

The role of dispersal in range change in birds

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Abstract

Eurasian reed warbler *Acrocephalus scirpaceus* expanded its range in Great Britain in the late 20th and early 21st centuries. The role of dispersal in this range expansion was investigated. Inference of the mechanisms underlying the range dynamics drew on fieldwork, analysis of large observational datasets, and a simulation model; this model was run in a reedbed map of Britain, generated from satellite data using machine learning.

Breeding season temperature sets up reed warbler's range limit in Britain directly, by influencing occupancy in the current year, perhaps mediated through reed *Phragmites australis* phenology. Although components of productivity were positively related to temperature, these and adult survival did not decline to the range edge. There was therefore no evidence that demography plays a role in limiting reed warbler's range in Britain; however, not all aspects of demography were investigated. Survival was negatively related to temperature, and simulations suggested that this may allow reed warbler to maintain a more northerly range limit than without such a relationship.

Reed warbler's range expansion can be explained by a gradual equilibration with climate space, enabled by long-distance dispersal: only rare long-distance dispersing individuals matched the rate of range expansion. Reed warbler's range edge tracked climate change, but the bulk of the population lagged behind. This could be due to dispersal-limitation, or perhaps newly established populations grow too slowly to generate sufficient emigrants. Simulations suggested that reed warbler's range size is more sensitive to demography than to dispersal. The number of fledglings per breeding attempt increased over time, probably due to climate warming, and could have increased emigration; if so, this may be the cause of a more rapid movement in the range centroid later in the study period. Emigration, transition and immigration may therefore play different roles in reed warbler's range dynamics in space and time.

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Author's declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

The 'Geneshifter' model used in Chapter 6 is an IBM adapted by Dr Phil Platts to my specification, using the structure and parameters in Chapter 6, from an existing IBM by Phil Platts and Calvin Dytham (available on GitHub). All model scenarios and inputs were set by me. I ran the model, collected and analysed the outputs.

1. Introduction

1.1 Introduction

The question ‘Why are species found where they are?’ predates the science of ecology. At the core of the question is a simple fact: an individual of a species only exists in a location if it moved there, or if one of its predecessors did. But the simplicity ends there. Every aspect of ecology comes together with evolutionary forces, environmental change and historical accident, in complex and non-linear ways, to determine a species’ geographical range. Tensions between gene flow and selection in unusual environmental conditions make range edges highly evolutionarily complex areas. The study of ranges and their dynamics has therefore been an enduring field within ecology throughout its history as a science.

Although there is much we do understand about ranges, we are still unable to predict successfully the future range of most species (Sofaer et al. 2018). This is a problem, because several important current challenges in applied ecology relate to species’ ranges and their dynamics. Due to anthropogenic environmental change, many species are threatened with extinction, particularly through habitat loss and climate change (Thomas et al. 2004). Species can respond to such existential threats by adapting in situ, changing their range, or by going extinct.

Adaptation to environmental change in situ requires a change in phenotype, and can take the form of either phenotypic plasticity (e.g. Barshis et al. 2013) or evolutionary adaptation (e.g. Kettlewell 1955). Range change can take place without phenotypic change (due to individuals dispersing into uncolonised areas - e.g. Svenning & Skov 2007), or through phenotypic change: due to phenotypic plasticity (e.g. Macgregor et al. 2019) or evolutionary adaptation (e.g. Buckley and Bridle 2014). Over the last 1.6 million years, plant taxa have responded to variation in Earth’s climate by dramatic distributional change, but little macroevolutionary change (Huntley and Webb 1989). The current rate of climate change is unprecedented in recent decades to millenia (IPCC 2014), and is not expected to be matched by the rate of evolutionary adaptation (Franks et al. 2014). This may suggest that species are more likely to successfully endure climate change by shifting their range than by adapting evolutionarily.

Therefore, understanding whether and how species will change their range is of critical importance for conservation science. Currently many species are changing their range poleward or to higher elevations (Pecl et al. 2017). As environmental change increases in pace, how we target conservation effort will increasingly depend on where species will be in the future, and the pathways they will take

to get there, rather than just where they are in the present. Furthermore, being able to predict species' range dynamics will allow us to assess their extinction risk under climate change (e.g. Thomas et al. 2011).

A better understanding of the factors determining and causing change in range is therefore a priority in both pure and applied ecology. Much theoretical work has been carried out on range dynamics, but we lack empirical studies of range, partly because studying species' ranges generally requires long-running data collection campaigns over large geographical areas. In this thesis I investigate the role of dispersal in range change in a passerine bird, the Eurasian reed warbler *Acrocephalus scirpaceus* (hereafter 'reed warbler'). In the first part of this chapter I introduce the field of range dynamics and outline my broader aims. In the second part of this chapter I review potential causes of range limitation and change in reed warbler in Britain and introduce my specific research aims.

1.2 Range dynamics: current state of knowledge and research questions

A species' range is the geographical area within which it exists. Two key areas of research into species' ranges are: what limits them, and what causes them to change.

1.2.1 Range limits

Most of our understanding of species' range comes from observational records of species' presence/absence, and is thus very heavily biased towards macroscopic species, due to the difficulty of observing microorganisms. For the remainder of this section I focus on what we know about determinants of range dynamics for macroscopic species.

Most species are absent from most places on earth, due to a combination of abiotic and biotic factors and dispersal ability. Some species are limited in range by abiotic factors acting directly on components of population growth rate (the sum of births, deaths, immigration and emigration). For example, the northern range limit of fiddler crabs *Uca pugnax* in the northern hemisphere is determined by the positive effect of temperature on larval survival (Sanford et al. 2009). Within their potential abiotic range, most species are limited to some extent by dispersal: they do not occupy their full potential range because they cannot get there. For example, many alien species can quickly invade new geographical areas once introduced; and many species of tree are still not at equilibrium across their European range after the last glacial maximum (Svenning & Skov 2007). Within their potential range that they can access by dispersal, species are typically limited by biotic interactions: such as the absence of suitable habitat or prey species, or the presence of competitors or natural enemies.

Overall, any factor that influences productivity (the number of offspring an individual produces), survival or dispersal can limit a species' range. We can also consider range limitation in terms of inability to adapt to novel conditions outside of the range. Gene flow from the centre to the edge of the range may swamp local adaptation at the edge of the range, preventing expansion (Kirkpatrick & Barton 1997).

Although it is simple to characterise the processes behind range limitation, diagnosing the causes of range limits can be very challenging. The spatial autocorrelation of species' occurrence and of environmental variables typically produces strong hump-shaped relationships between species' occurrence and environmental variables, even when there is no biological link between the two. For example, the relationship between climate and distribution for the majority of European bird species is no better than random (Beale et al. 2008). Partitioning abiotic and biotic causes of range limitation can therefore be very difficult, especially when some of the interspecific interactions that limit species may themselves be closely linked to climate (Gross & Price 2000). Furthermore, multiple factors can combine simultaneously to limit species' range, and different factors can affect different parts of a species range, or can change in importance over time (Gaston 2003). Studying individual potential causes or demographic parameters in isolation can therefore give an incomplete understanding.

1.2.2 Range change

Species' ranges can change by expansion or contraction. For a range to expand, species must disperse into and establish populations within the un-colonised area. For a range to contract, populations at a range edge go extinct. Thus the ecological processes involved in both trajectories differ: for example, dispersal is needed for range expansion, but not for contraction. Hereafter I focus mainly on range expansion.

As for range limitation, any factor increasing productivity, survival or dispersal can cause range expansion, and its influence can vary spatially and temporally along the range limit. Also, the rate of range change for a species can vary over time or in space. For example, a range expansion in American mink *Neovison vison* varied in rate by more than an order of magnitude over a 52 year period, and varied spatially, the rate being negatively related to habitat suitability (Fraser et al. 2015).

1.2.3 The role of dispersal in range dynamics

Dispersal – the movement of an individual from its natal site to its first breeding site, or between subsequent breeding sites – plays a crucial role in range limitation and expansion. Fundamentally,

dispersal is the only process allowing colonisation of new areas. A key finding in dispersal ecology is that long-distance dispersal can be more important than mean dispersal distance for determining the rate of range expansion. For example, the spread of tree populations since the end of the Pleistocene is too fast to have been carried out by the mean dispersal distance, but is consistent with a 'fat-tailed' dispersal kernel (Clark 1998). The role of dispersal in range change can also be considered in terms of the inverse of dispersal: site fidelity. When site fidelity is high, species should be less likely to colonise all of their potential range (Matthiopoulos et al. 2005). On the other hand, high site fidelity can maintain tiny populations in range-edge areas even if population growth rate is low (Smith & Summers 2005). The direct role of dispersal in range change can be very difficult to disentangle, because dispersal often covaries strongly with other traits (Rodriguez et al. 2007; Stevens et al. 2014).

In practice, the realised spatial distribution of dispersers is a combination of the shape of the dispersal kernel (the frequency distribution of dispersal distances in a population) and the number of emigrants. This means that a species' abundance trend, influencing the total number of dispersers, can be considerably more important than dispersal ability in determining how species change their range (Mair et al. 2014). The relative importance of this propagule pressure and long-distance dispersal can change over time (Fraser et al. 2015). For example, atmospheric CO₂ enrichment is expected to boost fecundity in some North American trees in the near future; this is likely to elevate the importance of propagule pressure relative to long-distance dispersal in determining the spread of these species (Nathan et al. 2011).

The other key role of dispersal in range dynamics is its role as the mechanism for gene flow. When dispersal is itself under strong selection at the range edge, especially during a range expansion, this can cause very complex eco-evolutionary feedbacks. Increased dispersal should be favoured during a range expansion, as it allows exploitation of unoccupied habitat (Travis & Dytham 2002). This, especially in combination with assortment of individuals with higher dispersal ability towards the range edge, should create positive feedback in the rate of range expansion (Phillips et al. 2008). Indeed, In North America, lodgepole pine *Pinus contorta* in populations founded most recently have more dispersible seeds (Cwynar & Macdonald 1987), and recently founded bush-cricket populations had higher frequencies of more dispersive individuals (Thomas et al. 2001). Dispersiveness may then decline after the expansion has finished (Hanski et al. 2004). Alternatively, reduction of emigration from the range core to the range edge, perhaps due to a population decline, could reduce 'gene swamping' at the range edge, allowing increased adaptation and potentially causing a range expansion (Kirkpatrick & Barton 1997).

1.2.4 Range dynamics in the Anthropocene

As climate change and other anthropogenic environmental change has accelerated in recent decades (IPCC 2014; IPBES 2019) species have responded by changing their ranges: generally poleward, uphill, and to deeper depths (Chen et al. 2011; Pecl et al. 2017). However, there is great variation in how species have changed their range (Gillings et al. 2015). For example, globally, 22% of species are shifting their range in the opposite direction expected to match climate change (Chen et al. 2011). In some areas very few species are shifting in the direction expected from temperature changes (Tayleur et al. 2015). Similarly, species responded in highly idiosyncratic ways to Quaternary climate change (Le Galliard et al. 2012; references therein). This suggests that different dispersal abilities, environmental tolerances and local geography come together to shape species' range shifts. The individualistic nature of species' range shifts makes it difficult to predict them.

Current species' range shifts have knock-on consequences for biodiversity, ecosystem function and services, and enhance climate change feedbacks (Pecl et al. 2017). In order to tackle these issues, we need to be able to be able to predict how species will change their range. Species distribution models (SDMs) have been a much-used tool in predicting species' response to climate change, but they overwhelmingly fail to predict observed range shifts, and they predict shifts where there are none (Sofaer et al. 2018). There are indications that SDMs that incorporate some of the biological mechanisms underlying range change have better predictive power.

1.2.5 This study

Much of the study of range has been theoretical, and lacks empirical testing. Many empirical studies of how species' ranges are limited and change have been narrow in scope, just testing one variable for its role (Gaston 2009). We do not have a comprehensive understanding of what limits range or causes range change for any one species. There is therefore a real value in single-species studies that examine every aspect of range dynamics for that species, from all angles. Such studies may allow us to better predict how species will change their range, or evaluate the level of data and analysis required to do so.

It is likely that for a considerable proportion of species, dispersal will progress far too slowly for them to be able to track climate change (Keith et al. 2008; Nathan et al. 2011). Understanding the role of dispersal in range change is therefore particularly important, because it determines whether we aim to help species to track climate by prioritising their population growth rate or their dispersal ability.

In this thesis I study the causes of range limits and range change in reed warbler in Great Britain (hereafter 'Britain') in the late 20th and early 20th century. Using large, spatially detailed, multi-decadal datasets collected over the course of a range expansion, I aim to analyse in depth how range limitation and range change occur in practice. In particular, I will evaluate evidence for the relative roles of dispersal (emigration, transition and immigration) and demography (here defined as productivity and survival) in range change. In the next section of this chapter I introduce the study system, review potential causes of range limitation and change in reed warbler, and outline the specific research aims of this thesis.

1.3. Study system

The domain of my study is the range change in reed warbler in Britain in the late 20th and early 21st centuries. Reed warbler (Figure 1.1) is a small insectivorous passerine bird. Reed warblers largely breed in stands of common reed *Phragmites australis* (hereafter 'reed') in western Eurasia, and spend the winter in sub-Saharan Africa. This is an excellent study system with which to study the role of dispersal in range change in birds, for two main reasons.

Firstly, the ecology of reed warbler is well understood, having been studied much in its own right, and also as a model organism for understanding, for example, brood parasitism (York & Davies 2017) and migratory navigation (Chernetsov et al. 2017). A literature search on Google Scholar with the search term 'Acrocephalus scirpaceus' generated 8,260 results (retrieved 16th August 2019). This detailed understanding of reed warbler's ecology allows me to generate sensible hypotheses for the causes of reed warbler's range limitation and change. It also allows me to delineate in detail the life history of reed warbler, allowing the construction of detailed models to fit to data or with which to make predictions. So our understanding of reed warbler's ecology allows me to both generate and test hypotheses more effectively for the role of dispersal in range change.

Secondly, reed warbler's range expansion in Britain is richly documented by a variety of data types. Large quantities of census, ringing and nest record data have been collected for reed warbler in Britain over the course of the range change. For each of the British Trust for Ornithology's integrated population monitoring data collection schemes, reed warbler is one of the best represented of all British breeding birds. Furthermore, these data have been collected from a large number of sites over this period. This allows me to estimate demographic parameters with an unprecedented level of spatial resolution, enabling the comparison in these parameters between the range core, the colonised areas and the range edge, to understand how demography drives range limitation and range

change. Very large amounts of ringing data exist, much of it involving chicks ringed in the nest, with which to estimate dispersal. Furthermore, climatic data exist in high spatial and temporal resolution for Britain over the course of the range expansion, allowing me to explore how climate drives mechanisms of range limitation and range change.



Figure 1.1. [Clockwise from top] Reed warbler (Flamborough Head, East Yorkshire, UK); reed warbler breeding habitat (Watermill Broad NR, Norfolk, UK); reed warbler nest with eggs hatching (Watermill Broad NR, Norfolk, UK).

In the remainder of this chapter I describe changes in reed warbler's global and British range, and present and evaluate potential causes of reed warbler's range limitation and change in Britain.

1.4 Reed warbler range limitation and change

1.4.1 Limits and change in reed warbler's global range

Reed warbler's breeding range has probably been expanding for tens of thousands of years. Reed warbler consists of three subspecies: *scirpaceus*, *fuscus* and *avicenniae*. In this study I focus on the nominate subspecies, which breeds in Europe, north Africa, west Russia and west Asia Minor (Figure 1.2). The three subspecies of reed warbler spent the Pleistocene in separate glacial refugia, one of which was probably Iberia (Procházka et al. 2011). Populations of the nominate subspecies began expanding approximately 35,000 years ago, admixed with each other 14,000-17,000 years ago and underwent a rapid expansion over the last 10,000 years, coincident with Holocene warming (Arbabi et al. 2014; Ceresa et al. 2015).

In documented history, reed warbler's range has been increasing in Europe, especially in the north and west. In Fennoscandia, reed warbler generally increased in distribution from the latter half of the 19th century onwards (Järvinen & Ulfstrand 1980). The Swedish reed warbler population expanded north and north-north-east from the 19th century until the mid-1970s, also growing markedly in abundance towards the end of the period (Österlöf and Stolt 1982; Stolt 1999). From 1975 to 1992 the population increased, and was then stable until 1997 – although captures at Swedish bird observatories declined non-significantly from 1980 to 1999 (Karlsson & Ehnbohm 2005). Reed warbler colonised Finland in the 1920s (Järvinen & Ulfstrand 1980), and the range has continued to move northwards in recent years (Brommer et al. 2012). Reed warbler was first seen in Norway in 1937, and first bred in the south-east of the country in 1947 (Røed 1994). There was particular range expansion during the latter half of the 20th century, with considerable variation in total population size between years. Since then, reed warbler's distribution in Norway is generally unchanged, leaving some suitable habitat further north un-colonised (Shimmings & Øien 2015).

South of the Baltic, trends in reed warbler's distribution and abundance have been more variable. In Denmark, populations were stable from the latter half of the 19th century until 1970 (Järvinen & Ulfstrand 1980), and then declined, particularly (-1.71% year⁻¹) from 1996 to 2005 (Heldbjerg & Fox 2008). Reed warbler increased in population size in northern Germany between 1950 and 1985 (Marchant 1992). There was no trend in the number of reed warblers trapped at three sites in Germany and Austria from 1972 to 1996 (Berthold et al. 1998). Reed warbler increased in abundance

and distribution in the Netherlands up until the early 2000s, and has since remained stable (van Turnhout et al. 2010; although see Johnston et al. 2016). Reed warbler's population increased in France (+2% year⁻¹) and declined strongly in Catalonia (-9% year⁻¹) from 1983 to 2008.

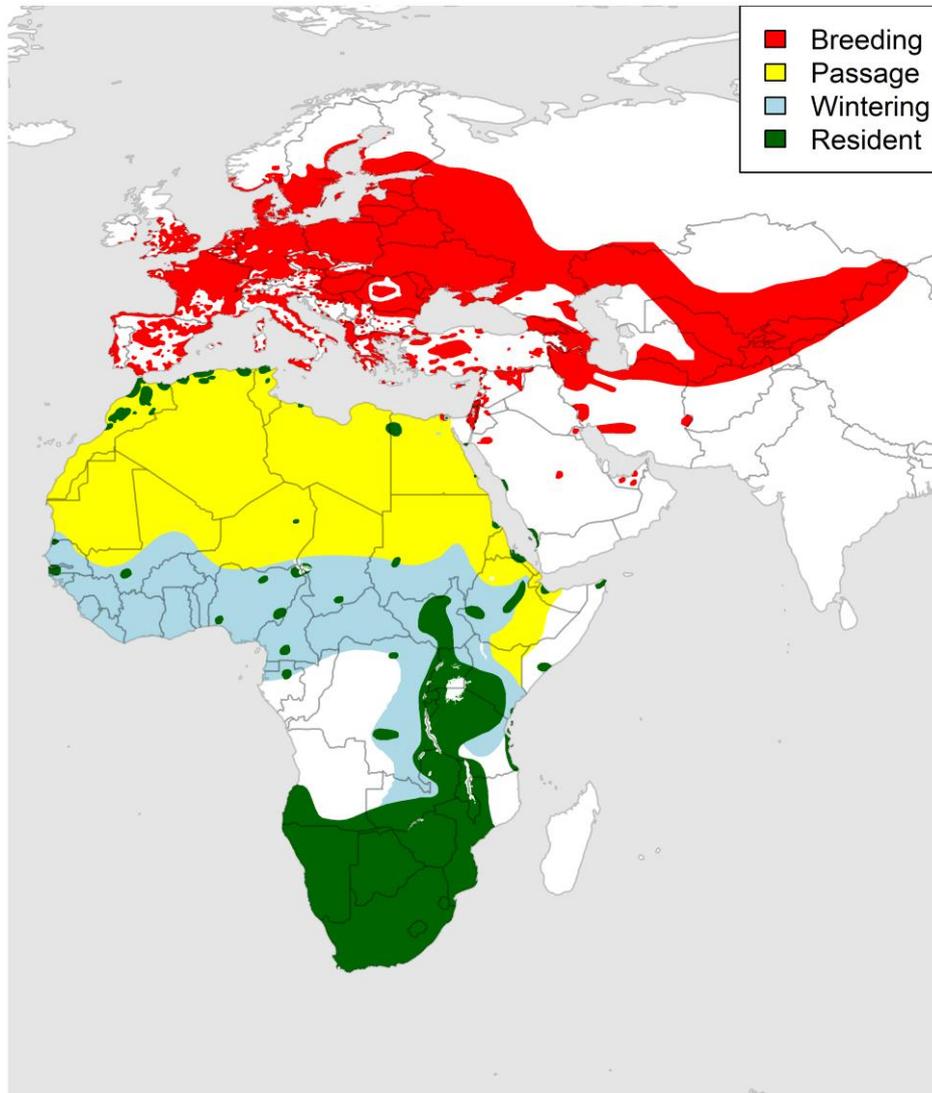


Figure 1.2. Global range of the three subspecies of Eurasian reed warbler and the closely related resident species African reed warbler *Acrocephalus baeticatus* (Birdlife International 2017).

Reed warblers migrate between Europe and Sub-Saharan Africa by a variety of pathways (Procházka et al. 2017). Generally western European populations pass west of the Mediterranean, while eastern European and Asian populations pass east, while a small proportion of birds pass directly through central north Africa (Procházka et al. 2008). Western European populations crossing the Sahara use oases and the wetlands of the lower Senegal River valley for fuelling (Bayly et al. 2012; Hama et al. 2013). These routes are not known to have changed recently.

Reed warblers winter in sub-Saharan Africa, in a broad curve following the humid savannah zone approximately between Senegal and Chad. Detail in reed warbler's wintering distribution is poorly understood (Procházka et al. 2017). Of 51,612 re-encounters of European-ringed reed warblers between 1933 and 2014, only 12 were made south of 20°N between November and February. Ringing recoveries suggest that wintering populations of reed warbler are distributed longitudinally in approximately the same way as their European breeding populations (Procházka et al. 2008). Feather stable-isotope values suggest that reed warblers vary greatly in the feeding habitats used by different individuals in the wintering grounds (Procházka et al. 2008). In the humid savannah zone, reed warblers are typically found in low trees and tall rank grass (Dowsett-Lemaire & Dowsett 1987). In some areas of coastal mangroves in West Africa, reed warbler is the commonest insectivorous bird species, migrant or resident (Zwarts et al. 2014). Coastal mangroves, which are very difficult to access and survey, probably support a large proportion of the breeding population of European reed warbler, especially British breeders. As for the migration routes, it is not known if reed warbler's wintering range has changed recently.

1.4.2 Limits and change in range in British-breeding reed warbler

In Britain, reed warbler's breeding range has a south-easterly distribution. From this core, the range has extended north and west over the last century. Between the 1930s and 1968-72, reed warbler extended its regular breeding range into Devon, Cornwall, Scilly in the west, and probably North Wales and Yorkshire in the north (Sharrock 1976). From 1968-72 to 2008-11, reed warbler colonised west Wales, the north of England and southern Scotland (Figure 1.3; Balmer et al. 2013). Although expanding its range, between 1983 and 2008 reed warbler populations declined in the UK: more so in the north (-1.3% year⁻¹) than in the south (-0.7% year⁻¹) (Johnston et al. 2016). Within this period, there has been variation in the population trend: reed warbler increased in population size in the UK from 2000 (219,000 individuals) to 2006 (257,000 individuals) (Newson et al. 2008).

Much of reed warbler's range change since the late 20th century has taken place in the north of Britain, especially in Scotland. Since it was first seen in Scotland in 1908, reed warbler became an increasingly common passage migrant, particularly in autumn. Reed warbler first bred in Scotland in 1973, in Unst (Shetland), more than 500 km beyond the British range edge at the time (Bruce 2007). Reed warblers were present in suitable habitat in the late 1970s and early 1980s but did not breed on the Scottish mainland until 1987 (Bruce 2007). Thereafter there were a series of colonisations in the south and east of the Scottish mainland.

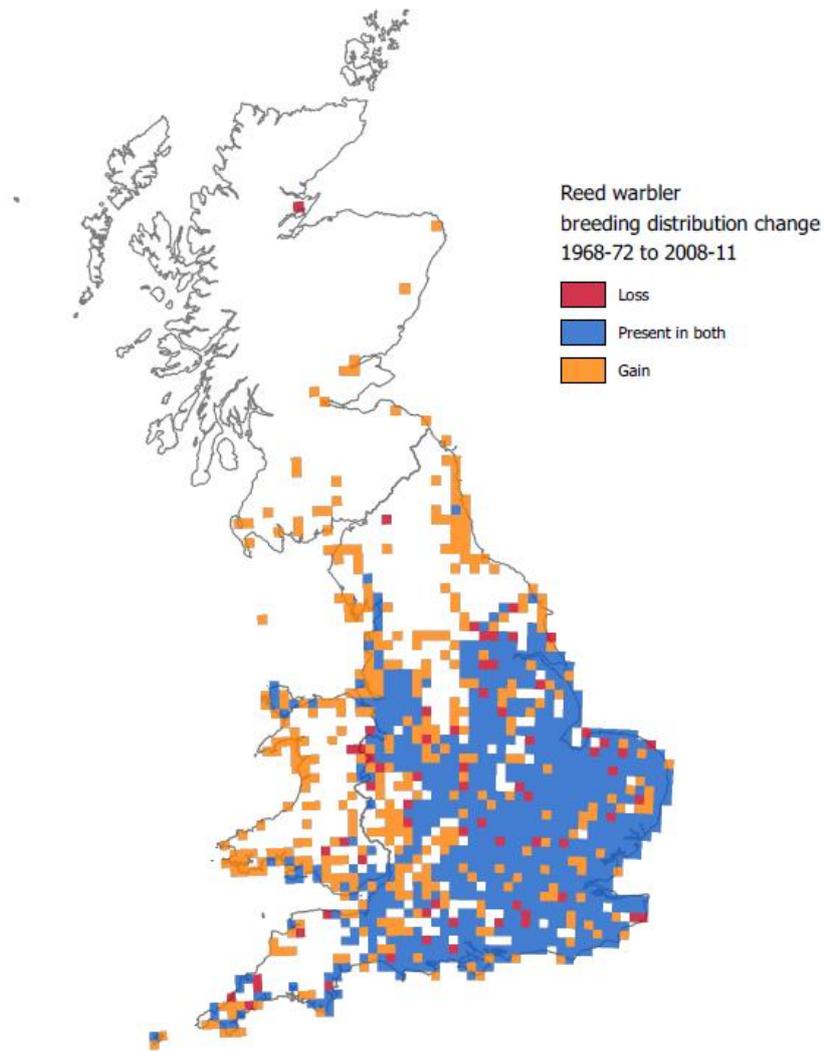


Figure 1.3. Breeding range change in reed warbler in Britain, 1968-72 to 2008-11 (Balmer et al. 2013).

The two first site colonisations in Scotland are well documented and provide potentially useful information about the cause of range limitation and expansion. The sites differ markedly in their latitude and rate of colonisation, but both were preceded by the presence of individuals in late summer or autumn. The first site, Tay reedbeds, is the largest contiguous reedbed (habitat dominated by reed) in Britain, being approximately 4.1 km² in extent (Malzer & Hansell 2017). Reed warblers were caught at Tay reedbeds in summer and autumn from 1981 onwards (Robertson 2001). Reed warbler first bred at Tay reedbeds in 1987, followed by breeding in 1988, 1990 and 1991. Male song had not been heard at the site before breeding in 1987, and was thereafter not heard every year that breeding took place. Rate of colonisation thereafter was slow, reaching eight apparently occupied territories by 2006 (Scottish Bird Report n.d.).

The second site to be colonised, Lochrutton Loch, is 95 miles SSW of Tay reedbeds. This site was much closer to the nearest English populations at the time, in Cumbria, which itself only had 2-3 pairs when Lochrutton Loch was colonised (Bruce 1997). The reedbeds at Lochrutton Loch are much smaller, being scattered around a waterbody about 1 km in length. At this site, a juvenile reed warbler was trapped in late September 1992, the first to be caught by the local ringing group (Bruce 1997). The bird was suspected to be locally fledged, but this is also peak autumn migration time for the species in Scotland (Bruce 2007). In 1993 the first breeding at Lochrutton Loch was confirmed, with two singing males holding territory and two recently-fledged juveniles caught in September. In the following years the population increased rapidly, with seven singing males and 20 juveniles caught at the site in 1996. In 2010, Lochrutton Loch had at least 12 breeding pairs, with 58 individuals caught (Scottish Bird Report n.d.).

Outside of these two sites, there were no known breeding attempts on the Scottish mainland before the late 1990s. Reed warblers were first known to breed at other sites in Dumfries & Galloway, Borders and Fife respectively from 1996, 1997 and 1999 onwards. Since then, range expansion has been slow. Pairs possibly bred in Moray, North-east Scotland, and Orkney in 2008, breeding was confirmed in Upper Forth in 2011 and singing males have been seen elsewhere in north and west Scotland (Scottish Bird Report n.d.). The current Scottish breeding population numbers just 40-60 pairs (Bruce 2007).

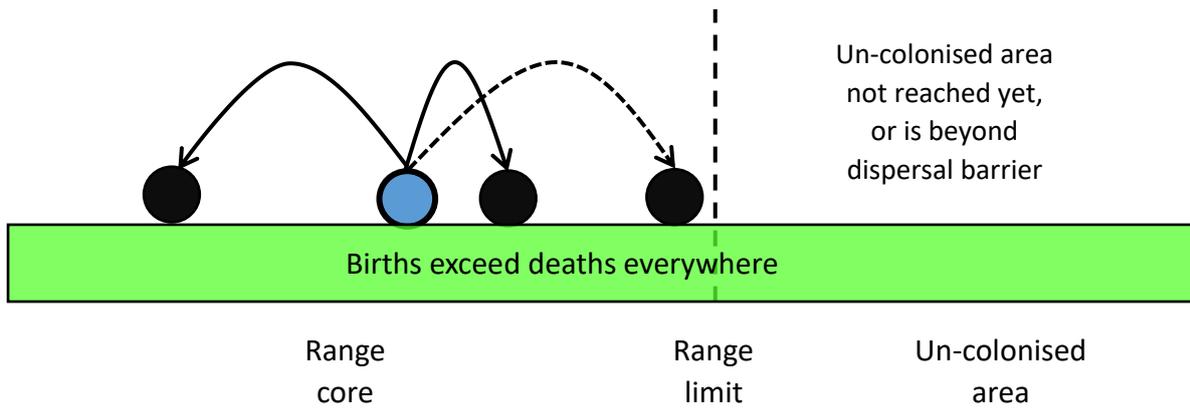
British-breeding reed warblers follow a slightly more westerly migration route than other populations in western Europe, passing through western France and western Iberia (Bibby & Green 1981; Andueza et al. 2014). Ringed British and Iberian birds have been found wintering in westernmost West Africa, mostly west of 12°W: i.e. in Senegal, Guinea-Bissau and Mauritania (Procházka et al. 2008); British-breeding birds appear to winter slightly further south within these areas than Iberian birds. It is not known if these migration routes or wintering range have changed recently.

1.4.3 Potential causes of range limitation and range change in reed warbler in Britain

1.4.3.1 Causes of range limitation

Range limits delineate the boundaries between where species do and do not exist. Diagnosing the causes of range limits is difficult. For example, finding a negative effect of a variable beyond the range edge does not necessarily mean that variable is limiting (Gaston 2003). To caricature, we might find that a reed warbler cannot survive in space, but that does not mean oxygen limitation is a key variable limiting reed warbler range. No transplant experiments have been carried out to directly test the causes of range limitation in reed warbler.

a) Range is limited by dispersal



b) Range is limited by deaths exceeding births, due to environmental gradient

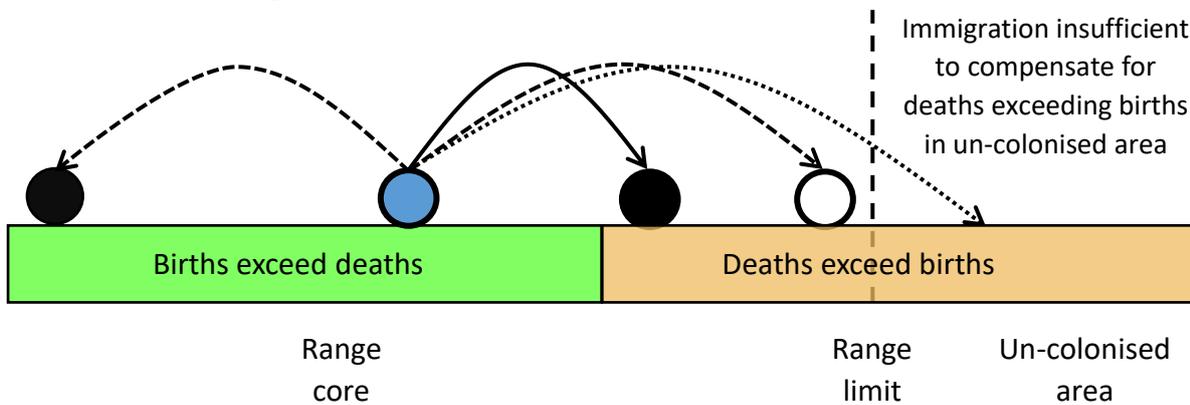


Figure 1.4. Two scenarios of range limitation in a hypothetical species: a) dispersal-limited; b) limited by deaths exceeding births, due to an environmental gradient. Circles represent populations (filled for population growth rate ≥ 1 ; empty for population growth rate < 1), arrows represent dispersal (solid = high; dashed = moderate; dotted = low). Dispersal only shown from blue-filled population for clarity. Green-filled rectangle represents habitat where births exceed deaths; brown-filled rectangle represents habitat where deaths exceed births. If there is no dispersal barrier in scenario (a), the range will advance to the right.

There are many potential proximate and ultimate causes of range limits. We can categorise these into two broad categories: those that cause insufficient dispersal, and those that cause deaths to exceed births. The species is at equilibrium with its potential range in the latter category, but not the former. Figure 1.4 describes these two categories.

In scenario (a), dispersal limitation prevents the species colonising available habitat to the right, even though in all habitat, births would potentially exceed deaths. From an existing population (blue-filled) near the range edge, most dispersal takes place over short distances, but does not reach available habitat further from the range core. If there is no barrier to dispersal, then this scenario only produces

a temporary range limit, even if dispersal distances are small: so this scenario is more likely during environmental change. However, if there is a barrier to dispersal then dispersal limitation could set up a permanent range limit.

In scenario (b), due to an environmental gradient, beyond a certain distance from the range core the potential birth rate no longer exceeds the potential death rate. From an existing population within the range, individuals can disperse well into the zone where deaths exceed births, but they may not always establish populations (right-most arrow). Although deaths exceed births in this zone, for some populations this is more than offset by immigration, and population growth rate is therefore above 1 (filled circle). For a more distant population, established in a year with favourable conditions or high immigration, immigration is insufficient to maintain a population growth rate above 1 and the population declines to extinction (empty circle). For both scenarios (a) and (b), populations do not establish at all beyond the range edge, even in years of favourable conditions or high immigration.

These two scenarios are a simplification and not mutually exclusive. For example, in scenario (a), dispersal could be limiting because birth rate is too low to provide enough dispersers. Also, a large population may take some time to decline to extinction where the population growth rate is just below 1, allowing populations to persist outside of a neat range limit. Reed warbler's range limit could therefore be caused by dispersal limitation, by insufficient births to exceed deaths, or a combination of both. Below I review literature on reed warbler ecology to identify potential causes of reed warbler's range limit in Britain. The range limit could be generated by one of these, or by several working together.

Ultimately reed warbler's breeding range is limited by habitat: relatively little of the Earth's surface is covered in reedbed. Next, reed warbler's breeding range is probably limited by dispersal: reedbeds are found on every continent except Antarctica (Packer et al. 2017), but reed warbler only breeds in Europe, western Asia and north Africa. Within reed warbler's European range, different range limits are likely to have different causes (Gaston 2003; Hersteinsson & Macdonald 1992): the cause of the range limit in Britain might be different to that in Asia. Little direct work exists on the causes of reed warbler's range limits, within or outside of Britain; however, much is known about reed warbler's ecology, which narrows down the potential causes of its range limits. Most reed warbler studies have been carried out at single sites: it is often impossible to reconcile apparently solid conclusions between site-based studies for reed warbler (e.g. Brown & Davies 1949; Catchpole 1974). I thus attempt to

present the variation in findings between sites, but this is not always possible where specific aspects of reed warbler ecology have been researched at relatively few sites.

1.4.3.2 Potential mechanisms of dispersal limitation

Dispersal limitation should be more likely during environmental change, as some species cannot keep up with the rate at which new habitat becomes available. Some species of tree are still recolonising Eurasia after the Last Glacial Maximum (Svenning & Skov 2007). Although birds typically have much higher rate of dispersal than trees, there is dependency between trophic levels, and so it may be that some bird species are still recolonising northern Europe after displacement by ice sheets (Tayleur et al. 2015).

As for most migratory birds, dispersal rate and distance are generally considered to be high in reed warbler. Although neither study took account of bias in observable dispersal distances, both Paradis et al. (1998) and Ceresa et al. (2016) found site fidelity is high in reed warbler, but a considerable number of longer-distance movements are made. Due to the methodological shortcomings of these studies, the relative frequency of no-, short- and long-distance dispersal remains unknown. Reed warbler populations in Eurasia and north Africa have high gene flow and low genetic differentiation, suggesting that dispersal between populations is high but not unrestricted (Procházka et al. 2011; Ceresa et al. 2015). Reed warblers can rapidly colonise new habitat that is well within the range (Shy et al. 1998; Eertman et al. 2002; Beauchard et al. 2013). There are two scenarios by which dispersal rate and distance could be limiting for reed warbler: if the rate at which new habitat becomes available is high relative to dispersal distances; or if the habitat is too sparse relative to dispersal distances. The climate in Britain is warming, but it is not known *per se* whether this is creating new available habitat for reed warbler, nor the rate at which it might be doing so. Reedbed is generally sparser in the north of Britain (Packer et al. 2017), but it is not known whether this is so at a scale relevant to reed warbler dispersal distances. Reed warblers are strong fliers, crossing the Sahara and small sea crossings, so it is unlikely that any habitat in Britain is inherently inaccessible to them.

If reed warblers do not attempt to settle in all suitable areas, dispersal rate or distance could be high while dispersal remains limiting. First, if individuals assess the suitability of reedbed before settling, but are conservative in doing so, then they may explore but not settle in suitable habitat. Although much is known about reed warbler densities in different habitat within reedbed, little is known about how reed warblers directly assess habitat. Secondly, if there is conspecific attraction and individuals are biased towards already-occupied sites, then high dispersal may not cause a high rate of range

expansion. Reed warblers are easily lured into unsuitable habitat using playback of reed warbler song during migration (Schaub et al. 1999), but also during juvenile exploration (Grinkevich et al. 2009). This suggests that reed warblers do use the presence of other reed warblers as an information regarding the suitability of a breeding site.

The number of reed warblers passing through Scotland on both spring and autumn passage has always considerably exceeded the number of breeders (Bruce 2007), suggesting that reed warblers have ample opportunities to assess the suitability of unoccupied habitat in the north of Britain. Reed warblers will rapidly re-colonise stopover sites in suitable areas when well within the range (e.g. Procházka et al. 2008); however, for most examples of this it is not known whether the populations actually went extinct. It therefore seems that reed warblers largely do not judge unoccupied habitat in the north of Britain as suitable: but it is not known whether they are conservative or efficient in this judgement; nor whether this is because there are no existing populations there to attract birds in.

The strength of evidence for the above scenarios for direct dispersal limitation could be enhanced if a) abundance is naturally lower towards the range edge, and b) positive density-dependence causes a decline in population growth rate to the range edge, thereby providing fewer dispersers overall, even if the relative frequency of long-distance dispersers within dispersers is not low.

It could be that the global population size of reed warbler, and therefore the number of dispersers, is ultimately limited by the carrying capacity of the wintering grounds. Eurasian migratory birds are less likely than resident birds to exhibit breeding ranges spanning Eurasia (Bensch 1999), and are less likely than resident birds to expand east-west into suitable vacant areas (Böhning-Gaese et al. 1998). Similar findings have been made in North America (Stralberg et al. 2017). This has been interpreted as evidence that colonisation of new breeding areas is more constrained in migratory species, or that the global population size of a migratory species is as likely to be limited by the non-breeding range size as by the breeding range size. It could be the case that density-dependent survival on the wintering grounds prevents population expansion in Britain. The exact size of reed warbler's wintering range is poorly known, making this hypothesis difficult to evaluate.

One final scenario of dispersal limitation is that the northern edge of reed warbler's range in Britain is too far from the wintering grounds. However this is unlikely: the Central Asian breeding grounds are further than Britain is from the African wintering grounds.

1.4.3.3 Potential mechanisms of limitation by deaths exceeding births: abiotic

We can broadly split the second scenario of British range limitation in reed warbler – deaths exceeding births – into abiotic and biotic causes.

We might expect reed warbler's northern range edge to be limited by abiotic effects on the balance between births and deaths. Poleward range edges are often limited by abiotic factors. For example, Arctic fox *Vulpes lagopus* in its Icelandic range is limited in the north by abiotic factors, and in the south by interactions with red fox *Vulpes vulpes*, whose own northern range limit itself is set by abiotic factors (Hersteinsson & Macdonald 1992). Reed warbler's range is at least consistent with being limited by climate. The current distribution of reed warbler in Europe correlates well with a model based only on climate variables (Harrison et al. 2003). The lower range of the distribution of temperature of occupied cells in Europe is especially truncated in June and July (Figure 1.6). Reed warbler presence in the 1986-1989 bird atlas in Finland is strongly positively related to temperature (Virkkala et al. 2005). In France, reed warbler is unusually narrow among passerines in the thermal breadth of its breeding range (Moussus et al. 2011). In continental Europe, some reedbed exists well beyond the northern range limit of reed warbler (Røed 1994; Shimmings & Øien 2015; although see Stolt 1999).

Likewise, it has long been proposed that reed warbler is limited by climate in Britain (Sharrock 1976). Although reedbeds are sparser in the north and west of Britain (Packer et al. 2017), large areas of reedbed beyond the northern edge of reed warbler's range are un-colonised by reed warbler (pers. obs.). Apart from areas of central Asia (where the extent of occurrence is more poorly known), reed warbler's northern range edge in Britain is in the coldest part of reed warbler's global range, particularly in June and July when the distribution of temperatures in occupied cells is most truncated (Figures 1.5, 1.6).

Some apparent limitation by climate is caused by indirect relationships with climate via biotic interactions. Nevertheless there is a wide range of studies that document a link between climate and reed warbler demographic rates, which propose or prove either abiotic or biotic mechanisms, or do not speculate on the mechanism. I present all climate effects on reed warbler together in this section, for simplicity. Most of these studies have been carried out some distance back from the range edge, where different climate-demography relationships may exist, due to the relatively extreme conditions there.

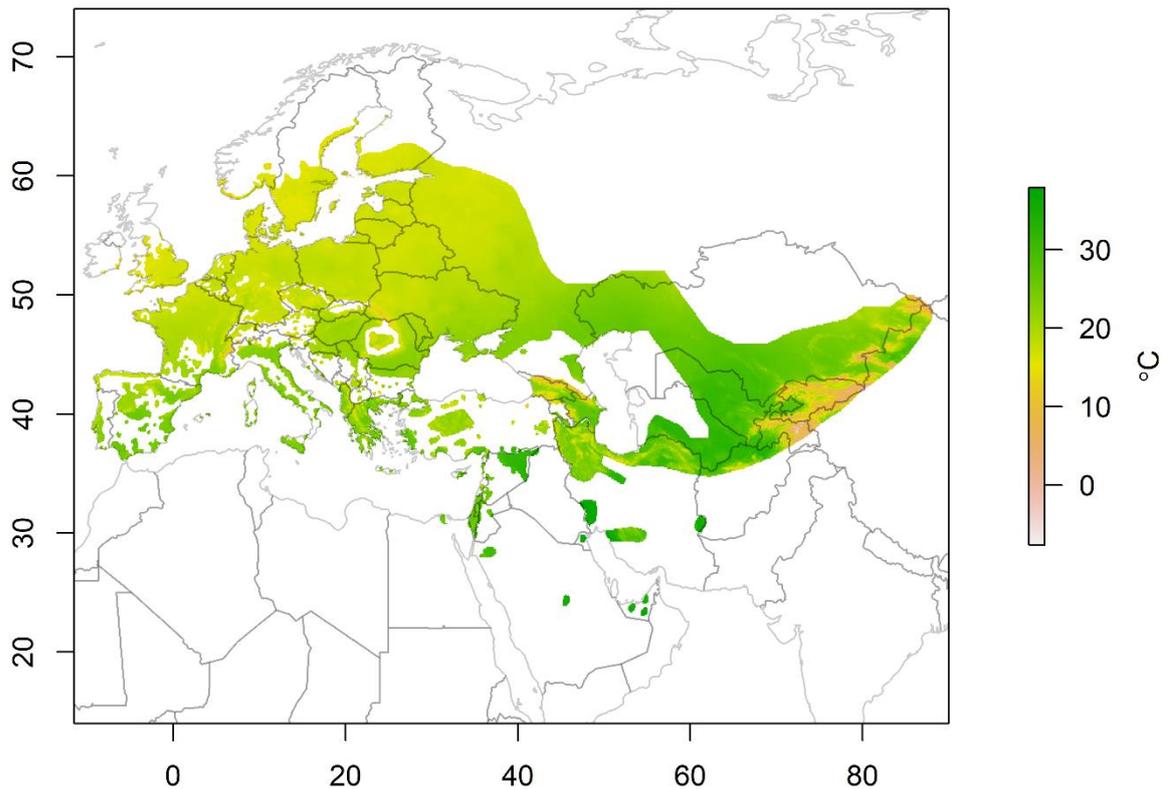


Figure 1.5. Mean July temperature (1970-2000; Fick & Hijmans 2017) across reed warbler Eurasian breeding range (Birdlife International 2017).

One of the best-known effects of climate change on our biosphere is that of advanced spring phenology in birds (e.g. Both et al. 2004). Reed warbler is no exception. Reed warbler spring passage dates and spring arrival dates across Europe are negatively related to local temperature and the North Atlantic Oscillation (Hüppop & Hüppop 2003; Sparks et al. 2007). Reed warbler spring arrival dates in Leicestershire moved later from the 1950s to the 1960s, perhaps because spring temperatures declined during that period (Mason 1995). In France, spring migration dates were related to local late winter temperatures before reed warblers had left Africa (Péron et al. 2007), perhaps due to a teleconnection (a relationship between climate anomalies at large geographical distances), and/or impacts on reed growth.

Reed warbler breeding phenology is also strongly related to temperature in all studies, although its breeding phenology has little or no relationship with migration phenology (Bibby 1978; Bergmann 1999). However, the nature of the relationship of breeding phenology with temperature differs between sites. Generally, the relationship between temperature and season start and median is negative (Bergmann 1999; Schaefer et al. 2006; Halupka et al. 2008; Vafidis et al. 2016). In France, the peak of the ratio of juvenile-to-adult captures moved later in years with high winter and spring temperatures; this is harder to interpret in terms of phenology (Moussus et al. 2011). The relationship

of the end of the season with temperature is variable: none at sites in England and Poland (Sparks et al. 2007; Halupka et al. 2008), negative at a site in Germany (Schaefer et al. 2006), and positive for juveniles but not adults at a site in Hungary (Miholcsa et al. 2009). Precipitation had a strong positive effect on season end at a site in Poland (Halupka et al. 2008). At a site in France, autumn migration dates had no relationship with autumn temperature, but were negatively related to late winter temperature. (Péron et al. 2007).

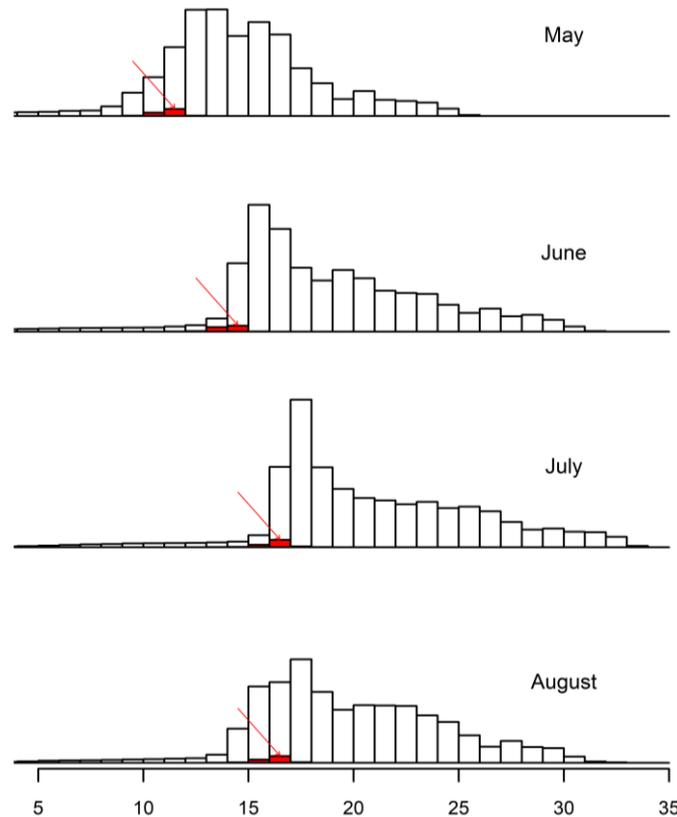


Figure 1.6. Histograms of monthly mean temperature (°C, 1970-2000, Fick & Hijmans 2017) across reed warbler's range (Birdlife International 2017) within Britain (red) and outside of Britain (no fill).

Clutch size increased with spring temperature at a site in Germany, purely due to the breeding season moving earlier (Schaefer et al. 2006): clutch size decreases over the season in reed warbler (Dyrce 1981). However, no such relationship was found at sites in Poland or Wales (Halupka et al. 2008; Vafidis et al. 2016). At a site in Wales, incubation period increased with rainfall (Vafidis et al. 2016).

The causes of nest failure in reed warbler are variable and differ substantially across the range. In the UK, the most important cause of nest failure is weather (Bibby 1978); across Europe, direct losses from bad weather are quite low in reed warbler relative to other factors (Schulze-Hagen et al. 1996). The

effect of bad weather can be indirect or direct: at sites in central and eastern Europe, some broods starved in cold rainy weather, while up to 15% of nest losses were caused by wind (Dyrz 1981). Reed warbler nest survival increased with temperature at a site in Poland, and increased non-significantly at a site in Germany (Schaefer et al. 2006; Halupka et al. 2008). Runts are frequent in reed warbler, which could make post-fledging survival more sensitive to bad weather (Bibby 1978). At a site in Cambridgeshire, chick post-fledging survival was positively correlated to chick weight in a wet year, but not in a dry year (Bibby & Thomas 1985).

Reed warbler productivity generally increases with spring temperature (Schaefer et al. 2006; Vafidis et al. 2016; Meller et al. 2018). At a site in Wales, first brood productivity was negatively related to total breeding season rainfall (Vafidis et al. 2016), although there was no effect on productivity of spring or summer rainfall at a site in Cambridgeshire (Harrison et al. 2000). Non-breeding season conditions can influence breeding season productivity, too: at a site in Cambridgeshire, reed warbler productivity increased with the magnitude of highest winter flood, perhaps due to habitat effects (Harrison & Whitehouse 2012).

No study has found effects of breeding season climate on reed warbler survival. Studies vary in non-breeding-season effects of climate on survival. For all western European breeding populations except France, winter Sahel rainfall was positively related to survival, with autumn North Atlantic Oscillation (NAO – an atmospheric pressure differential in the North Atlantic) explaining less (Johnston et al. 2016). At a site in Poland, only autumn rainfall in Spain had a (positive) effect on survival (Halupka et al. 2017). At a site in Germany, survival was positively related to NAO and Sahel rainfall and negatively related to rainfall in Spain; but these variables explained little absolute variation in survival (Salewski et al. 2013). In the closely related African reed warbler, survival varies positively with breeding season temperature (Jansen et al. 2015). Reed warblers are able to adequately compensate for some wind drift during migration (Åkesson et al. 2002), and can identify geographical displacement because they navigate with a bi-coordinate system (Chernetsov et al. 2008). However, the increased number of reed warbler drift migrants on the east coast of Britain during easterly winds in the migration periods suggests wind has the potential to deflect migrant reed warblers from their migration paths, potentially causing longer migration or death.

So overall, reed warbler productivity broadly increases with breeding season temperature, but apparently through different mechanisms in different part of the breeding range: through clutch size, breeding season length or nest survival. The season start generally advances with increasing

temperature, but the effects of this on productivity differs with local responses to temperature in clutch size and season end. The effects of precipitation can be negative on nest survival and post-fledging survival, but the overall effects of precipitation on total productivity are less clear. There is no evidence for effects of breeding season climate on reed warbler survival, but some varying evidence for effects of non-breeding season climate, particularly from rainfall. I could find no studies that investigated the effects of climate on juvenile survival or recruitment.

As breeding temperature declines north and west across Britain, productivity may likewise decline to the north and west. This could mean that beyond a certain isotherm, productivity causes births to decline below deaths, setting up a range limit. It seems less likely that temperature gradients could cause a gradient in survival. However, few of the studies investigated the effects of climate on demography near the range edge.

1.4.3.4 Potential mechanisms of limitation by deaths exceeding births: biotic

It is easier to determine the role of abiotic factors in species' ranges than the role of biotic factors (Hoffman & Blows 1994). Most species exist well within their fundamental niche, and so we should typically expect biotic rather than abiotic causes of limits (Gaston 2003). Several salient biotic factors impact on reed warbler's demographic rates and population density, and thus have the potential to limit range: habitat quality and configuration, interspecific competition, predation and brood parasitism.

Reed warblers largely breed in reedbed, and occasionally in other wetland habitats and crops. In Britain, reed exists on a wide variety of substrates, from the high water mark to 470 m above sea level and is catholic in its tolerated hydroperiods and pH values (Packer et al. 2017). Reedbed, as large stands of reed suitable for breeding reed warblers, occupies a narrower range of conditions but may still vary importantly in habitat quality for reed warbler across Britain. For example, eight reed-specialist moth species respectively occupy 1.4% to 67.1% of reed's Britain distribution, and are almost all biased in their distributions towards the south-east of Britain (Quinn et al. 1997). If this is representative of the general diversity or abundance of reedbed invertebrates, then there may be a lower diversity and/or abundance of food sources for reed warbler in reedbed in the north-west of Britain. Within reedbed, reed warblers often have strong habitat preferences, not occupying all available reedbed. However, these preferences vary from site to site, even over short distances (Dyrce 1981; Martínez-Vilalta et al. 2002; Prokešová & Kocian 2004; Báldi 2006). For example, reed warblers at different sites display opposite responses to reed-cutting (Catchpole 1974; Graveland 1999; Poulin

& Lefebvre 2002; Mortelliti et al. 2012). This could be due to habitat-linked predation which could vary with local predator guilds. As reed warblers carry out much of their foraging outside of reedbed, the composition of surrounding habitat can (but not always - Báldi (2006)) influence reed warbler abundance. For example, reed warblers in Poland show a preference for nesting near oilseed rape *Brassica napus* (Surmacki 2005). Re-analysis of data in Benassi et al. (2009) from a site in Italy showed that reed warbler density is unrelated to total reedbed area in marshlands, but almost all the variation in reed warbler density is explained by a model containing both marsh area and reedbed area (both effects positive).

In terms of potential influences on population growth rate, habitat quality appears to have effects through invertebrate supply and through nest predation rate. Reed warblers are opportunistic feeders, with a broad trophic niche. This means that diet composition can vary significantly between sites, with reed warblers generally feeding on a wide range of prey types from most available nearby habitat types (Grim & Honza 1996). Given this, and the broad peak in temporal invertebrate availability in reedbeds, it has therefore been suggested that reed warblers are not subject to phenological mismatch. However, the link between overall food supply and population growth rate is not simple in reed warbler. Although invertebrate availability may have been covarying with reed growth, Vafidis et al. (2016) found a positive effect of invertebrate availability and a negative effect of supplementary feeding on lay date, suggesting that not all invertebrates are valuable to reed warbler. Batey (2018) found that double-brooding (making further breeding attempts after a successful attempt) increased with invertebrate availability. Comparing two sites, Bibby & Thomas (1985) found a lower productivity but higher density at the site with greater invertebrate abundance. Poulin et al. (2002) found a positive relationship between invertebrate abundance and reed warbler density. It could therefore be that invertebrate availability has an overall positive effect on productivity, but also on site selection, potentially leading to density-dependent effects on productivity in high-density high-invertebrate areas.

Reedbed is sparser in the north and west of Britain (Packer et al. 2017). The relative importance of habitat quality and spatial configuration of habitat in determining reed warbler presence varies between landscapes. In an area of Italy, reed warbler's distribution was better predicted by characteristics at the landscape scale than at the reedbed patch scale (Sozio et al. 2013). A range of studies have found that reed warbler density or occurrence probability is greater in large habitat patches (Foppen et al. 2000; Virkkala et al. 2005; Surmacki 2005; Báldi 2006). It is not known whether this is due to higher preference for or higher population growth rate in larger patches. At some scales,

reed warblers are less likely to cross larger gaps between reedbeds (Bosschieter & Goedhart 2005). However, the spatial cohesion of patches has a more minor positive or no effect on incidence (Foppen et al. 2000; Báldi 2006; Mortelliti et al. 2012).

If reedbed or its surrounding habitat declines in quality to the north-west of Britain, either due to natural variation or different management, it is likely to cause reduced productivity or settlement probability. This may cause systematic variation in recruitment and thus in population growth rate which could set up a range limit. No clear evidence exists of an effect of habitat quality on post-fledging survival, juvenile survival or adult survival. If reedbeds decrease in size or increase in fragmentedness to the north-west of Britain, it could reduce patch occupancy probability (through an unknown demographic mechanism) and therefore incidence, setting up a range limit.

Especially in Europe, reed warblers mainly compete with two species for breeding territories. Great reed warbler *Acrocephalus arundinaceus* often outcompetes reed warbler (Hoi et al. 1991; Honza et al. 1999; Schaefer et al. 2006), but is not known to have bred in Britain. Sedge warbler *Acrocephalus schoenobanus* is a common breeding bird in Britain, with about 260,000 territories (Musgrove et al. 2013). Given that reed warbler is typically dominant over sedge warbler (but see Catchpole 1974), even near its range edge (Svensson 1978), it is unlikely that sedge warbler's distribution causes the range limit in reed warbler.

Predation during the breeding season can affect both fully-grown reed warblers and nest contents. For adult reed warblers, the majority of mortality during the breeding season seems to be due to predation (Wierucka et al. 2016); however, survival during this period is generally high and so adult predation is unlikely to contribute much to annual survival variation (Procházka et al. 2017). Nonetheless predation of fully-grown reed warblers is hard to study (Mukhin et al. 2009), and it could be considerable for vulnerable juveniles and contribute to variation in post-fledging juvenile survival. The most likely avian predator of reed warbler, sparrowhawk *Accipiter nisus*, does not increase in relative abundance towards the north and west of Britain (Balmer et al. 2013), and so it is hard to conceive a scenario by which predation of fully-grown reed warblers is limiting range.

Nest predation can be the main or even only cause of nest losses in reed warbler at certain sites, seemingly particularly so in mainland Europe (Dyrz 1981; Borowiec 1992; Schulze-Hagen et al. 1996; Schaefer et al. 2006). Egg predation is typically higher than nestling predation (Schulze-Hagen et al. 1996; Halupka & Wróblewski 1998; Bibby & Thomas 1985). The effects of habitat and food supply can

be mediated through nest predation in reed warbler. Nest predation can differ between wet and dry areas, cut and un-cut reed, and between reed and non-reed nests; the direction of this effect differs by site, presumably depending on the local predator guild (Catchpole 1974; Bibby & Thomas 1985; Graveland 1999). At sites in Wales, supplementary-fed reed warblers had dramatically lower nest predation (Vafidis et al. 2016; 2018), perhaps due to increased adult nest presence or reduced begging (e.g. Dyrce 1981). Given the range of ecological factors that could cause variation in nest predation, which can be the main source of variation in productivity in reed warbler (Bibby & Thomas 1985), there is a variety of ways in which nest predation could increase to the north and west of Britain and cause a range limit.

Reed warbler is one of the main hosts in Britain of the brood parasite, cuckoo *Cuculus canorus*. Reed warblers readily accept cuckoo eggs, and so cuckoo parasitism can be one of the most important influences on productivity in reed warbler (Schulze-Hagen et al. 1996). Additionally, cuckoos will also predate clutches from large numbers of nests (Bibby 1978), even if they do not go on to parasitise them. Therefore cuckoo have a negative effect on productivity that goes beyond parasitism. Cuckoo parasitism is very strongly density-dependent in reed warbler (Stokke et al. 2007), and is potentially therefore a source of the density-dependence in reed warbler productivity (Schulze-Hagen et al. 1996). However, although cuckoo density is high in the north of Britain, almost all these cuckoos probably belong to gens that parasitise other hosts (e.g. meadow pipit *Anthus pratensis*). It is not known how cuckoo density varies within reed warbler's range, so no assessment of the probability of cuckoo limiting reed warbler range can be made.

1.4.3.5 Causes of range expansion in reed warbler in Britain

Species can be prevented from colonising an area due to insufficient dispersal into the un-colonised area, or by deaths exceeding births in the un-colonised area. Range expansion can likewise result from change in the same two factors. Firstly, dispersal can increase or change such that immigration into the un-colonised area becomes sufficient to sustain populations or to colonise new sites. Secondly, the potential ratio of births to deaths can increase in the un-colonised area such that the population growth rate becomes 1 or greater. Additionally, the above two scenarios could be provoked or enhanced by adaptation at the range edge, perhaps due to reduced gene flow from the range core (Kirkpatrick & Barton 1997).

There is no need for the ecological cause of the range limit in reed warbler to be the same as the cause of the range expansion. For example, nest survival could decline with temperature north and west to

the range edge. If survival (due to a change in the African wintering grounds) increases for the whole population, then the potential population growth rate beyond the range limit will increase, leading to a range expansion, even without any changes in nest survival. Similarly, there is no need for there to only be one cause of range expansion: multiple ecological and evolutionary causes can act at the same time to cause a range expansion (Thomas et al. 2001). Next, I outline potential causes of the range change in reed warbler.

1.4.3.6 Increased dispersal as a cause of range expansion

There are several ways in which reed warbler's range change in Britain could be caused by increased immigration into the un-colonised area.

If reed warbler's range limit is caused by slow dispersal, but suitable habitat remains available and there is no barrier to dispersal, then range expansion may take place without any changes in dispersal parameters. Under this scenario, range expansion should remain relatively similar in rate over time, although it may vary as the range edge passes through different landscape habitat configurations. If constrained by dispersal rate, then the rate of reed warbler's range expansion could increase due to an increase in dispersal distances, or due to an increase in abundance within the range increasing the absolute number of emigrants.

If reed warbler's range limit is caused by over-conservative habitat selection, then range expansion may take place without any changes in dispersal parameters. Range expansion would require a change in the potential ratio of births to deaths in the un-colonised area. Reed warblers would then newly identify some of the un-colonised area as suitable for colonising. Under this scenario, the range edge would move at the rate that the ratio of births to deaths improves, but the population growth rate would remain above 1 at the range edge. Habitat selection can itself evolve during a range expansion (Thomas et al. 2001): reed warblers could become less conservative in their habitat selection.

Immigration into the un-colonised area could increase without changes in Britain. The first breeding record for Scotland was in the far north, leading to suggestions that these pioneering birds may have come from growing Scandinavian populations, rather than the English populations (Sharrock 1976). In the 1990s, shortly after the Tay reedbeds were colonised, two Norwegian-ringed reed warblers were caught in Tayside in autumn, one of which in the Tay reedbeds themselves (Robertson 2001). Some Scandinavian bird species make more breeding attempts in Scotland after easterly winds during spring migration (Harvey 2007; Thorpe 2007). Also, some Scandinavian-ringed reed warblers arrive in eastern

Britain during autumn, especially during easterly winds (Bruce 2007). It is not known whether individuals discovering potential breeding habitat during autumn migration consider those locations for future breeding attempts. Either way, an increase in the number of Scandinavian reed warblers arriving in Britain in spring or autumn, due to an increase in the Scandinavian populations or due to a change in wind patterns, could have caused an increase in the number of attempted colonisations. However, much of the range expansion has taken place in the west of Britain, and so this scenario is unlikely to have caused all of the range expansion.

Finally, reed warbler is one of a group of species inhabiting eutrophicated water bodies that expanded their ranges in northern Europe in the 20th century (Järvinen & Ulfstrand 1980), over a time when eutrophication increased in Europe (Keatley et al. 2011). It has been suggested that eutrophication caused a growth in reedbeds in Europe in the middle of the 20th century, causing an increase in reed warbler populations (Karlsson & Ehnbohm 2005). However, it is not known whether reedbed increased in Britain over the 20th century. Reed warblers breed in *Miscanthus* (Burton et al. 1999; Bellamy et al. 2009), which could have increased in extent. If reedbed or *Miscanthus* has increased in the un-colonised area, it could have allowed more immigration events.

1.4.3.7 Increased births-to-deaths ratio as a cause of range expansion

There are several plausible mechanisms by which reed warbler's range change could have been caused by an increase in the potential births-to-deaths ratio in the un-colonised area, leading to births newly exceeding deaths. All of these pertain to potential mechanisms by which reed warbler's population growth rate has improved. I split these into abiotic and biotic.

Reed warbler's population growth rate could have been increased by climate change. As detailed above, there are numerous known mechanisms by which reed warbler productivity is influenced by climate. The climate during reed warbler's breeding season has warmed in recent decades in Britain (Figure 1.7), and therefore has changed in a potentially beneficial way for reed warbler. Under all future climate projections, reed warbler is predicted to expand its range in Britain (Harrison et al. 2003). Reed warbler, in moving north and west, is among a group of species that have changed their range in a direction consistent with climate change. Generally species are moving in directions consistent with climate change: poleward and to higher elevations. The highest rates of range shift are in geographical areas that have experienced the highest rates of warming (Chen et al. 2011). This suggests that climate change is responsible for the range shifts of a large proportion of range-shifting species.

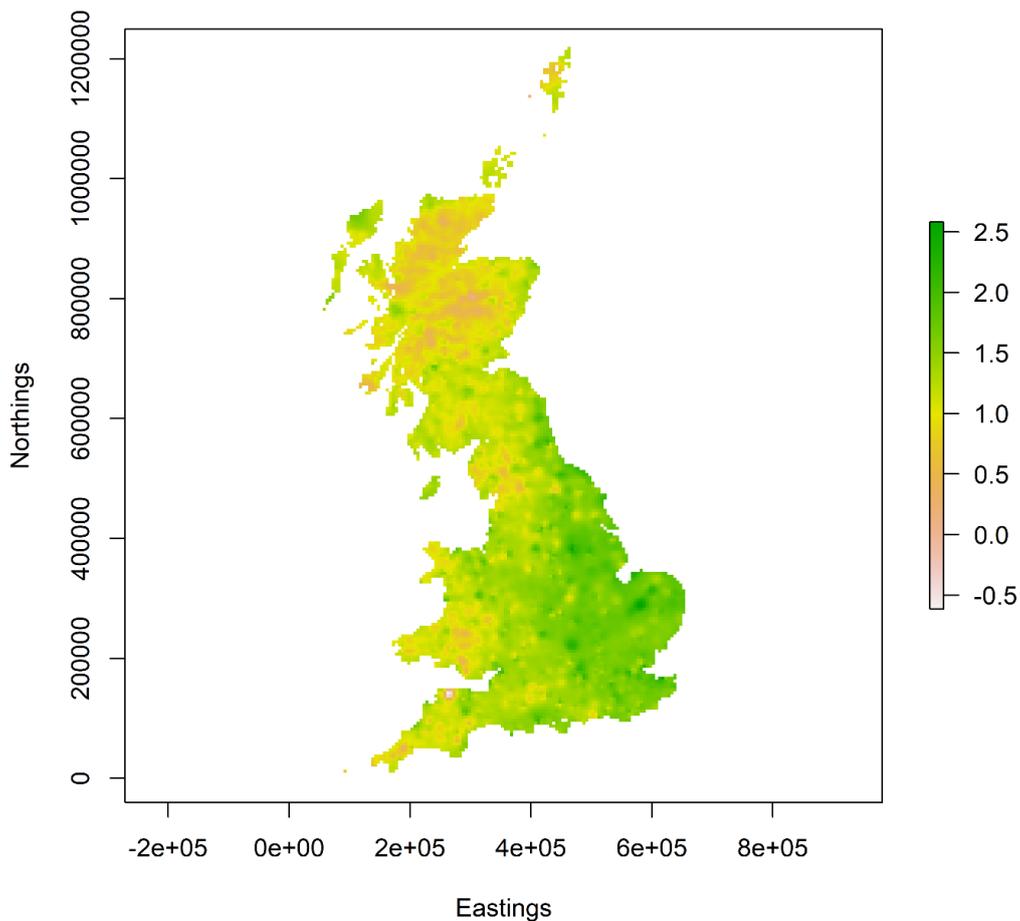


Figure 1.7. Estimated reed warbler breeding season temperature change (°C) from 1968 to 2011 in Britain (UKCP09 data; Met Office 2017). For each 5 km x 5 km cell, the mean was taken of the mean monthly temperature for May-Aug each year. A linear model was fitted with annual breeding season temperature as the response variable and year as the explanatory variable. The coefficient multiplied by 49 (n. years) is presented, representing the estimated temperature change over the time period.

It should be easier for reed warbler to track climate change in Britain than elsewhere in northern Europe. There is a steep gradient in climatic variables in Britain, especially in summer. Reedbeds in northern Scotland, less than 100 miles from reed warbler's current range edge, have the same mean July temperature as areas of the Arctic coast of northern Scandinavia and Russia, 500-1000 miles beyond reed warbler's current range limit.

An improvement in breeding season climate is not necessary for a range expansion: for example, some species are rapidly increasing in the UK as their climate suitability decreases (Green et al. 2008). Reed warbler population growth rate is influenced by climatic changes in its non-breeding range (Johnston et al. 2016). For example, in the 1970s and 1980s, large areas of mangrove forests in the west of reed warbler's wintering range dried out and reduced in extent (Dieye et al. 2013). This, through decreased survival, perhaps explains the loss of some of the breeding range core between 1968-72 and 1988-91 in Britain (Balmer et al. 2013). Therefore, climate or environmental improvement elsewhere in reed

warbler's range could have caused the range expansion. If climate has improved in reed warbler's non-breeding range, then that could improve juvenile and adult survival, increasing the population growth rate across Britain and increasing the births-to-deaths ratio in the un-colonised area.

There are several potential biotic causes of an increase in reed warbler's population growth rate. If reedbed has increased in extent, it could increase the incidence of reed warbler in a landscape. Considering the species with which reed warbler interact, it is not known whether reed warbler prey species have increased or changed in distribution over the course of the range expansion. Sedge warbler, with which reed warblers compete, has declined moderately in abundance in the core of reed warbler's range since the 1960s (Balmer et al. 2013; Woodward et al. 2018); however, reed warbler is dominant over sedge warbler and so reed warbler's population growth rate is unlikely to have been affected. Reed warbler is parasitised and predated by cuckoo, which have recently declined dramatically in the south of Britain, including much of reed warbler's range (Balmer et al. 2013). However, brood parasitism of reed warbler increased steeply between the middle and late 20th century, over a period when reed warbler was increasing in range (Brooke & Davies 1987). It is therefore unlikely that an increase in productivity from reduced cuckoo parasitism could have caused reed warbler's range expansion, but it could have contributed to it.

I have outlined several reasons why reed warbler's population growth rate might have improved. All the above mechanisms of increased population growth rate could operate by elevating births above deaths in the un-colonised area. However, they could also operate by increasing the absolute number of dispersers from the range into the un-colonised area.

1.4.3.8 Summary: range limitation and change in reed warbler in Britain

Reed warbler is an able disperser, suggesting it should be unlikely to be limited in range by dispersal distance; however, this depends on the relative rate of new availability of suitable habitat, which is not known. There is evidence that reed warblers actively choose to avoid breeding in reedbeds beyond the northern range edge in Britain, and conspecific attraction could prevent range expansion even if dispersal is high. It seems unlikely that the northern range edge of reed warbler's range is too far from the wintering grounds. It is not possible currently to evaluate whether the size of reed warbler's wintering range limits the size of the breeding range.

There is widespread evidence that productivity in reed warbler increases with temperature, through a range of mechanisms that may apply differently in different locations. There is tentative evidence

that productivity in reed warbler decreases with rainfall. There is no evidence that adult survival is influenced by breeding season conditions; effects of breeding season conditions on juvenile survival are unstudied. Breeding season temperature declines to the north and west in Britain, and so could limit reed warbler's range through insufficient productivity. There are mechanisms (e.g. invertebrate availability) by which habitat quality could limit reed warbler's range in Britain, but no evidence either way to say this is the case. However, habitat configuration (especially patch size but also connectivity) appears more important than quality in determining reed warbler's distribution: reedbed is sparser in the north and west of Britain, potentially too sparse to support a reed warbler metapopulation. Distributions of reed warbler's competitor species, brood parasite and predators do not suggest competition or predation limiting reed warbler's range in Britain.

If dispersal rate is limiting reed warbler's range, range expansion could occur as reed warbler equilibrates with its potential range, without any changes in dispersal or demographic parameters. There are mechanisms by which habitat selection could have changed to allow more of the potential range to be occupied. There is evidence that an influx of Scandinavian birds into eastern Scotland could have supplemented the range expansion. An increase in reedbed distribution in Britain could have allowed a range expansion, but there is no evidence either way for this. The climate has changed in Britain in such a way as to allow reed warbler's range expansion in Britain. It is uncertain whether climate or environmental change in reed warbler's non-breeding range has acted in a way to increase reed warbler's population growth rate in Britain. Apart from unknown potential changes in reedbed extent or prey distribution and abundance, it is unlikely that biotic interactions have allowed range expansion in reed warbler in Britain.

Some of these mechanisms for the drivers of range limitation and change will produce distinctive patterns in range change, dispersal and demographic parameters. As explained above, particular causes of range limitation make particular causes of range change more likely. I will attempt to estimate reed warbler's range change, occupancy, demographic parameters and dispersal in space and time, and the relationships of some of these quantities with climate, in order to attempt to diagnose the causes of range limitation and change in reed warbler in Britain.

1.5 Thesis structure and methodology overview

The structure of this thesis is as follows. I will estimate reed warbler's range change and occupancy (Chapter 2), dispersal (Chapter 3) and demographic parameters (Chapter 4) in Britain, in order to evaluate support for different hypotheses for causes of reed warbler's range limitation and change in

Britain. I do this primarily using large volunteer-collected datasets on reed warbler in Britain, held by the British Trust for Ornithology (BTO): Bird Atlas, the Breeding Bird Survey, and the Constant Effort (CES), Nest Record (NRS), and Ringing Schemes. These include datasets from which one can estimate occupancy (Bird Atlas; BBS; CES), productivity (CES; NRS), survival (CES) and dispersal (CES; Ringing Scheme).

One of the key methods I use for estimating reed warbler occupancy and demographic parameters is hierarchical models. In hierarchical models, the realisation of a random variable at one level is the parameter of another random variable, the level below. Much of the variation in the datasets I use arises from (known) variation in observer effort; by modelling process error and observation error separately, hierarchical models can account for these types of error separately, allowing for more accurate estimation of quantities of interest (Kéry and Schaub 2011). Additionally, this flexible modelling approach allows for bespoke, complex likelihood definitions, allowing fitting of custom survival models and integrated population models (IPMs). IPMs combine datasets to allow more accurate estimation of demographic parameters, and also estimation of latent parameters which cannot otherwise be estimated directly. Finally, I aim to understand how reed warbler demographic parameters, and their relationships with time and climate, vary in space. I therefore fit the models in a Bayesian framework, for pragmatic reasons: it is easier to fit large hierarchical models with many parameters or spatial random effects in this framework than in a frequentist paradigm.

The second main modelling approach I use is individual-based models (IBMs). IBMs allow the simulation of large numbers of agents (e.g. individual animals), given particular rules (e.g. survival rates, dispersal movements, number of offspring produced) about their behaviour. I design an IBM of the British reed warbler population, with which to further investigate the relative roles of demography and dispersal in range limitation and change in reed warbler in Britain. This IBM is structured and parameterised according to autecological information from the literature and from the previous chapters. How reed warbler short-distance dispersal takes place, and its parameters, are poorly known; I therefore carry out two seasons' fieldwork (Chapter 3) to inform the characterisation of this process in the IBM. I create a reedbed map of Britain from remotely-sensed data (Chapter 5) in which to run the IBM. To make this map, a machine learning classification model is trained on Sentinel-2 data; this model is predicted over Britain and then validated in the field. The Methods for the IBM are presented in the Appendix, and preliminary results are presented in Chapter 6. Additionally in Chapter 6 I synthesise the information from Chapters 2-5 to evaluate the

role of dispersal in range change in birds, and discuss the implications for the field and for future research.

2. Range change in Eurasian reed warbler *Acrocephalus scirpaceus*

2.1 Abstract

In this chapter I studied the patterns of reed warbler's range expansion in Britain, in order to narrow down potential causes of range limitation and change in the species. Occupancy is strongly related to temperature, suggesting that climate sets up the range limit directly or indirectly. Occupancy is much more strongly related to temperature in the current year than in the previous year, suggesting that climate sets up the range limit through behavioural choices, rather than through demography. Reed warbler's range expanded in a similar direction and distance to that of climate change, suggesting that climate change has played a role in this species' range expansion. Although the temperature of reed warbler's range edge did not decrease over time, the velocity of the range edge was slower than the velocity of the far edge of climate space. The frequency of occupied hectads at the cool edge of reed warbler's climate space decreased during a period of rapid warming, and only recovered slowly during climate stasis. This implies that reed warbler lagged behind its climate space, suggesting that the species is dispersal-limited during rapid climate change.

2.2 Introduction

The study of species' geographical ranges has continued to increase over recent decades, out of both opportunity and necessity (Gaston 2003). Large, long-running spatial datasets on species occurrence and abundance have proliferated in recent years, as have the tools with which to analyse them (Pimm et al. 2015), providing the opportunity to test predictions from spatial ecology. As anthropogenic environmental change progresses (IPCC 2014; IPBES 2019), many species are responding by shifting their ranges, and their conservation partly depends on our ability to predict those shifts (Pecl et al. 2017).

Globally, many species are shifting their ranges in directions consistent with climate change (Chen et al. 2011; Pecl et al. 2017). Species are typically shifting their ranges at rates sufficient to track temperature change (median 16.9 km poleward and 11.0 m uphill decade⁻¹; Chen et al. 2011). However, the nature of the range shift varies greatly between species, with some species failing to move in the direction expected due to climate change, or moving in the opposite direction (Mair et al. 2012). Furthermore, many species move with climate change, but lag behind their climate space (Tayleur et al. 2015; Pecl et al. 2017). These idiosyncratic responses may be due to variation in dispersal abilities, abundance trends, environmental tolerances and local geography (Hill et al. 1999; Mair et al. 2014). Also, as many species' ranges are limited by biotic interactions (Gaston 2009), then

we might expect the effects of climate change on species' ranges to be lagged as the effects cascade through other species, depending on the time-scale of these cascades (Suttle et al. 2007).

There are several plausible, possibly interacting, causes of reed warbler's range limit and range change (see 1.4). To narrow these down, in this chapter I analyse reed warbler occupancy and climate to answer three questions about the mechanisms of range dynamics in this species. First, by analysing the relationship between climate and reed warbler occupancy, I evaluate whether climate sets up reed warbler's range limit. Second, by comparing patterns in reed warbler's range expansion with spatial patterns in climate change, I evaluate whether climate change may have caused reed warbler's range expansion. Third, by comparing the velocity of the range edge to the velocity of the edge of suitable climate space, and by examining the shift in climate space occupied by reed warbler over time, I evaluate the extent to which reed warbler has successfully tracked its climate space. Additionally, I generate estimates of range shift velocity to compare with estimates of dispersal rate and distance (Chapter 3) for additional insight into the role dispersal has played in reed warbler's range change. Overall, this chapter addresses the role of climate and dispersal in reed warbler's range dynamics.

2.3 Methods

2.3.1 Occupancy and climate

2.3.1.1 Data and modelling approach

In order to evaluate whether climate sets up reed warbler's range limit, I modelled reed warbler occupancy as a function of climate. Reed warbler capture data from the BTO's CES were used for occupancy data. Under the CES, volunteers operate multiple mist-nets after dawn according to a standardised methodology (Robinson et al. 2009), over 12 visits at approximately 10-day intervals across the breeding season. Mist-net locations are kept the same and habitat is managed in order to prevent capture probability changing. A large number of sites are run every year (median 92 over dataset used here), with some sites running for long periods (more than 25 years). This scheme produces capture data and parallel effort data. Data were used from the initiation of the scheme in 1983 until 2014.

Occupancy was modelled with a hierarchical structure: with an observation error component and a latent ecological process component (see 1.5). All models assumed that the underlying demographic parameter varies with a covariate (year, temperature or rainfall) according to a slope and an intercept.

There is expected to be spatial autocorrelation in occupancy, for example due to dispersal or relationships with spatially autocorrelated ecological variables (Beale et al. 2010). This means that data from closely-located sites are likely to be non-independent. I incorporated this structure into the model as a spatial random effect, with each level of the random effect corresponding to a 100 km x 100 km grid square. I used this scale as a trade-off between flexibility and the number of data-contributing sites per grid square. Each level of the random effect was correlated to the levels around it (intrinsic conditional autoregressive model; Besag et al. 1991). The variation between grid squares was determined by a term estimated by the model. One spatial random effect was added each for occupancy and its slope with a given covariate. The spatial discretising of the random effects presents additional advantages by allowing estimation of occupancy, and its slope with covariates, for each grid square across Britain (e.g. Saracco et al. 2010).

2.3.1.2 Technical details of Bayesian modelling

Models were fitted in a Bayesian framework; details of the Bayesian modelling in this chapter and in Chapter 4 (modelling of demographic parameters) are described here. For inference, the models used Markov Chain Monte Carlo sampling (MCMC), which explores parameter space according to the prior probability and the likelihood of the data in order to sample from the posterior probability. With enough MCMC samples, the frequency distribution of MCMC samples matches the posterior probability distribution, which can then be summarised (e.g. with a mean and credible interval) for each parameter in the model. To assess confidence in the posterior probability distribution this process can be carried out independently several times, and the traces (hereafter 'chains') of each set of MCMC samples can be compared.

MCMC chains may take many iterations to arrive from an initial value to a stationary distribution. In order to solely focus on the posterior probability distribution, I discarded the first set (e.g. 5,000) of MCMC samples (hereafter 'burn-in'); the remaining set were used for estimating the posterior probability distribution. The MCMC samples should be relatively independent, and so in order to minimise autocorrelation in the MCMC chains I retained only one in every six samples from each. For each model I ran three independent chains, and assessed their convergence by eye and using the Gelman-Rubin statistic, $R\text{-hat}$ (Kéry and Schaub 2011). $R\text{-hat}$ compares the within- and between-chain variance; if $R\text{-hat}$ was below 1.1 for a given parameter then I assumed that the chains had converged on the posterior probability distribution (e.g. Kéry and Schaub 2011). The length of the total sampling and the length of the burn-in were adjusted such that all pre-convergence sampling was in the burn-in, and that the chains had long enough to adequately explore the posterior probability distribution

after convergence. Large models ran slowly, and so the length of the total sampling was set to be no longer than necessary.

In a Bayesian model, the prior probability (i.e. a probability distribution and the values of its parameters; hereafter ‘prior’) represent the prior belief in a parameter’s value, and must be defined for each parameter to be estimated in the model. This is an opportunity to input prior knowledge about a parameter’s expected value into the model. If no knowledge is held about a parameter’s expected value, then priors must be left vague (i.e. as close to uniform as possible over the range of potential values). However, if there are few data, then completely vague priors can encourage exploration of nonsensical parameter space. In my modelling I aimed to use uninformative priors where possible. However, sometimes priors had to be more informative to avoid numerical problems; these cases are identified in the text.

Due to the large number of parameters in some models (especially the IPM – Chapter 4), and the fact that runtime can be slow for large Bayesian models, I fitted one model for each covariate: year, temperature and rainfall. Although both temperature and rainfall followed trends over the survey period (Figure 4.3c & d), neither has done so monotonically. Year and climate will therefore differ in their covariance with demographic parameters. By comparing the estimated relationship of reed warbler occupancy or demographic parameters with year and climate separately, I can infer whether an apparent relationship with climate is a real one (resulting in a stronger relationship with climate than with year) or if it arises from a spurious relationship with an unknown ecological variable that has followed a trend over time (resulting in a stronger relationship with year than with climate).

Models were fitted in WinBUGS from R (R Core Team 2018), using the package R2WinBUGS (Sturtz et al. 2005).

2.3.1.3 Occupancy and climate: model details

Sites were defined as being occupied in a year if at least one adult reed warbler was captured on at least one of the 12 visits of that year: 254 sites were thus ‘occupied’ in at least one year; these formed the dataset. Being a binary variable, the observed occupancy of a site was assumed to be Bernoulli-distributed with parameter λ (equation 2.1). For site i in year j ,

$$z_{i,j} \sim \text{Bern}(\lambda_{i,j}) \quad \text{Eq. 2.1}$$

The logit of λ was assumed to be the product of the true occupancy and whether the CES site was operated on any visits in that year eff (equation 2.2). The true occupancy was assumed to vary across a global intercept α according to a spatially varying trend against the covariate (year, temperature or rainfall) with slope $\gamma + \delta$, local intercept β and random annual residual ϵ . Random effects β and δ were spatially discretised by 100km x 100km grid square (identity $gridid$). For site i in year j

$$\text{logit}(\lambda_{i,j}) = (\alpha + \beta_{gridid_i} + ((\gamma + \delta_{gridid_i})covariate_{i,j}) + \epsilon_j)eff_{i,j} \quad \text{Eq. 2.2}$$

Preliminary analysis showed that the global intercept ω could be given a reasonably vague prior, and so was assumed to be drawn from a normal distribution with mean 0 (being on the logit scale) and precision (1/variance) 0.001. Being a slope parameter, α was assumed to be drawn from a normal distribution with mean 0; preliminary analysis showed that α needed a more informative prior, and so was given a precision of 0.1. Values of the precision of the random effects δ , γ and ϵ had to be drawn from positively-skewed positive real numbers, and were therefore drawn from gamma distributions. The precision of these random effects needed relatively narrow priors: thus all three were given shape parameter 10 and rate parameter 1.

The presence of reed warblers at a site could be influenced by breeding season climate in under two non-exclusive scenarios. Firstly, reed warblers might only occupy a site if the climate is suitable. This would produce a relationship between occupancy and the current year's climate. Secondly, reed warbler demography could be a function of climate: for example, productivity might be higher in a warm year. Climate-linked demography would then only influence occupancy (through recruitment and survival) the following year. Therefore, this second scenario would produce a relationship between occupancy and the previous year's climate. To discern between these two scenarios and ascertain the mechanism through which climate may influence occupancy, I ran five models for occupancy, each with one of the following covariates: current year's temperature; previous year's temperature; current year's rainfall; previous year's rainfall; year.

UKCP09 data (Met Office 2017) were used for temperature and rainfall (see Figure 4.3a & b for summary maps): monthly 5 km x 5 km data were summarised annually (mean for temperature, total for rainfall) over the main months of reed warbler's breeding season (May to August), and extracted for each CES site. All covariates were scaled to mean 0 and standard deviation 1 to ease model running (Kéry and Schaub 2011) and allow comparison of slopes between covariates.

2.3.2 Range change

Next, I described patterns in reed warbler's range expansion, to be compared with patterns in climate change, to evaluate whether climate change may have caused reed warbler's range expansion, and the extent to which reed warbler has successfully tracked its climate space. To describe reed warbler's range, I used reed warbler presence/absence data from the BTO's Bird Atlas (Balmer et al. 2013). For the Bird Atlas, fieldwork was carried out over three different surveys (1968-1972; 1988-1991, 2008-2011), in order to estimate the presence or absence of bird species in as many as possible of the 3984 10 km x 10 km squares (hereafter 'hectad') containing land in Britain, Ireland, the Isle of Man and the Channel Islands, in the period April-July. The aim was to produce complete bird species lists for each square. Fieldwork methods varied slightly between survey periods, and lists were supplemented with records from other contemporary surveys. The proportion of hectads assessed as being surveyed well was high, and differed little (89.7-92.3%), between Bird Atlas surveys (Gillings et al. 2019). The level of survey effort in Bird Atlas is much higher than in similar nationwide surveys of other taxonomic groups in Britain (Mason et al. 2015). However, coverage was consistently lower in the central Highlands and north-west Scotland in all periods, especially in 1988-1991: it is more likely that reed warblers present here would be incorrectly classed as absent than elsewhere in Britain.

Range change can be considered in two broad ways: change in the central tendency of the range, or change in the range edge. Range change can be estimated in many different ways (Yalcin & Leroux 2017). Central tendency was estimated by taking the mean eastings and mean northings of all occupied hectads, for a given Bird Atlas survey. When estimating change in range edge, many studies focus on movements in the poleward-equatorward dimension (e.g. Mason et al. 2015). However, many species are moving in other directions (Chen et al. 2011), and different parts of the range edge can move in different directions. Gillings et al. (2015) adapted Thomas & Lennon (1999)'s method for estimating poleward range margin shifts, and generalised it to estimate range margin shifts in all directions. The authors applied this to Bird Atlas, estimating range margin shifts between 1988-91 and 2008-11 for 122 species. I applied this to reed warbler to estimate the range margin in 1968-72, 1988-81 and 2008-11 as follows. From the 1968-72 range centroid in Britain, a line was defined at bearing 000° (i.e. north) to an outer point 10,000 km away. The 20 hectads occupied by reed warbler that are closest to the outer point were identified, and the mean distance from the 1968-72 centroid to those hectads was calculated. This was taken as an index of reed warbler's range edge in bearing 000°, and was repeated every 15° up to 345° to give a multidirectional index of the range edge. Applying the same method to reed warbler's occupied hectads in the other Bird Atlas surveys allowed estimation of the rate of shift of the range edge in the intervening periods. In some directions, the range edge

was often already at the coast and so there was no capacity for range expansion. To give a simple multidirectional index of capacity for range expansion, the method for identifying the range edge was repeated, but identifying the 20 outermost land hectads, regardless of reed warbler occupation. My only deviations from Gillings et al. (2015)'s methods were to use pure presence/absence (the authors used additional visit data to account for variation in effort), to estimate also the range edge for 1968-72, and to present the results for an individual species.

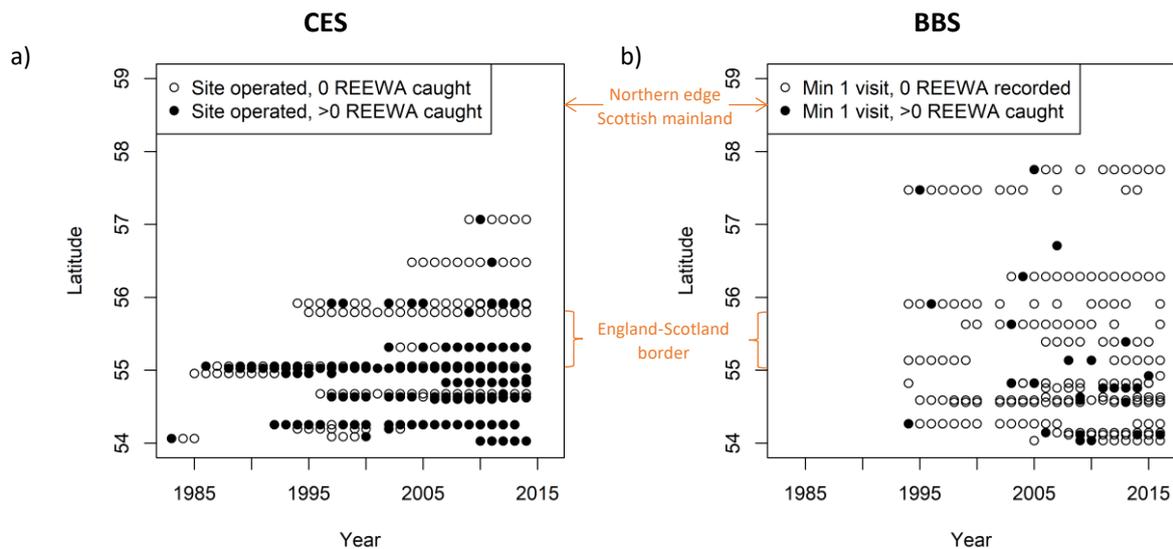


Figure 2.1. CES captures (a) and BBS observations (b) of reed warbler in northern England and Scotland, 1983-2016. CES data were only retrieved up until 2014; the BBS scheme began in 1994.

Bird Atlas data give us snap-shots of a species' range at a point in time. However, extra insight could be gained by estimating a species' range limit annually, in order to, for example: analyse covariates of the annual location of the range edge; to analyse how demography or dispersal vary as a function of distance from the range edge. Both analyses would provide evidence for particular causes of range limitation or change. Preliminary data exploration was carried out for two of BTO's annual demographic monitoring datasets well suited to this: the CES and the BBS (Noble et al. 2001). For the CES sites in northern England and southern Scotland where reed warblers have been frequently caught, most already had reed warblers present in their first year of operation (Figure 2.1). It is therefore possible that reed warblers were present at these sites before operation began. Of the BBS sites, only one had more than three years' consecutive reed warbler records, perhaps because BBS covers a wider range of habitats than CES, and therefore is potentially more susceptible to passage reed warblers than CES sites (Figure 2.1). Therefore for both the CES and the BBS datasets, it was not possible to identify the year of colonisation for enough sites to robustly estimate the location of the range edge in a given year, and this avenue of analysis was therefore not pursued.

2.3.3 Climate change

To evaluate whether climate change may have caused reed warbler's range expansion, and the extent to which reed warbler has successfully tracked its climate space, I summarised spatial patterns of climate change between the Bird Atlas surveys.

To compare species' range shifts to multidirectional shifts in climate space, Gillings et al. (2015) compared the range edge shifts, and range centroid shifts, to climate space centroid shifts. The authors took the centroid of the climate space (between 2.5th and 97.5th percentiles of temperatures of all occupied hectads) occupied by a given species in the first period, and computed the vector to the centroid of the same space in the second period. However, as reed warbler's climate space moves northwards in Britain, novel warmer climate space in the south is still suitable for reed warbler (being still cooler than most of the European breeding range). I therefore made the same calculation, but I defined climate space as all temperatures above the 2.5th percentile of the 1968-72 hectad temperatures, in every Bird Atlas survey; I calculated the climate space centroids from this.

In order to compare range centroid shift with climate space centroid shift, and to compare range edge shift with climate space edge shift, I estimated a multidirectional index of the distance to the cool edge of reed warbler's climate space, extending the multidirectional paradigm of Gillings et al. (2015). This was carried out using the same method used to define the indices for range edge and capacity for range expansion; here I defined the cool edge of climate space (in each bearing) as the mean distance to the 20 most distant hectads in that direction with: a) temperature above the 2.5th percentile of the temperatures of hectads occupied by reed warbler in 1968-72 hectad; and b) altitude below the 97.5th percentile of the altitudes of hectads occupied by reed warbler in any Bird Atlas survey (to exclude warm areas in non-lowland habitats unsuitable for breeding reed warbler). I repeated this for each of the Bird Atlas surveys.

To understand how successfully species have responded to climate change, it is important to describe their movement in climate space as well as in geographical space (Tayleur et al. 2015). Firstly, to compare reed warbler's changes in climate space with changes in geographical space, I produced histograms of the northings and temperature of occupied hectads in each Bird Atlas survey. Secondly, as a summary of the position of reed warbler's range edge in climate space, I calculated the mean breeding season temperature of the 20 most distant hectads north of the 1968-72 centroid in each Bird Atlas survey. Thirdly, I also presented the frequency of occupied hectads with mean breeding season temperature below 14C, to summarise reed warbler's relative incidence near its cool range

edge. As in 2.3.1, I used UKCP09 (Met Office 2017) monthly mean temperature at 5 km x 5 km resolution to characterise reed warbler's climate space. For each year of the three Bird Atlas surveys, I took the mean of these monthly temperatures across May-August (the main months of reed warbler's breeding period), and then took the mean across all the years of that Bird Atlas survey.

2.4 Results

2.4.1 Occupancy and climate

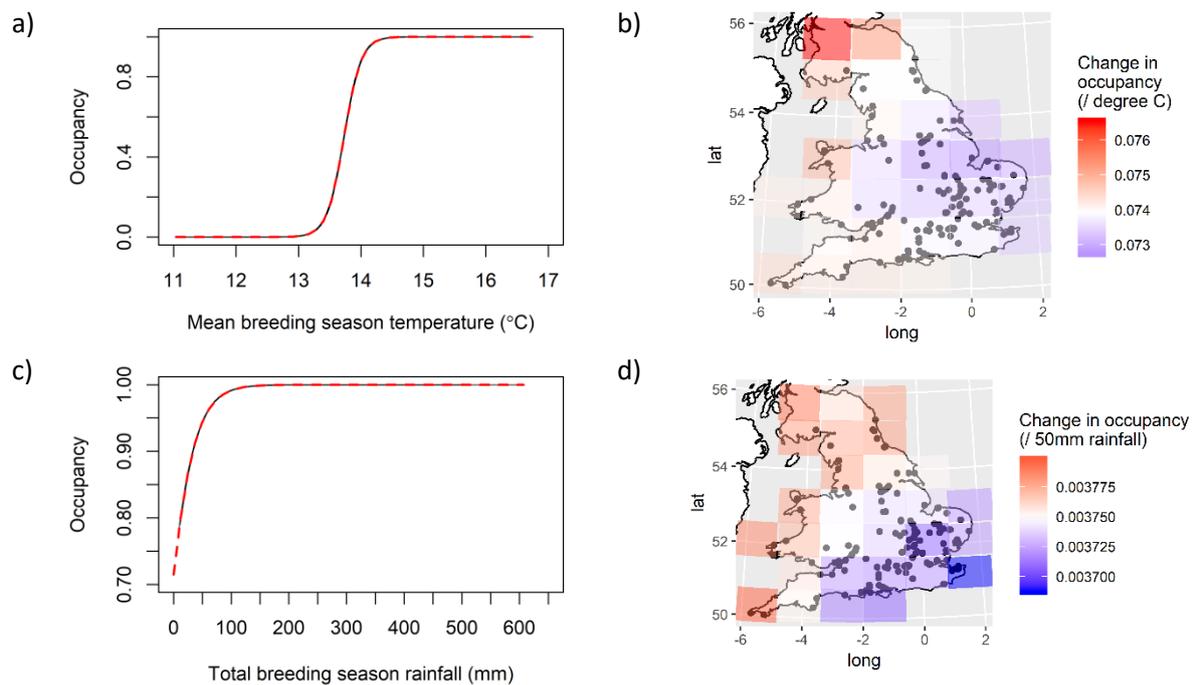


Figure 2.2. Modelled relationship between climate and occupancy. a, c): red dashed line describes the global relationship; black lines describe the relationship for each 100 km x 100 km square containing a data-contributing site. The estimated precisions of the spatial random effects are very high (little estimated variation in occupancy or its slope with covariates across the study sites), so the black lines for each 100km x 100km square are very tightly clustered under the red dashed line. b, d): points show the data-contributing CES sites.

For all five model runs, model was updated 10,000 times, of which a burn-in set of 5,000 samples was discarded. After this burn-in, values of R-hat were below 1.1 for all parameters, and chains had visually converged. There was a very strong relationship between occupancy probability and mean breeding season temperature (Figures 2.2a, 2.4). Modelled occupancy was close to zero below 13°C, and close to 1 above 14.5°C. There was very little spatial variation in this relationship, but 100km x 100km grid squares in the far north and west of the range had a slightly steeper positive relationship between occupancy and temperature (Figure 2.2b). There was a much weaker relationship between occupancy probability and the temperature in the previous year (Figure 2.4). Occupancy probability seemed to increase with total breeding season rainfall (Figure 2.2c); however, the credible interval of the global

slope overlapped with zero (Figure 2.4). This relationship varied little across the range, perhaps with a steeper relationship in the north and west than in the south and east (Figure 2.2d). There was no relationship between occupancy probability and the total rainfall in the previous breeding season: the credible interval for the global slope overlapped with zero (Figure 2.4).

Occupancy probability increased slightly from 1983 to 2014 across the breeding range (Figure 2.3a); however, the credible interval of the global slope overlapped with zero (Figure 2.4). There was little variation in occupancy across the range (Figure 2.3b); however, occupancy was slightly lower in the north and west, and there was a hint of a slightly more rapid increase over time in the same area (Figure 2.3c).

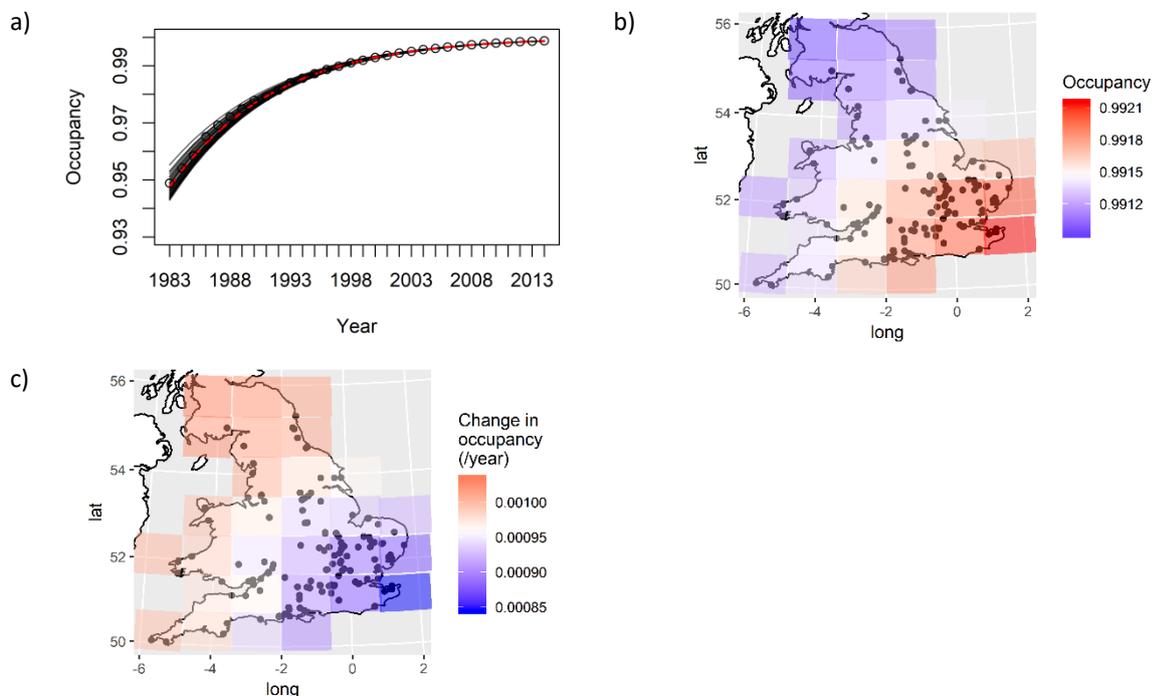


Figure 2.3. Modelled change in occupancy over time. a): red dashed line describes the global relationship; black lines describe the relationship for each 100 km x 100 km square containing a data-contributing site; points represent the mean relationship plus the annual residual. The estimated precision of the spatial random effects and the random effect for year is very high (little estimated variation in occupancy, or its slope with time, across the study sites or away from the time trend), so the black lines and points are very tightly clustered under the red dashed line. b, c): points show the locations of the data-contributing CES sites.

2.4.2 Range change

From 1968-72 to 1988-91, reed warbler colonised much of Wales and northern England (Figures 2.5, 2.6). This was contemporary with a thinning out of the range: although the range increased considerably in extent, the overall increase in occupied hectads was just 1.0% (Table 2.1). Thus the range edge moved almost 10 times faster than the centroid over this period (range edge 6.2 km year^{-1} ;

centroid 0.7 km year^{-1}). The maximum change in the range edge over this period was more northerly in direction (Figure 2.7) than was the change in the centroid (Table 2.1).

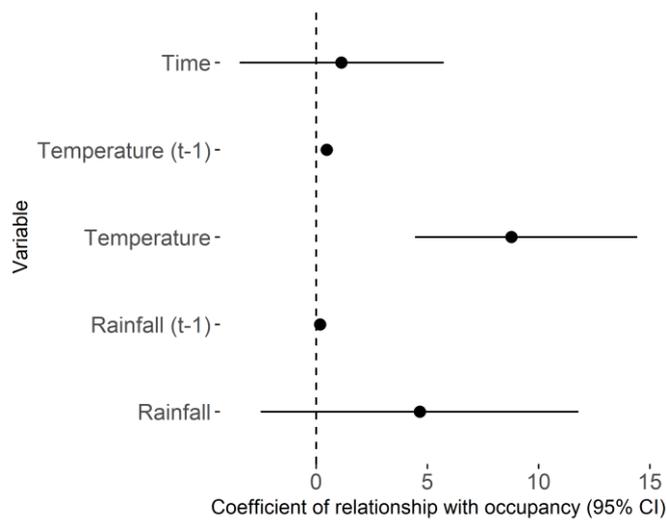


Figure 2.4. Forest plot of coefficients of relationships between occupancy and climate or year. For each model run with a given variable, the estimate of its global slope (γ in equation 2.2) with occupancy is presented (points), with 95% credible intervals (bars). Covariates are scaled to allow comparison.

Between 1988-91 and 2008-11, reed warbler filled out much of its range (Figures 2.5, 2.6), with a 35% increase in the number of occupied hectads (Table 2.1). The main expansion of the range edge was northwards into Scotland, but there was also an expansion in the south-west of England (Figure 2.7, solid green line), using up much of the capacity for expansion there (Figure 2.6). Between the latter two Bird Atlas surveys, the centroid moved twice as fast (1.3 km year^{-1}) as between the first two periods, but the maximum change in the range edge was much lower than between the first two periods (3.6 km year^{-1} ; Figure 2.7). The maximum change in the range edge was just east of north over this period, whereas the centroid moved in a similar direction to the previous shift, west of north-west (Table 2.1).

Table 2.1. Magnitude, direction and distance of reed warbler’s range change and movement of climate space between Bird Atlas surveys.

	1968-1972	1988-1991	2008-2011
Number of occupied hectads	775	790	1087
Change in occupied hectads	15	297	
Change in centroid	13.1 km, 302.3°	26.1 km, 307.6°	
Maximum change in range edge	120.3 km, 345°	71.0 km, 015°	
Change in centroid of climate space	45.2 km, 337.3°	12.6 km, 339.6°	
Maximum change in climate space edge	172.2 km, 000°	22.7 km, 315°	

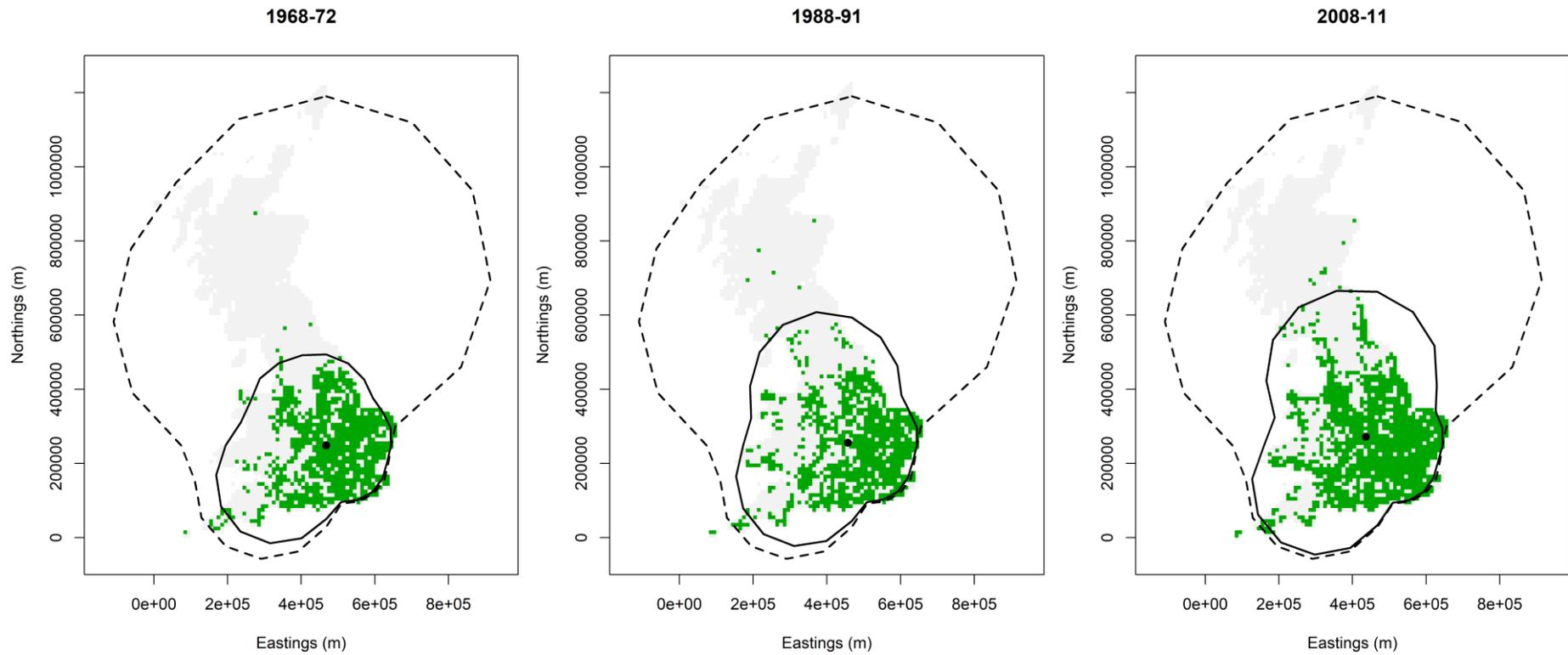


Figure 2.5. Reed warbler range centroids, range limits and potential for expansion over three Bird Atlas surveys in Britain: 1968-72; 1988-91, 2008-11. Green cells denote hectads occupied by reed warbler in each Bird Atlas survey. Black point is mean eastings and northings of occupied hectads. Solid lines link, for each 15° increment from 0-345°, the mean location along that axis of the outermost 20 hectads occupied by reed warbler. The equivalent margin for outermost 20 Bird Atlas hectads, regardless of occupancy status by reed warbler, is shown with the dashed lines (same in all years).

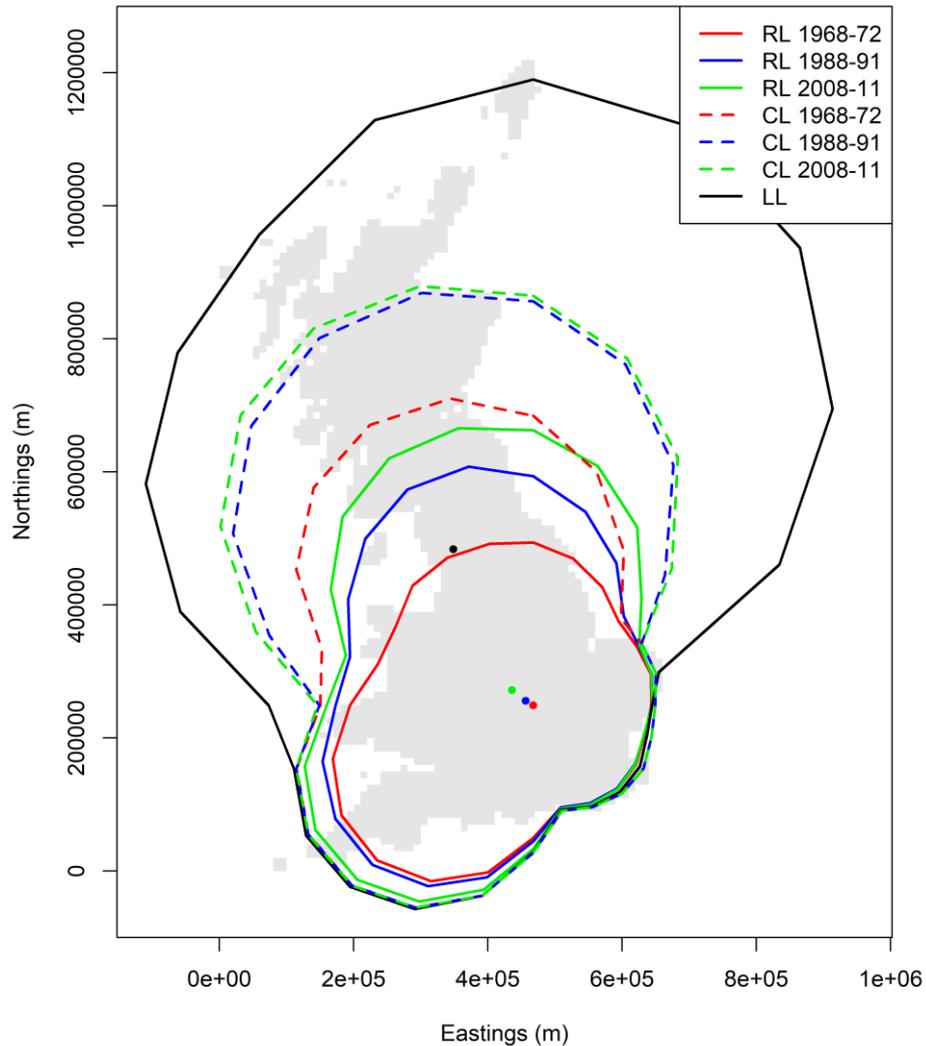


Figure 2.6. Reed warbler range centroids, range limits and potential for expansion over three Bird Atlas surveys in Britain: 1968-72; 1988-91; 2008-11. Coloured lines link, for each 15° increment from 0-345°, the mean location along that axis of the outermost 20 occupied hectads (RL, solid) or climatically suitable hectads (CL, dashed) from each Bird Atlas survey. Coloured points are mean eastings and northings of occupied hectads from each Bird Atlas survey (colours same as RL and CL). The equivalent centroid and margin (LL) of all Bird Atlas hectads, regardless of occupancy status by reed warbler, is shown in black.

2.4.2 Range change and climate

The climate warmed over the period from 1968-72 to 2008-11, generally with a higher rate of warming in the south and east of Britain than in the north and west (Figure 2.8). In 1968-72, 97.5% of hectads occupied by reed warbler had mean breeding season temperatures warmer than 13.2°C (Figure 2.9). The largest area of land that newly became above 13.2°C over the study period was in north-east England (Figure 2.8).

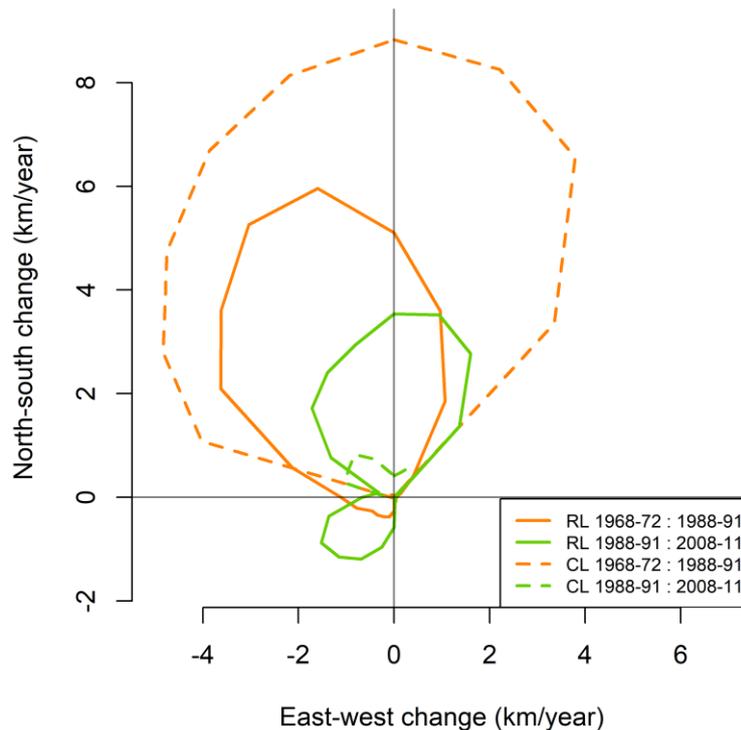


Figure 2.7. Annual change in reed warbler range limit (RL; solid line) and potential climatic limit (CL; dashed line) between three Bird Atlas surveys (1968-72; 1988-91; 2008-11) in Britain. Lines show difference in km in RL or CL (see Figure 2.5) between the first and second surveys (orange), or between the second and third surveys (green); distances divided by the number of intervening years between the pairs of surveys to give annual change.

The rate of movement of climate space was much greater from 1968-72 to 1988-91 (Figure 2.7, dashed orange line) than from 1988-91 to 2008-11 (Figure 2.7, dashed green line). As the climate warmed from 1968-72 to 1988-91, reed warbler's northern range edge did not keep pace with the movement of the far edge of climate space (Figures 2.6, 2.7). Reed warbler's range centroid therefore moved 69% slower (0.7 km year^{-1}) than the centroid of reed warbler's climate space (2.3 km year^{-1} ; Table 2.1). Also, the centroid of reed warbler's range moved with a more westerly element than the centroid of reed warbler's climate space over this period (Table 2.1). The movement of reed warbler's range edge was 30% slower than the movement of the far edge of reed warbler's climate space, but the direction of the maximum change in range edge was intermediate between the change in the centroid and the far edge of climate space (Table 2.1). From 1988-91 to 2008-11, warming slowed and the rate of movement of reed warbler's range edge (Figure 2.7, solid green line) and centroid were faster than the rate of movement of the far edge (Figure 2.7, dashed green line) and centroid of climate space.

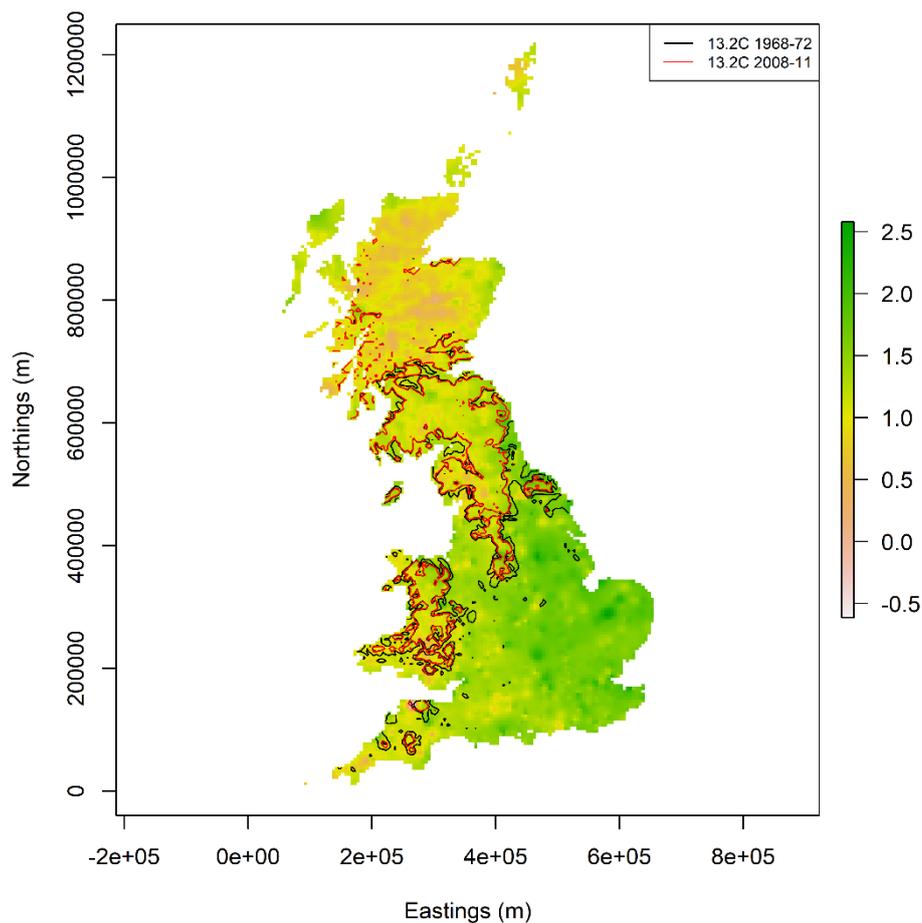


Figure 2.8. Estimated temperature change ($^{\circ}\text{C}$) during reed warbler breeding season from 1968 to 2011 in Britain. For each 5 km x 5 km cell, the mean was taken of the mean monthly temperature for May-Aug each year. A linear model was fitted with annual temperature as the response variable and year as the explanatory variable. The coefficient multiplied by 49 (n. years) is presented. Contours are presented for 13.2 $^{\circ}\text{C}$ (2.5th percentile of temperatures of hectads occupied by reed warbler in 1968-72), for all areas with altitude less than 220m (97.5th percentile of altitudes of hectads occupied by reed warbler in any Bird Atlas survey), for the first and last Bird Atlas surveys (for the mean temperature over each 5 year period).

Although reed warbler's northern range edge did not track movement in the far edge of climate space (Figure 2.6), reed warbler's range edge maintained its position in climate space: temperatures at reed warbler's northern range edge did not increase over time (Table 2.2). However, the frequency of occupied hectads at the cool edge of the range ($<14^{\circ}\text{C}$) decreased substantially from 1968-72, and only partially recovered by 2008-11 (Table 2.2, Figure 2.9). The mean temperature of hectads occupied by reed warbler increased by 0.67 $^{\circ}\text{C}$ between 1968-72 and 1988-91, and by 0.04 $^{\circ}\text{C}$ between 1988-91 and 2008-11 (Figure 2.9).

Table 2.2. Climate characteristics of reed warbler's range limit over three Bird Atlas surveys.

	1968-1972	1988-1991	2008-2011
Mean breeding season temperature, 20 most distant hectads north of 1968-72 centroid	13.5°C	12.9°C	13.0°C
Number of occupied hectads with mean breeding season temperature below 14°C (Figure 2.5)	235	47	101

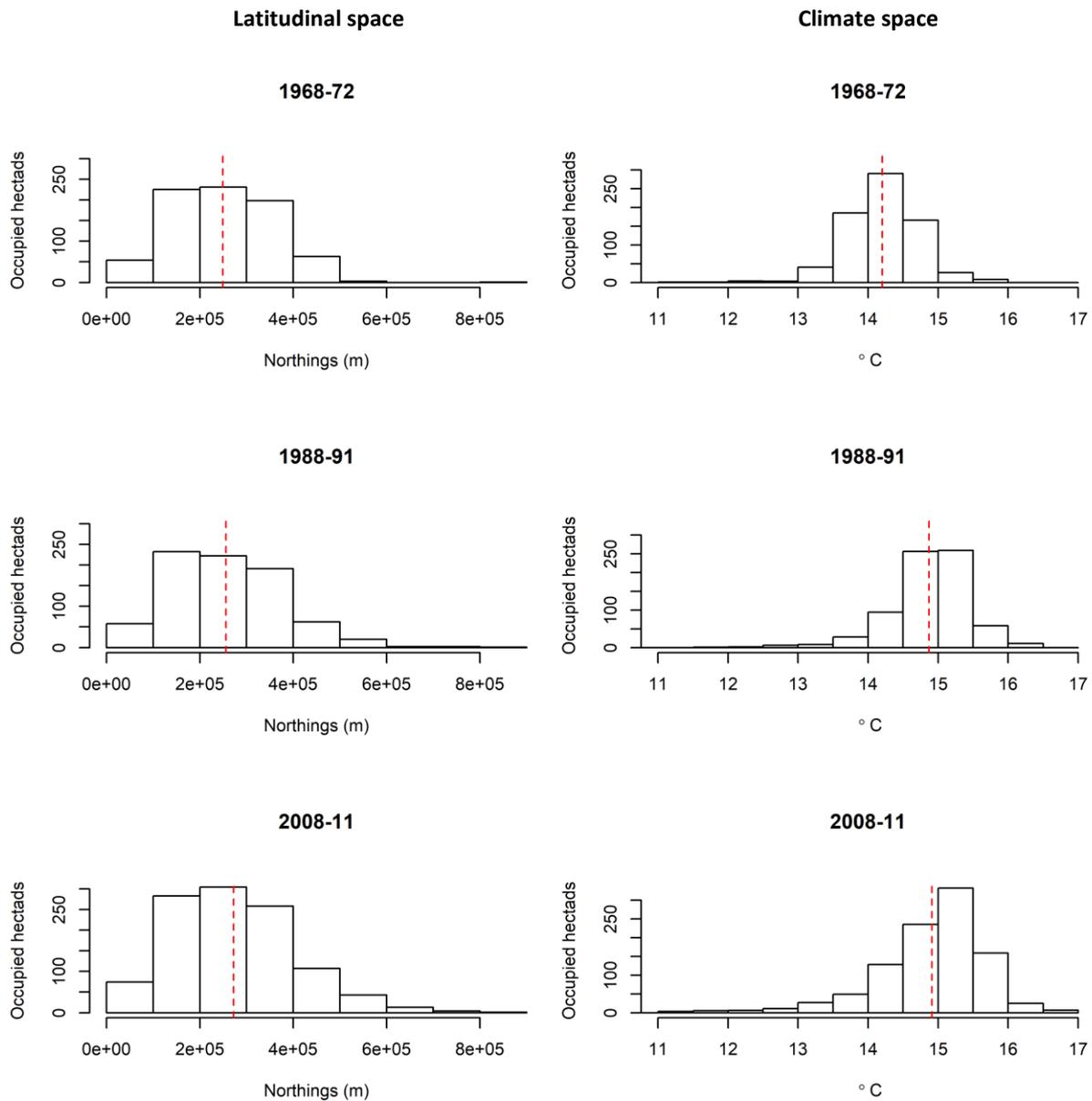


Figure 2.9. Reed warbler in latitudinal and climate space in Britain over three Bird Atlas surveys. Each panel is the histogram of latitudes or mean breeding season temperature of all occupied hectads in that year (red dashed line = mean).

2.5 Discussion

2.5.1 Reed warbler range limitation

Reed warbler occupancy was very strongly positively related to current breeding season temperature. This relationship was much stronger than the relationship between occupancy and time, suggesting that the relationship with temperature was genuine, rather than arising from covariance with a latent variable that also followed a trend over time. A similar strong positive relationship between reed warbler presence and temperature was found near reed warbler's cool range edge in Finland (Virkkala et al. 2005). I found that a step-change in occupancy probability occurred between 13 and 14°C, which also defines the cool edge of occupied Bird Atlas hectads. This suggests that the limit to reed warbler's breeding range in Britain is imposed by climate, directly or indirectly. The relationship between occupancy and the current breeding season's temperature was much stronger than the relationship between occupancy and the previous breeding season's temperature. This suggests that reed warbler's range limit is imposed through climate in the current year, rather than through productivity and survival from the previous year being climate-linked. Reed warbler's range limit is thus apparently generated by insufficient dispersal into the un-colonised area, rather than by deaths exceeding births in the un-colonised area.

Although the range limit is ultimately caused by current climate, it is not clear whether this is a direct effect of current climate, or an indirect effect of another factor itself affected by current climate. It could be that reed warbler survival is positively related to temperature, and reduced occupancy arises from higher mortality below a given temperature. The temperatures reed warblers experience in spring at the cool edge of their range are the coolest they experience over their entire life-cycle (see Figures 1.5, 1.6). However, most species survive far beyond the edge of their range (Gaston 2003), so it is unlikely that climate-linked mortality is causing the range limit for reed warbler. This will be explored more in Chapter 4.

Reed warblers depend on stands of reed for breeding. Reed growth rate, growing season length and maximum height in Britain are strongly positively influenced by temperature (Haslam 1972). Reed emergence is delayed by cold or dry spring weather, and is prolonged by spring frosts. Reed below a constant temperature of 14°C takes much longer to achieve a suitable height for reed warbler nesting than above 14°C (Vafidis 2014). Therefore at sites with low temperatures, reed warblers might arrive early in the season, perceive the lack of reed growth for a given day length, and move on before attempting to breed. The suppressive effect of dry weather on reed emergence (Haslam 1972) could also explain the non-significant but positive relationship between breeding season rainfall and reed

warbler occupancy probability. However, early-nesting reed warblers do occasionally nest in dry reed before the current season's growth is available (e.g. Halupka et al. 2008); perhaps relatively few individuals do this, with enough of an effect to influence occupancy. Further investigation would be required to ascertain whether reed warblers do not occupy cold reedbeds because they choose not to attempt to breed in a reedbed if it appears too cold (i.e. a behavioural choice), or because they cannot breed there because the phenology of the reed there is not advanced enough for nesting.

2.5.2 Reed warbler range expansion

Reed warbler expanded its range northwards and westwards between 1968-72 and 2008-11. As for many other species (Mair et al. 2012; Brommer et al. 2012), its rate of range change varied over time: the range change was slow at the centroid and fast at the range edge between 1968-72 and 1988-91, and fast at the centroid and slower at the range edge between 1988-91 and 2008-11. Reed warbler's poleward shifts in the range edge (5.1 and 3.5 km year⁻¹) are considerably faster than the average (2.3 and 1.8 km year⁻¹ over two recent intervals) poleward range edge shift found in a study of birds, butterflies, macromoths, dragonflies and damselflies in Britain (Mason et al. 2015).

Although, like many other species (Pecl et al. 2017), reed warbler shifted its range poleward, there was also a strong westward element especially in the range centroid. To consider only the poleward shift would cause underestimation of the magnitude of the shift, by 47% and 17% (1968-72 to 1988-91), or 39% and 3% (1988-91 to 2008-11) for the centroid and range edge respectively. The vectors of the centroid shift and the maximum shift in the range edge were in different directions: the latter generally more northerly. Together they gave a faithful description of the overall range shift that neither could give well on its own.

As Britain warmed, the area climatically available to reed warbler moved generally northwards between 1968-72 and 2008-11, especially between 1968-71 and 1988-91. Reed warbler generally expanded its range in the direction of newly available climate space, suggesting that reed warbler's range expansion has been caused by climate change. Interestingly there was a range expansion into the south-west of England in the second interval, into an area that had already been climatically suitable since 1968-72. This could be due to dispersal limitation, and suggests that the causes of range expansion in reed warbler may even differ within Britain.

Although the range edge was not able to match the velocity of the far edge of climate space, the range edge did not warm over time. The apparent conflict between these two measures may be because

temperature does not decline monotonically towards the edge of reed warbler's potential climate space (Figure 2.8). While some climatically suitable but un-colonised land lies well beyond reed warbler's range edge, there is climatically unsuitable land between this un-colonised land and reed warbler's range edge. Therefore reed warbler's range edge can lie at the edge of its climate space (and thus 'track climate change') without lying at the most geographically distant manifestations of its climate space. The relative geographical location of the far edge of climate space can instead be considered as a measure of the extent of climatically-available but un-colonised land. However, the geographical location of the edge of climate space partly depends on my definition of the edge of climate space. I defined the edge of reed warbler's climate space as the 2.5th percentile of temperatures of hectads occupied by reed warbler in 1968-72. Using a different definition (e.g. the 10th percentile) would give a different geographical location of the edge of climate space, and therefore potentially a different velocity of the far edge of climate space, depending on the topography of the geographical area the edge was passing through. Therefore I propose that the temperature of the range edge is a better measure of its ability to track climate space than the location of the far edge of climate space, which is sensitive to a (somewhat arbitrary) numerical definition.

Reed warbler's range edge tracked the edge of climate space, insofar as its temperature did not increase over time. However, the frequency of occupied hectads at the cool edge of reed warbler's climate space decreased during a period of rapid warming. Crucially, this frequency recovered slowly during relative climate stasis. This implies that even though reed warbler moved unusually fast compared to other species, the bulk of the population failed to track its climate space through time during a period of rapid environmental change. This is in common with many other species (e.g. Tayleur et al. 2015). This suggests that only a minority of individuals disperse far enough to match the rate of climate change, or that once established, reed warbler populations grow too slowly to generate significant numbers of dispersers. The difference in the abilities of reed warbler's range core and range edge to track climate space demonstrates the value of describing range shift with more than one metric (Yalcin & Leroux 2017).

This disequilibrium with climate space is particularly surprising in a species with high dispersal ability (Procházka et al. 2011), and in an area with a relatively steep geographical gradient in environmental variables: reed warbler has had to move shorter distances to track its climatic niche in Britain than elsewhere in its Eurasian breeding range. However, the range thinned out between 1968-72 and 1988-91 over a period where British climate was ameliorating. It could be that over this time, population growth rate declined because of factors unrelated to breeding season climate, perhaps due to biotic

changes in Britain or environmental change in the non-breeding range. Interestingly, between 1972 and 1986, droughts caused major declines in extent of West African mangrove forests (Dieye et al. 2013), which are thought to be an important component of western European reed warbler's wintering range (Zwarts et al. 2014; Procházka et al. 2008). Such habitat loss could have reduced survival and therefore population growth rate, causing reduced occupancy in some areas in Britain. This occupancy decline in some areas between 1968-72 and 1988-1 meant that although the range edge was able to move at 63% of the velocity of the edge of climate space, the range centroid barely moved. This is consistent with findings that species' range change ability is better explained by abundance trend than by dispersal (Mair et al. 2014).

2.5.3 Conclusion

In summary, there is good evidence that reed warbler's range in Britain is ultimately limited by climate, through climate-linked settlement probability. The similarity between the range expansion and the extension of suitable climatic space is consistent with climate change having caused most of the recent range expansion. Although the range edge was able to track climate space during rapid warming, the bulk of the population lagged behind. The estimated rate of movement of reed warbler's range edge, and of the far edge of its climate space, will be compared in Chapter 3 with the frequency distribution of reed warbler dispersal movements, in order to evaluate further the role of dispersal in this species' range dynamics.

3. Dispersal in Eurasian reed warbler *Acrocephalus scirpaceus*

3.1 Abstract

Dispersal in reed warbler, allowing range change, is carried out overwhelmingly by juveniles rather than by adults. Only about a quarter of individuals recruit to their natal (1km radius) area, but those that do so breed closer than random to their precise nest site, suggesting that there are multiple stages to the decision about how far to disperse. Only 5.3% of individuals dispersed far enough to match the rate of maximum range change, suggesting that reed warbler's range expansion has been enabled by long-distance dispersal. However, the extent to which reed warbler is dispersal-limited is unclear, because some individuals dispersed very long distances. Data were generated on exploration, capture probability, dispersal and seasonal variation in recruitment in juveniles, and dispersal in adults, in order to inform the structure and plausible parameter values of the IPM and IBM.

3.2 Introduction

In allowing colonisation of new areas, and as the mechanism for gene flow, dispersal plays a pivotal role in range dynamics (see 1.2.3). For many species, dispersal is the least known aspect of its life history, because it can be difficult to study. If emigrating, individuals are likely to leave finite geographical research areas. If travelling, individuals might be more difficult to observe than if they were static. Migrating individuals can be mistaken for dispersers. Immigration and emigration can be mistaken for productivity or mortality respectively. In this chapter, I take advantage of hundreds of thousands of ringing records in order to estimate adult and natal dispersal kernels (the frequency distribution of dispersal distances in a population) in reed warbler, which are both poorly described in this species to date.

Describing dispersal in reed warbler contributes towards two main aims of this thesis. Firstly, this will allow me to evaluate support for different causes of range limitation and change in reed warbler. The spatial patterns of reed warbler's range change suggest reed warbler may be dispersal-limited, particularly during rapid environmental change (Chapter 2). Comparing the dispersal kernel to the velocity of range change may corroborate this inference. Furthermore, it is thought that long-distance dispersal plays an important role in range expansion, with some range expansions impossible to explain without long-distance dispersal (e.g. Clark 1998). By estimating the proportion of individuals dispersing fast enough to match the rate of range spread, I will be able to ascertain whether the rate of range expansion was enabled by long-distance dispersal.

Secondly, describing dispersal in reed warbler will allow me to build a more accurate characterisation of dispersal in the IPM (Chapter 4) and IBM (Chapter 6). The structure of the IPM and IBM both depend on a faithful description of reed warbler's life history. For example, the dynamics of an IBM would differ depending on whether it is mostly juveniles that disperse, or if juveniles and adults have an equal probability of dispersing. I describe reed warbler dispersal by analysing following-year-recaptures of birds ringed as chicks or adults. I extend this analysis to comprise recaptures of chicks in their juvenile year. This allows description of the spatial activity patterns of reed warblers in their early weeks and months; I build some of this information into the IPM and IBM. Finally, I also describe how fledging date influences recruitment probability to the next year; this relationship is also incorporated into the IBM.

3.2.1 State of knowledge of dispersal in reed warbler

Dispersal is the largest gap in our knowledge of reed warbler ecology. However, some aspects of reed warbler dispersal are well known, particularly juvenile exploration. There are indications that migratory birds have higher gene flow than resident birds, suggesting that migratory birds have higher dispersal (Arguedas & Parker 2000). Indeed, reed warbler populations in Eurasia and north Africa have high gene flow and low genetic differentiation, suggesting that dispersal between populations is high but not unrestricted (Procházka et al. 2011; Ceresa et al. 2015).

Little is known about reed warbler dispersal movements in Britain, even though considerable analysis was carried out on reed warbler (and other British breeding species) dispersal distances by Paradis et al. (1998). In that study the authors analysed the raw frequency distribution of observed dispersal distances as the true dispersal kernel. Like many dispersal distance studies, this failed to account for the unequal probability of detecting dispersal distances of different lengths in a finite study area (Van Noordwijk 1995). Among a given set of points, there are more available short distances between the points than long distances, and so the probability of detecting a dispersal movement declines with distance (Koenig et al. 1996). This means that an apparently positively-skewed dispersal kernel could arise from a truly uniform dispersal kernel measured over a finite area. The true dispersal kernel, instead, is the departure of the observed distribution of dispersal distances from the null distribution of possible dispersal distances (Van Noordwijk 1995).

Dispersal in reed warbler may be negatively related to population size: reed warbler populations in Britain are negatively synchronous with the previous year's size of distant populations (Martin et al. 2017). However, this pattern could also arise through conspecific attraction, which reed warblers

exhibit, and indeed negatively density-dependent dispersal appears to be rare in birds (Matthysen 2005).

Juvenile reed warblers have a remarkable period of activity, probably partly related to exploration for future breeding sites, in the weeks between fledging and migration. Over this period, juvenile reed warblers gradually switch from being largely diurnal to largely nocturnal (Mukhin et al. 2005). Juvenile reed warblers gain independence from their parents at about 25-29 days of age. From about 30 days after hatching, juveniles begin to be active for short periods at night. From about 38 days old, juveniles carry out short night flights over their natal reedbed. Between then and their departure for migration at age 49-55 days, most (63%) make one or several nocturnal off-site excursions of several kilometres (Mukhin et al. 2005). These movements have no preferred direction (Mukhin 2004). Birds may return during the same night after their excursion, but some birds remain at another site for 1-5 days before returning. Some juvenile reed warblers spend two weeks or even a month in the pre-migration period at a site 20 km from their natal site (Bulyuk et al. 2000). Some juvenile reed warblers move to other sites very young: juveniles were trapped up to 20 km away from their nests, in the opposite direction from autumnal migration, as young as 33 days old (Chernetsov & Mukhin 2001). Movements between sites take place in ~1hr hops, 1-3hrs before dawn (Bulyuk et al. 2000; Mukhin et al. 2005). The pattern of captures suggests that birds move on their explorations by uninterrupted flights over habitat, rather than filtering through the intervening matrix (Mukhin 2004). Over the period from 30 days old to migratory departure, night flight initiations get earlier and earlier in the night.

There appear to be multiple functions of this behaviour. Firstly, apart from during their Sahara crossing, reed warblers migrate at night (Adamík et al. 2016). Therefore this pre-migratory process may ease them into a cycle of nocturnal wakefulness as migratory preparation. Next, reed warblers return on spring migration in the penultimate hour before sunrise (Bolshakov et al. 2003; Bulyuk 2006), and hence need to be able to recognise their migratory destination in nautical twilight. Moving around near their natal site at night may build up a navigational target to be returned to at night the following spring. During the post-fledging pre-migration period, reed warblers in Kaliningrad, Russia redistribute themselves towards wetter areas, with more plum aphids *Hyalopterus pruni*, suggesting that at least part of the movement is due to finding the best areas for pre-migratory fattening (Chernetsov 1998). Finally – especially given the fact that some reed warblers spend multiple days away from their natal site – it may be that their pre-migration behaviour constitutes exploration, allowing assessment of potential future breeding sites. It is possible that reed warblers visit other sites

during the exploratory period in order that at least one other site is known if the preferred reedbed isn't there, or is already at carrying capacity, the following year (Grinkevich et al. 2009).

Adult dispersal is poorly described in reed warbler, but is thought to be low. Individuals have been shown to build nests within less than one metre of the nest they built the year before (Long 1975). Although radio-tagging has shown that pairs may respond to simulated nest predation by leaving the site and relocating to other sites tens of kilometres away, it is not known whether breeding is attempted at the new site during the same season, nor whether it is a permanent move (Mukhin et al. 2009).

In this chapter I aim to describe reed warbler natal dispersal, breeding dispersal and exploratory movements in Britain. All of these will contribute to the design of the IPM and IBM. I also aim to compare the magnitude of reed warbler dispersal movements in a single year to the rate of movement of the range edge, and to the spatial rate of environmental change (Chapter 2). The latter comparisons will help determine whether dispersal limits reed warbler's range, and how important long-distance dispersal is in range change.

3.3 Methods

3.3.1 Dispersal kernels

Although dispersal is very unlikely to take place in a straight line, Euclidian distance between start and finish is the simplest way to describe dispersal. Not all individuals disperse the same distance, and so a characterisation of the frequency distribution of dispersed distances is more informative, especially as the proportion moving long distances can have important effects on spatial population dynamics (e.g. Clark 1998). There are two different approaches to measuring dispersal. Under the Lagrangian approach, individuals are tracked in real time. Under the Eulerian approach, the number of particles is measured at different distances from the source. Tracking devices are not yet sufficiently miniaturised to track individual reed warblers in real time at this spatial scale, so a Lagrangian approach is not available for estimating reed warbler dispersal. However, large numbers of reed warblers are ringed every year, allowing estimation of reed warbler dispersal by a Eulerian method.

I aimed to measure the distances from natal site to first breeding site (natal dispersal), and from a given breeding site to the next year's breeding site (adult dispersal). In my estimates of dispersal, I converted the frequency distribution of observed movement distances into the proportion of

individuals moving different distances. I did this by also using the frequency distribution of observable movement distances, for each individual, as follows. For each distance band (50 m for sub-1 km dispersal; 1 km for national-scale dispersal), I took the number of individuals x that were observed to make a movement that fell within that distance band. I then, for each individual, summed the number of dispersal movements that could have been observed in that distance band. This was calculated using known effort for the time period: for example, for a given individual that hatched in 2007, the number of CES sites that operated in distance band 23-24 km in 2008. This was then summed across individuals to give an index y of spatial observer effort for each distance band. I then divided x by y for each distance band to give a proportion p of observable distances moved by individuals. p for each distance band was then divided by the sum of p across all distance bands, to give a proportion of individuals moving distances within that distance band. I defined this frequency distribution of distances moved (adjusted for the uneven spatial probability of observing movements of different lengths) as the 'dispersal kernel'.

Although it would have been useful to analyse dispersal in relation to interesting covariates (such as year or latitude) preliminary analyses showed that there were too few data to do so. Therefore I provided simple quantitative descriptions of dispersal in reed warbler, rather than analysing dispersal.

Like any ecological process (Wiens 1989), dispersal is unlikely to take place in the same way on different scales. Whether reed warbler dispersal is scale-dependent affects how the IBM is designed. For example, dispersal could be characterised as emerging from a dispersal kernel, where probability of movement gradually fades away from the nest. Alternatively, it could be that dispersal is comprised of multiple decisions: a decision to leave or stay in the natal area; if an individual leaves its natal area, then it might disperse according to a different dispersal kernel. I therefore estimated dispersal kernels at both the national (3.2.2) and within-site ('sub-1km'; 3.2.3) scale, and compared the two kernels.

3.3.2 Dispersal at national scale

I used two ringing data sources from the British Trust for Ornithology (BTO) for estimating dispersal. In the first, the Ringing Scheme (Baillie et al. 1999), volunteer ringers seek to catch and ring birds without necessarily following a structured programme of ringing effort. Importantly for this chapter, this dataset contains birds ringed as chicks in the nest (Figure 3.1). Under the CES, volunteers operate multiple mist-nets after dawn according to a standardised methodology (Robinson et al. 2009), over 12 visits approximately 10 days apart across the breeding season. This scheme produces capture data

and parallel effort data. Data were available from 1928 to 2015, and from 1983 to 2014, for the respective schemes.

Natal dispersal, for a young reed warbler, is the movement from its natal nest location to the location of its first nest as a breeding adult. Some studies have attempted to measure this by taking the movements from any capture as a juvenile to any subsequent capture as an adult (e.g. Ceresa et al. 2016). However, reed warblers can be caught many kilometres from their natal site while still juveniles, or may be caught as adults while still on migration to or from their breeding site. Here, due to the large datasets available, I was able to use very strict criteria (for a natal site and first breeding site) for evidence of natal dispersal movements. I modified these dispersal movements with a null distribution (see 3.3.1) to estimate the true dispersal kernel.

I used two criteria for a reed warbler’s natal site (Table 3.1). Firstly, if a bird was ringed as a chick in the nest, I concluded that it was at its natal site (criterion A). Secondly, if a recently-fledged bird was caught before it had finished growing its flight feathers (Euring code ‘1J’), I assumed that it was at its natal site (criterion B). Birds at this age mostly move by hopping and are unlikely to have moved more than tens of metres.

Table 3.1. Criteria used as acceptable evidence of natal or first breeding site.

Acceptable evidence of natal site	Acceptable evidence of first breeding site
A. Ringed in nest	1. Caught on multiple occasions at a CES site in the bird’s second calendar year
B. Ringed as just-fledged bird	2. Caught on multiple occasions (> 10 days apart) at a non-CES ringing site in the bird’s second calendar year
	3. Caught at a CES site on at least one occasion in the bird’s second calendar year, and then again at the same site in any subsequent year
	4. Caught at a non-CES ringing site on at least one occasion in the bird’s second calendar year, and then again at the same site in any subsequent year

It is more difficult to be certain that an adult caught at a site is attempting to breed there: individuals caught as adults might just be passing through on migration. Ktitorov et al. (2010) found that reed warblers spent a median of four days at a stopover site. I propose therefore that it is unlikely that birds spending more than ten days at a site are just passing through. I therefore assumed that individuals caught at more than one CES visit, or on multiple occasions more than ten days apart on a non-CES ringing site, are resident. Given that migrant reed warblers are present at a stopover site for only a median of four days (Ktitorov et al. 2010), whereas resident birds may spend several months on a site, I assumed that the integrated probability of capture at least once over a whole season is

much higher for a resident than a migrant. The difference between residents and migrants in their probability of capture in two different years will be even higher, because the probabilities are squared. Therefore I assumed that it is unlikely that birds caught on multiple years at a site are just passing through. Applying these residency criteria in a bird's second year of life (i.e. the year subsequent to fledging) gave four possible criteria for acceptable evidence of a bird's first breeding site (Table 3.1).

All movements between a natal site and a first breeding site (Table 3.1) were considered to be natal dispersal movements. From these natal dispersal movements, and a null distribution (described below) for each natal dispersal movement, a natal dispersal kernel was estimated (see 3.3.1). Null distributions were created by taking, for each individual making a dispersal movement falling under a given criterion for adult breeding site (i.e. 1, 2, 3, or 4), all sites (CES sites if criterion 1 or 3; non-CES ringing sites if criterion 2 or 4) where enough survey visits were made to potentially have recorded that bird as 'breeding' at that site in that year. For example, if a bird made a dispersal movement under criteria A and 1, then the null distribution for that movement would be all distances from the natal nest to every CES site that operated two or more visits in the year subsequent to the bird's fledging year. Effort is recorded for CES sites, but not for general ringing: it was assumed that no ringing took place on a non-CES ringing site on a given day if no reed warblers were caught on that site on that day. 'Retraps' – bird movements of less than 5 km – were not processed by BTO widely, except for CES, before around 2004. Thus all null distributions were censored below 5 km, and all sub-5 km observed movements discarded, for all dispersal movements under criteria 2 and 4 before 2004.

To estimate an adult dispersal kernel, I repeated the process as for estimating the natal dispersal kernel, but solely used movements between any adult breeding locations in subsequent years (rather than between natal location and first adult breeding location).

In order to evaluate the proportion of individuals moving fast enough to match the rate of range change, I had to take account of the fact that not all individuals necessarily disperse in the direction of range change. The direction of reed warbler's range change has varied, but has been approximately northerly (direction of maximum rate of range change: 345°, 1968-72 to 1988-91; 015°, 1988-91 to 2008-11; Chapter 2). I therefore estimated a dispersal kernel in the north-south dimension. To do this, I repeated the calculation for estimating the juvenile dispersal kernel; instead of using distances between sites, I used distances in the northerly dimension only.

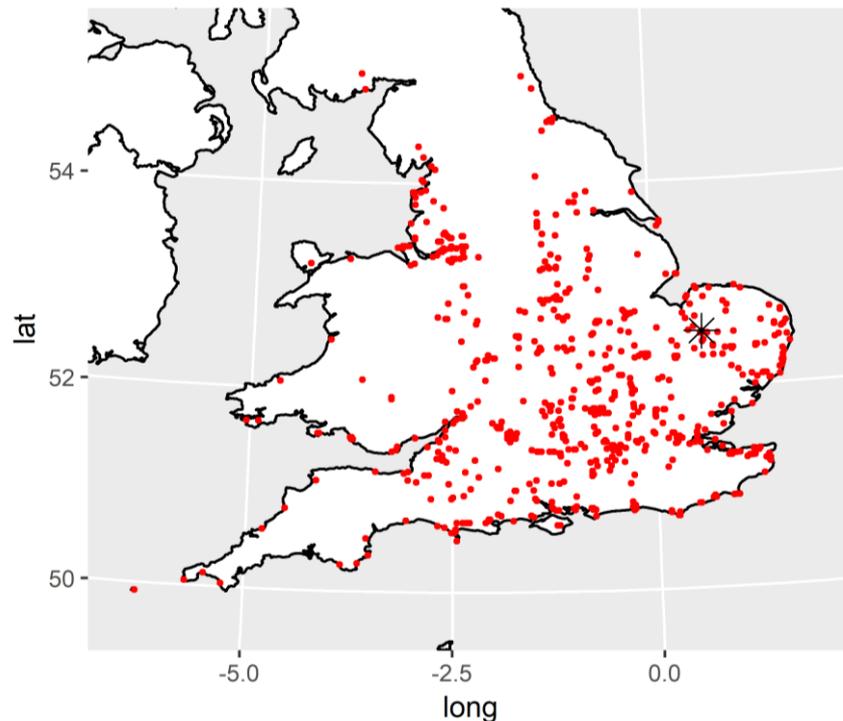


Figure 3.1. Locations of all (32,122) reed warblers ringed as chicks in Britain, 1928-2015. Asterisk is location of Watermill Broad NR.

3.3.3 Sub-1 km dispersal

Fieldwork was carried out at Watermill Broad Nature Reserve (52.53°N, 0.62°E; Figure 3.1), near Cranwich, Norfolk, UK in 2016 and 2017. The site is a system of flooded former gravel- and peat-extraction pits adjacent to the River Wissey, fringed by reed, sedges *Carex* spp. and willow *Salix* spp. and other trees. The site covers an area of approximately 700 m by 400 m, and supports a population of approximately 150 pairs of reed warblers (Figure 3.2a). At the site, reed warblers almost exclusively nest within reedbeds, but occasionally in sedge beds with reed stems, or in branch forks in willows in an event when the water level was high.

Fieldwork was carried out to estimate natal dispersal distances. All potential reed warbler breeding habitat was exhaustively searched approximately every five days for reed warbler nests. Reed warbler nests are relatively easy to find, and it is considered that almost all were found every year. The location of each nest was recorded with GPS. All chicks in all surviving nests were fitted with a metal BTO ring at age five-six days. Attempts were made to capture as many adults as possible, using mist-nets near the nest. A CES site exists in the north-west of the site, supplementing the number of adults caught. All adult reed warblers caught were fitted with a darvic (a rigid laminate) colour ring with a unique alphanumeric code (Figure 3.2b). This allowed the linking of the identity of any birds ringed as chicks with a darvic ring worn as an adult. As soon as the clutch was complete for a given nest, a video camera

was set to record on the nest for one hour (Figure 3.2c). Repeat video attempts were made on each nest (never in the same day) until the identity (un-ringed, metal-ringed or colour-ringed with code) of both of the pair visiting the nest was ascertained.

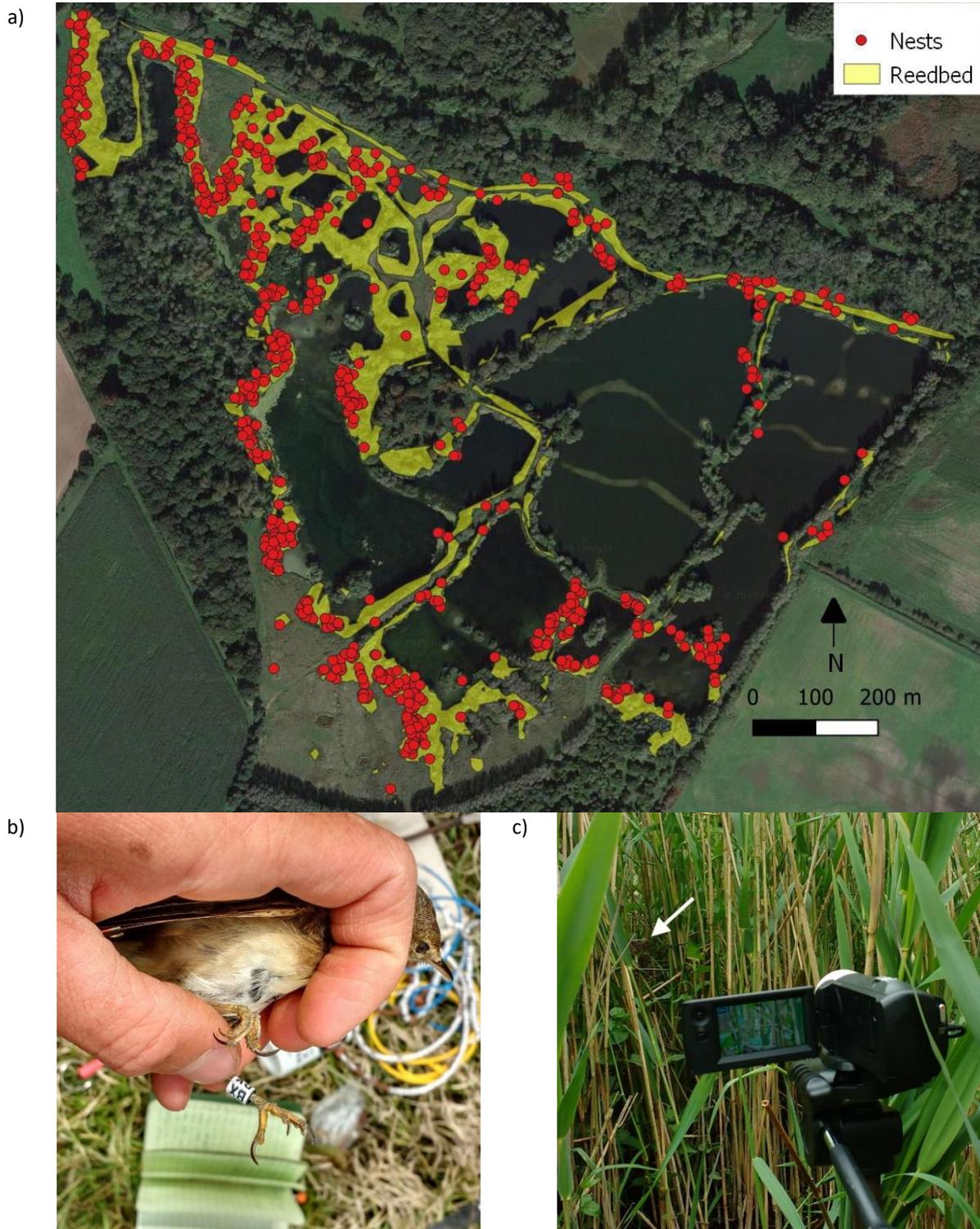


Figure 3.2. Fieldwork for sub-1 km dispersal. a) Watermill Broad NR with nest locations (2014-2017) and reedbed extent. b) Darvic colour ring 'BX' fitted to an adult reed warbler. c) Video camera filming a reed warbler nest (white arrow) to record identity of attending adults.

The distance from natal nest to first breeding nest was taken as the natal dispersal distance for an individual. The distribution of distances from the natal nest to all nests at which video attempts were made in the subsequent year was used as the null distribution. The natal dispersal kernel was estimated from the natal dispersal distances and null distributions, as in 3.3.2. Fieldwork was carried out by a small team, and had been carried out in previous years, allowing data from 2014-2017 to be used. To my knowledge, this is the first time a natal dispersal kernel has been described for a migratory bird at such a small spatial scale.

3.3.4 Juvenile reed warbler movements and seasonal variation in recruitment

Juvenile reed warbler movements, after fledging the nest and before migration, were described both at the national scale and at the sub-1km scale. Frequency distributions were described for the distance and direction juveniles moved between ringing in the nest and subsequent captures in the same year. Finally, a movement kernel was calculated from all recorded juvenile movement distances, as in 3.3.2. The null distribution for this calculation was the distribution of distances to any ringing site operated in the same year as the chick was ringed, after the date of first ringing. Seasonal variation in recruitment was estimated by comparing chick ringing date bands to the proportion of chicks ringed in that band that were subsequently caught on CES (at any site) in their first adult year.

3.4 Results

3.4.1 Reed warbler movements post-fledging pre-migration

In 2016, 23 chicks ringed in the nest at Watermill Broad NR were subsequently caught on CES there. At the sub-1 km scale, juvenile reed warbler captures increased with time since ringing as a chick, being initially very low (Figure 3.3a). At this scale, juveniles moved away from their immediate natal area as time went on (Figure 3.3b). Above approximately 40 days of age, using the national dataset, some individuals were caught many kilometres from their natal site (Figures 3.3c and 3.3e). Some of these individuals spent more than a week at other sites (Figure 3.3c). Sub-70 km and supra-70 km movements differed in direction (Watson's $U^2 = 0.187$ for $\alpha = 0.05$), with longer movements being more south-easterly (Figure 3.3d).

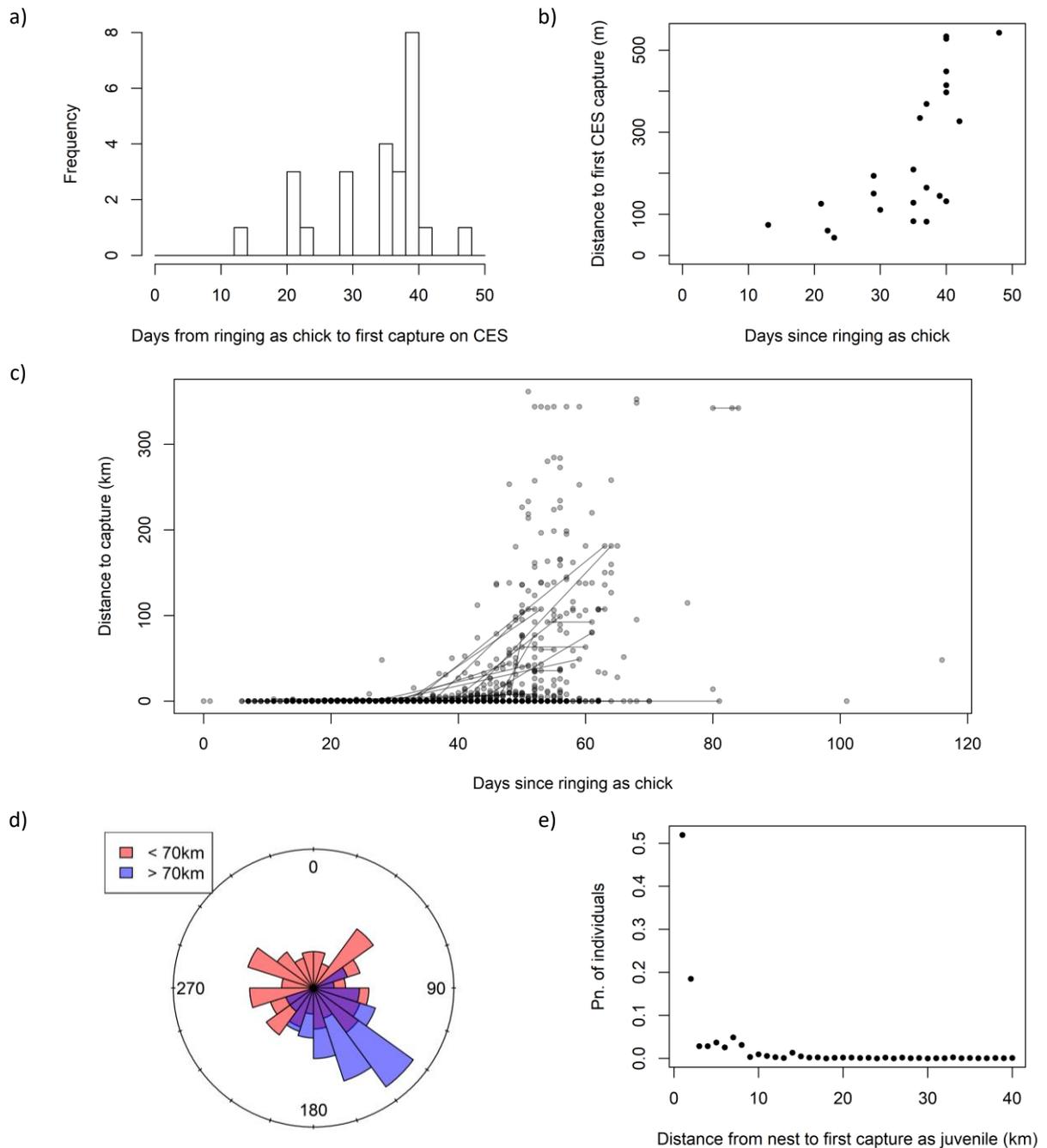


Figure 3.3. Summer movements in juvenile reed warblers ringed as chicks. (a & b) Chick movements, Watermill Broad NR, 2016 only. c) Duration vs distance of movements made in same year by juveniles ringed as chicks (lines link subsequent captures of individual birds). d) Rose diagram of all movements in (c). e) Movements in (c) as a movement kernel.

3.4.2 Reed warbler dispersal at national scale

Out of 25,024 reed warbler chicks ringed, 171 individuals met the criteria (see Methods) to have a known natal site and a known breeding site. Almost all (96.7%) natal dispersal movements were below 12 km, with a tendency for dispersal distance to decline with increasing distance below 12 km (Figure 3.4a). Only 23.3% of chicks recruited to within 1 km of their natal site. There were some relatively

long-distance dispersal movements, the maximum of which was 77 km. There was unevenness in the temporal distribution of long-distance dispersal movements: all natal dispersal movements greater than 12 km took place between 1995 and 2003 (Figure 3.4b).

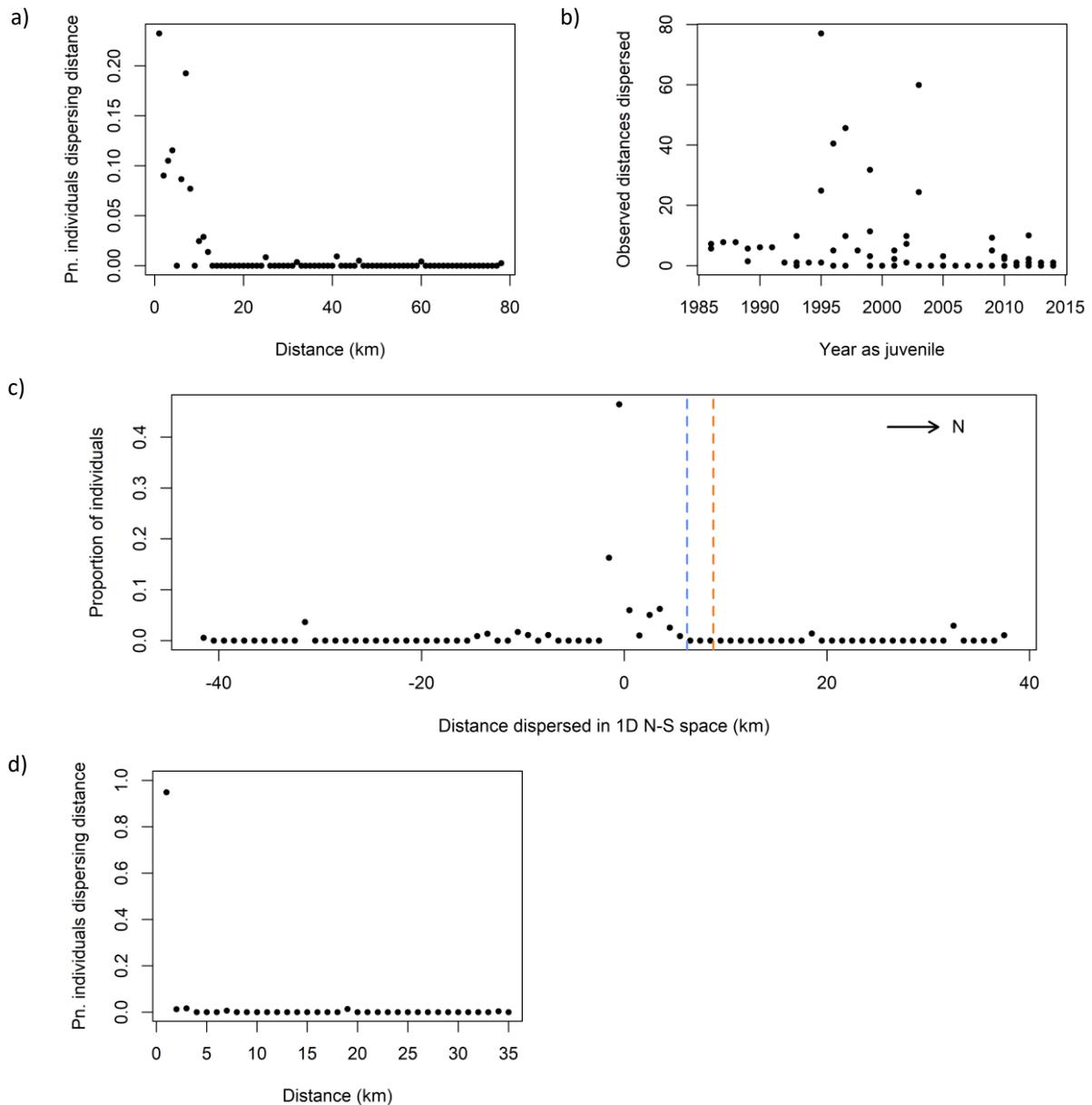


Figure 3.4. Reed warbler natal dispersal and adult dispersal across British range. a) natal dispersal kernel; b) raw natal dispersal distances vs time; c) natal dispersal kernel in north-south dimension (blue dashed line = maximum annual movement in range edge (Chapter 2); orange dashed line = maximum annual movement in edge of climate space (Chapter 2)); d) adult dispersal kernel.

In the north-south dimension, 5.3% of individuals dispersed faster than the maximum velocity of the range edge between 1968 and 2011 (6.2 km year^{-1} between 1968-72 and 1988-91, Chapter 2) or the

maximum velocity of the edge of climate space between 1968 to 2011 (8.8 km year⁻¹ between 1968-72 and 1988-91, Chapter 2) (Figure 3.4c).

1,871 adults were captured on multiple CES occasions in multiple years. These were considered to be adults which had known breeding locations in two or more years. 94.8% of these individuals did not move sites from the first to the second year in which they had multiple captures (Figure 3.4d). 2.8% of individuals moved 1-3 km and one individual moved 33 km.

3.4.3 Reed warbler natal dispersal and recruitment at sub-1km scale

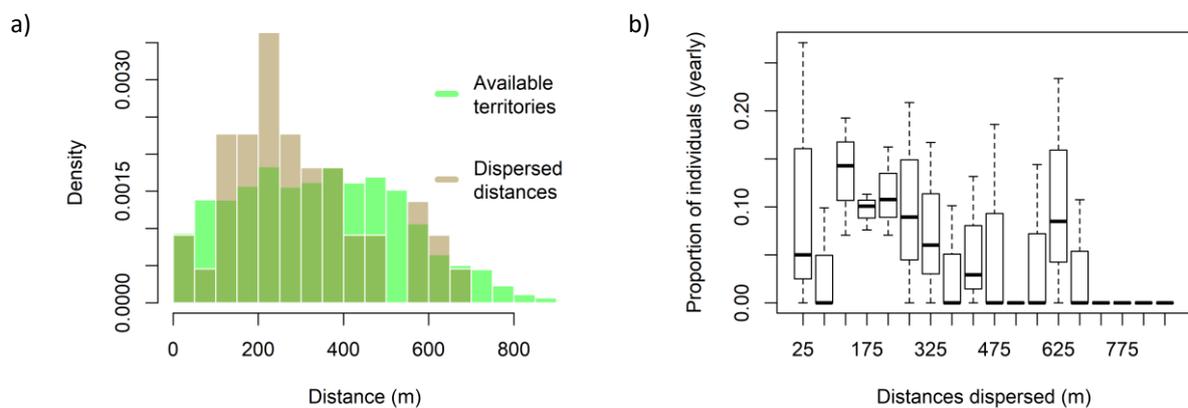


Figure 3.5. Reed warbler natal dispersal, sub-1 km. a) Histogram of dispersed distances and distances to available territories (in year of dispersal), pooled across 2015-2017. b) Annual variation in proportion of individuals dispersing into each distance band.

Out of 1,433 chicks ringed at Watermill Broad NR over the years 2014-2016, 44 were colour-ringed and videoed at the nest in their first adult year, allowing calculation of their natal dispersal distances. Within Watermill Broad NR, reed warblers dispersed shorter distances than a null distribution based purely on territory availability (Wilcoxon rank sum test; $W = 324$, $p < 0.001$) (Figure 3.5a). No individual dispersed more than 700 m, even though reed warblers bred in those more distant locations. Most individuals dispersed 100-200 m. Very few individuals dispersed between 50-100 m. The proportion of individuals dispersing less than 50 m was very variable between years (Figure 3.5b).

Recruitment to the following year declined strongly over the course of the season (Figure 3.6b). Although we would expect there to be a decline in juvenile-year capture probability over the course of the season (as there is less time left in which to be caught), there was no relationship ($F_{1,9} = 0.422$, $p = 0.532$) between chick ringing date and proportion captured on CES in their juvenile year (Figure 3.6a). However, there was a very strong relationship (linear model; $F_{1,8} = 36.08$, $p < 0.001$, $R^2 = 0.796$) between chick ringing date and the proportion captured on CES in their first adult year (Figure 3.6b).

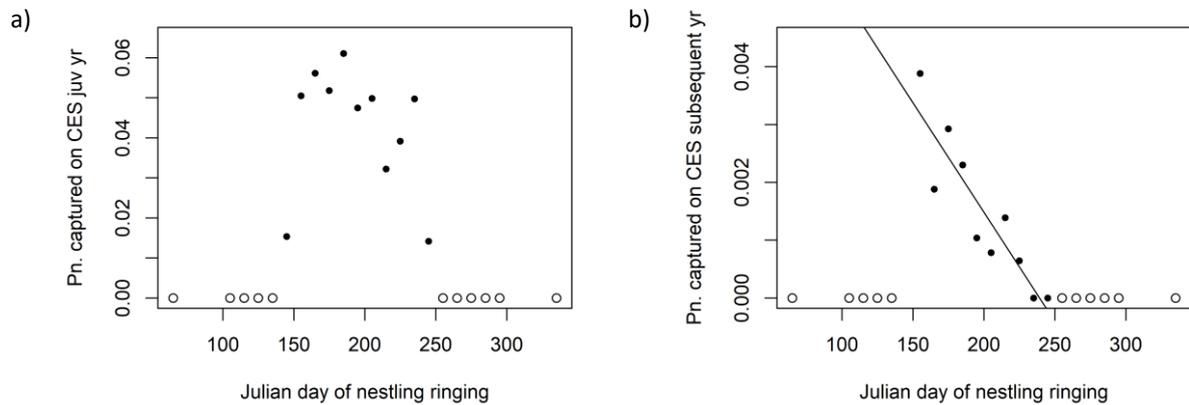


Figure 3.6. Seasonal variation in recruitment. a) Proportion of all chicks ringed that were subsequently caught on CES in their juvenile year, against date of ringing. b) Proportion of all chicks ringed that were subsequently caught on CES in their first adult year, against date of ringing. Relationships were solely fitted between date and non-zero proportions (filled points).

3.5 Discussion

3.5.1 Juvenile summer movements

Like others (e.g. Mukhin et al. 2005), I found that juvenile reed warblers undergo marked changes in their movement patterns as they age. Chicks are typically ringed at 5-7 days old, and fledge at about 10-12 days old: therefore at Watermill Broad NR very few chicks were caught on CES within two weeks of fledging, and most were caught at least four weeks after fledging. The period in the weeks immediately after fledging is typically especially high in mortality for passerines (Naef-daenzer et al. 2001); so potentially by the time reed warblers are caught at CES, they have passed the high mortality period. At the sub-1 km scale, juveniles start to move away from their immediate natal area about four to five weeks after fledging. At this age, some individuals moved away from their natal site, and spend some time at other sites: this finding is in common with Bulyuk et al. (2000). Therefore juvenile reed warblers caught at a given site in summer are not necessarily from that site, but are likely to be from the nearest tens of kilometres: stricter definitions of the natal site should be more accurate when estimating natal dispersal.

Like Mukhin (2004), I found that shorter distance juvenile movements in late summer are much more evenly spread throughout the compass than longer distance movements, which tended to be in a south-easterly direction consistent with migration routes. Furthermore, the shape and scale of the movement kernel of juveniles during their first year (Figure 3.3e) is similar to that of the actualised natal dispersal kernel (Figure 3.4a). This suggests that reed warblers may carry out at least some of their prospecting for available breeding sites during the late summer.

3.5.2 Dispersal and recruitment

I found that, like many birds (Greenwood & Harvey 1982; Winkler et al. 2005), most reed warblers breed relatively close to their natal site: reed warbler natal dispersal was positively skewed at both the national and sub-1km scale. It is especially striking that a species that migrates tens of thousands of kilometres a year disperses shorter distances than random at the sub-1 km scale. At both the national and sub-1km scale, there also appeared to be a non-random movement away from the exact natal site, perhaps to avoid competition with parents or to avoid inbreeding. At the sub-1km scale, there was great annual variation in the proportion of individuals dispersing less than 50 m, perhaps due to variation in adult survival leading to offspring inheriting their parents' territory in some years more than others.

Although at the national scale only about a quarter of individuals recruited to within 1km of their natal site, the dispersal kernel declined to zero well short of the maximum potential dispersal distances across Watermill Broad NR. This suggests that there is a decision whether or not to leave a site, before dispersing a longer distance, rather than the large-scale dispersal kernel simply being a continuation of the shorter one.

At the national scale, almost all reed warblers disperse less than 12 km. As for many species, there was a 'fat tail' to the dispersal kernel (i.e. the proportion of individuals dispersing long distances is higher than would be expected under an exponential distribution), with some species dispersing much further than 12 km. Intriguingly, all of these long-distance dispersal movements were detected over an 8 year period, even though the opportunity to detect long-distance dispersal movements has not decreased (not shown). This was during a period (1988-91 to 2008-11) when reed warbler's range centroid moved much more rapidly than over the preceding two decades (Chapter 2). It may be that during the range shift, dispersive behavior became more selectively favourable (e.g. Travis & Dytham 2002; Phillips et al. 2006), and then less so again as the rate of new availability of suitable climate space slowed (Hanski et al. 2004). However, the number of observed long distance movements is few, and it is not known if similar movements were made over the period when the range centroid moved more slowly.

Only 5.3% of individuals dispersed fast enough to match the fastest movements in range edge or climate space. This suggests that reed warbler's range change has been enabled by long-distance dispersal. Reed warbler's dispersal kernel is fat-tailed (Figure 3.4c), and so the individuals that surpassed the velocity of the range edge or the edge of climate space greatly surpassed that velocity.

It is difficult to assess from this alone whether reed warbler is dispersal-limited. This depends on whether the mean distance of the long-distance dispersal is long enough to compensate for the scarcity of long-distance dispersers (determined by demography). The fat-tail of the dispersal kernel may explain why the edge of reed warbler's range did not move in climate space, even though the frequency of occupied hectads near the range declined during rapid environmental change (Chapter 2). Perhaps a small number of individuals disperse far enough to match the rate of environmental change (although not the rate of movement of the far edge of climate space), but it takes some time for the bulk of the population to fill in remaining occupied sites through short-distance dispersal. The relative contribution dispersal and demography may make to reed warbler's range dynamics will be explored further using the IBM (preliminary results presented in Chapter 6). It is important to note that the data contributing to the dispersal kernel were taken from across the range core; few were from the range edge (not shown). It may be that dispersal distance has evolved to be markedly greater at reed warbler's range edge (e.g. Dytham 2009).

As for many other passerines, adult dispersal is very low in reed warbler in Britain. Adult reed warblers have been recorded leaving sites after predation or after breeding failure (pers. obs.; Borowiec 1992; Mukhin et al. 2009). The fact that only a very low proportion of individuals actually permanently moved breeding sites suggests that these departures after predation or failure are temporary.

Recruitment to the following year declined very steeply over the course of the season, while captures in the same year did not decrease so strongly over the same time period. This suggests that the seasonal decline in recruitment is determined by the length of time left before the end of the season, and mediated through over-wintering survival. Clutch size in reed warbler declines over the course of the season (Dyrzcz 1981), and some documented increases in clutch size across years have purely arisen from the season moving earlier (Schaefer et al. 2006). It could be that the seasonal decline in clutch size is due to adults reducing their investment appropriately in response to the decline in recruitment.

This chapter demonstrates the value of ringing data for studying dispersal, but also the difficulty of acquiring sufficient data to analyse relationships of dispersal with covariates. A trend towards more ringing of chicks would help with the study of avian dispersal. However, it is easy to understate the magnitude of the task involved in using ringing data to analyse variation in dispersal: even in this highly-captured species with 32,122 chicks ringed, only seven long-distance dispersal movements have been detected.

Information presented on exploration, capture probability, dispersal and seasonal variation in recruitment in juveniles, and dispersal in adults, is incorporated into the structure and plausible parameter values of the IPM (Chapter 4) and IBM (Appendix) as appropriate.

4. Estimating Eurasian reed warbler *Acrocephalus scirpaceus* demographic parameters and their relationship with time, space and climate

4.1 Abstract

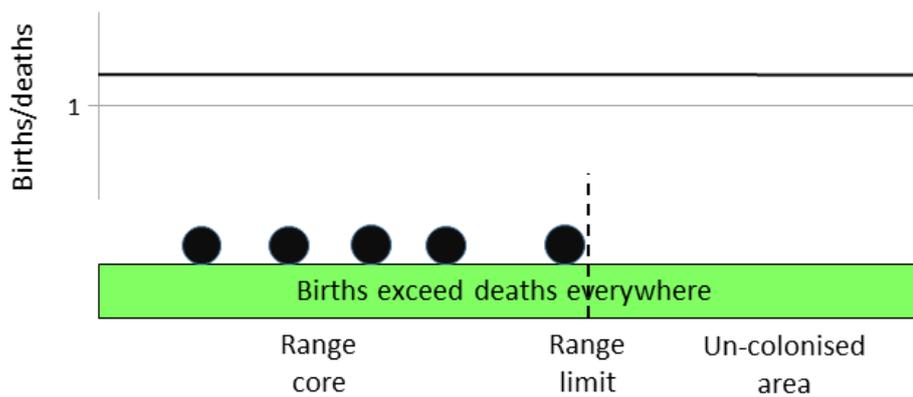
In this chapter I estimate reed warbler demographic parameters in Britain, and their relationships with time, space and climate, in order to establish the role of demography in reed warbler's range dynamics. An increase in reed warbler egg survival and chick survival in Britain between 1983 and 2014 may have been driven by an increase in temperature. Egg survival and chick survival were positively related to breeding season temperature, while adult survival was negatively related to the previous breeding season's temperature. A fully spatial IPM did not work, preventing estimation of some key demographic parameters and population growth rate. None of clutch size, egg survival, chick survival or adult survival declined to the range limit, suggesting that demography does not limit reed warbler's range in Britain; however, not all key aspects of demography were estimated. Likewise, an increase in fledglings per breeding attempt may have increased reed warbler's rate of range spread, but it is unclear how strongly the number of fledglings per breeding attempt is related to population growth rate.

4.2 Introduction

Range limitation and change can be considered in terms of spatial variation in population growth rate, which is itself determined by the relative balance of births, deaths, immigration and emigration (Gaston 2009). As such, the balance of births and deaths can play several important roles in range limitation and change; sometimes more important roles than dispersal (Sanford et al. 2009; Mair et al. 2014). Reed warbler expanded its range in Britain in recent decades (Chapter 2), but the role of demography in the range limit and the range change are unknown. Although I focus in this thesis on the role of dispersal in range limitation and change in reed warbler, I can also approach this by estimating the role of the balance of births and deaths in these phenomena. In this chapter I do so by estimating reed warbler demographic parameters and their relationship with time, space and climate.

Demography can play several roles in range dynamics. Firstly, demography can affect range dynamics directly through its effect on the potential population growth rate in the un-colonised area. Next, demography can have an indirect effect on range dynamics – through dispersal – by determining the density of available dispersers near the range edge. Similarly, demography influences the time it takes for populations to establish, grow, and themselves produce significant numbers of dispersers; this can be strongly influenced by positive density-dependence in births or survival (Travis & Dytham 2002).

a) Range is limited by dispersal



b) Range is limited by deaths exceeding births, due to environmental gradient

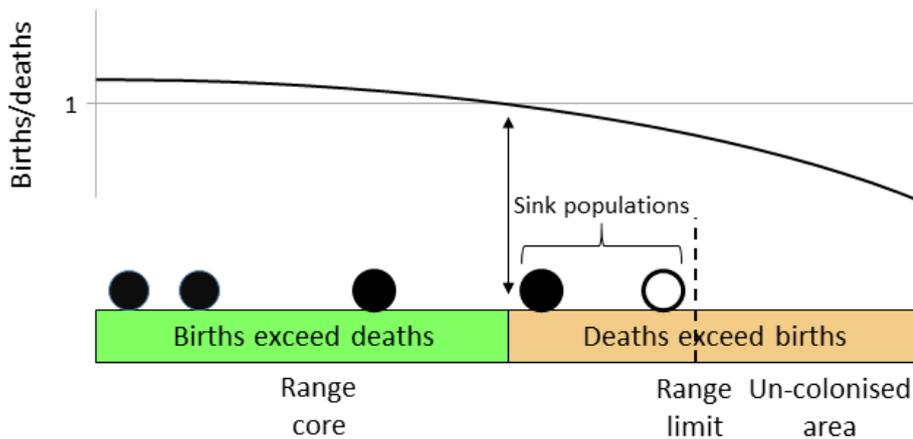


Figure 4.1. Two scenarios of range limitation in a hypothetical species: (a) dispersal-limited; (b) limited by deaths exceeding births, due to an environmental gradient. Circles represent populations (filled for population growth rate ≥ 1 ; empty for population growth rate < 1). Green filled rectangle represents habitat where births exceed deaths; brown filled rectangle represents habitat where deaths exceed births. In scenario (a), the range limit falls far short of the area where deaths exceed births. In scenario (b), immigration (not shown) sustains sink populations in the area where deaths exceed births. The two scenarios produce different spatial patterns in the balance of births and deaths.

In chapter 1, I introduced two broad potential causes of range limitation: lack of dispersal into the un-colonised area; or deaths exceeding births in the un-colonised area. These should create different spatial patterns in the balance of births and deaths. The two causes of range limitation are shown in Figure 4.1 (detailed explanation in 1.4.3.1). When the range limit is caused by lack of dispersal into the un-colonised area, the ratio of births to deaths should stay above 1 up to the range edge (Figure 4.1a). The ratio of potential births to deaths should remain above 1 past the range edge, perhaps for some distance. Conversely, if the range limit is caused by deaths exceeding births in the un-colonised area,

the ratio of births to deaths should decline below 1 at, or short of (if dispersal is considerable), the range edge (Figure 4.1b).

Similarly, there are two broad potential causes of range expansion (Chapter 1). Dispersal can increase or change such that immigration into the un-colonised area newly becomes sufficient to sustain populations or to colonise new sites. Alternatively, the potential ratio of births to deaths can increase in the un-colonised area such that the population growth rate becomes 1 or greater. As with range limitation, these two alternative scenarios should create different patterns in the un-colonised area. If the range expansion is caused by new increased immigration into the un-colonised area, then the ratio of births to deaths may not necessarily increase in the newly colonised area as the range edge moves northwards. If the range expansion is caused by an increase in the potential ratio of births to deaths in the un-colonised area, then this increase will be apparent there.

These two potential causes of range expansion may be difficult to distinguish through changes in demography alone. Changes in demography can cause range expansion through two main mechanisms: by increasing population growth rate beyond the range edge, or by increasing population growth rate short of the range edge, thereby increasing the number of dispersers. These two mechanisms may not be distinguishable if the location of the range edge is not precisely known.

If demography is causing the range limit in reed warbler in Britain, there are a number of potential ecological mechanisms for this. Broadly, there are more known mechanisms for productivity as the cause of the range limit than survival: most mortality occurs outside of the breeding season (Wierucka et al. 2016; Procházka et al. 2017), and variation in breeding season conditions appears to better explain variation in productivity than variation in survival (Chapter 1). Eglington et al. (2015) found that reed warbler productivity increases with latitude across Europe – the opposite relationship to what we would expect if it is limiting range. However, this study did not cover the northern edge of reed warbler's range, where productivity could begin to decline again.

Similarly, there is a range of ecological mechanisms for demography causing the range expansion in reed warbler in Britain. The possible causes of this are wider, because changes in demography leading to an increase in potential population growth rate in the un-colonised area need not only apply to that geographical area. For example, an increase in survival across the British range, due to changes in conditions on the wintering grounds, could cause an increase in the potential population growth rate in the un-colonised area. Studies investigating individual demographic parameters found that reed warbler's population growth rate is strongly related to survival (across Europe; Johnston et al. 2016),

and weakly related to productivity (in Finland; Meller et al. 2018). A study in France investigating multiple demographic parameters found that reed warbler's population growth rate is better explained by survival than by recruitment (Julliard 2004). Therefore we might expect variation in survival to have a more important effect on reed warbler's British range change than variation in recruitment.

Links between demographic parameters and climate could corroborate particular demographic roles in range dynamics. For example, if a demographic parameter increases with temperature, and decreases towards the range edge, then this would be consistent with that parameter limiting the range through population growth rate. I will thus estimate the relationship between demographic parameters and climate in this chapter. However, I cannot use the relationship between climate and demographic parameters to adjudicate either way on the ultimate mechanisms (dispersal or demography) for range limitation or range change. For example, a reduction in nest predation in the un-colonised area could cause an increase in productivity allowing range expansion, without there being a positive relationship between productivity and climate.

In this chapter I estimate reed warbler demographic parameters and their relationship with time, space and climate, from demographic and population size data. This fulfils two aims towards my overall research aims. Firstly, it allows me to assess the support for different scenarios of range limitation and expansion. In particular, it will allow me to evaluate the second plausible scenario of range limitation and change in reed warbler (Chapter 1): that the range limit and/or range change are caused by variation in demography between the range and the un-colonised area. Secondly, it allows me to estimate clutch size, nest survival and adult survival for the IBM (Chapter 6).

4.3 Methods

4.3.1 Data

4.3.1.1 Demographic and population size data

I modelled demographic parameters and population size from data collected under two BTO population monitoring schemes: the Constant Effort Scheme (CES) and the Nest Record Scheme (NRS). Under the CES, volunteers operate multiple mist-nets after dawn according to a standardised methodology (Robinson et al. 2009), over 12 visits across the breeding season. This scheme produces capture data and parallel effort data. Under the NRS, volunteers search for nests, and over successive visits, record the contents (Crick et al. 2003). This scheme produces data on clutch size, brood size,

and hatching and fledging success. The Constant Effort Site scheme began in 1983, later than the Nest Records Scheme, so analyses of both datasets were commenced in 1983. CES data were used to estimate survival and juvenile and adult population size; NRS data were used to estimate productivity. Data were available for both schemes until 2014. Data from 139 CES sites and 611 NRS locations were used (Figure 4.2).

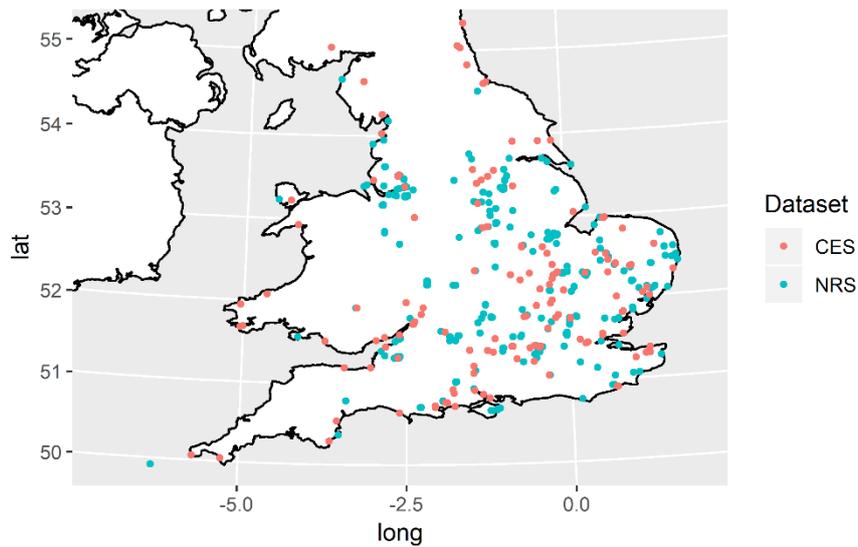


Figure 4.2. Data-contributing sites from CES and NRS.

4.3.1.2 Climate data

I summarised variation in reed warbler's breeding season climate using temperature and rainfall, because these variables are both known to influence reed warbler productivity (see 1.4.3.3). UKCP09 data (Met Office 2017) were used for breeding season temperature and rainfall. Monthly 5 km x 5 km data was summarised annually (mean for temperature, total for rainfall) over the main months of reed warbler's breeding season (May to August), and extracted for each CES site or NRS location. CRU precipitation data (Harris et al. 2014) were used for wintering grounds rainfall. The actual limits of reed warbler's wintering range, and the extent of British-breeding reed warblers within those limits, are poorly known. Most British-breeding reed warblers recaptured while wintering have been from west of 12°W (Procházka et al. 2008), and they probably winter further south of Senegalese-wintering Iberian breeders. Therefore I defined an extent of 18°W to 10°W, and 5°N to 16°N (Figure 4.3e), from within which to extract rainfall data: this may well include considerable areas of land in which reed warblers do not winter. Monthly precipitation data was summed for each 0.5° x 0.5° land cell within this extent over the period May to April each year. The mean total annual precipitation was then taken across all land cells within the extent, and used as an annual index of wintering grounds rainfall (Figure 4.3f).

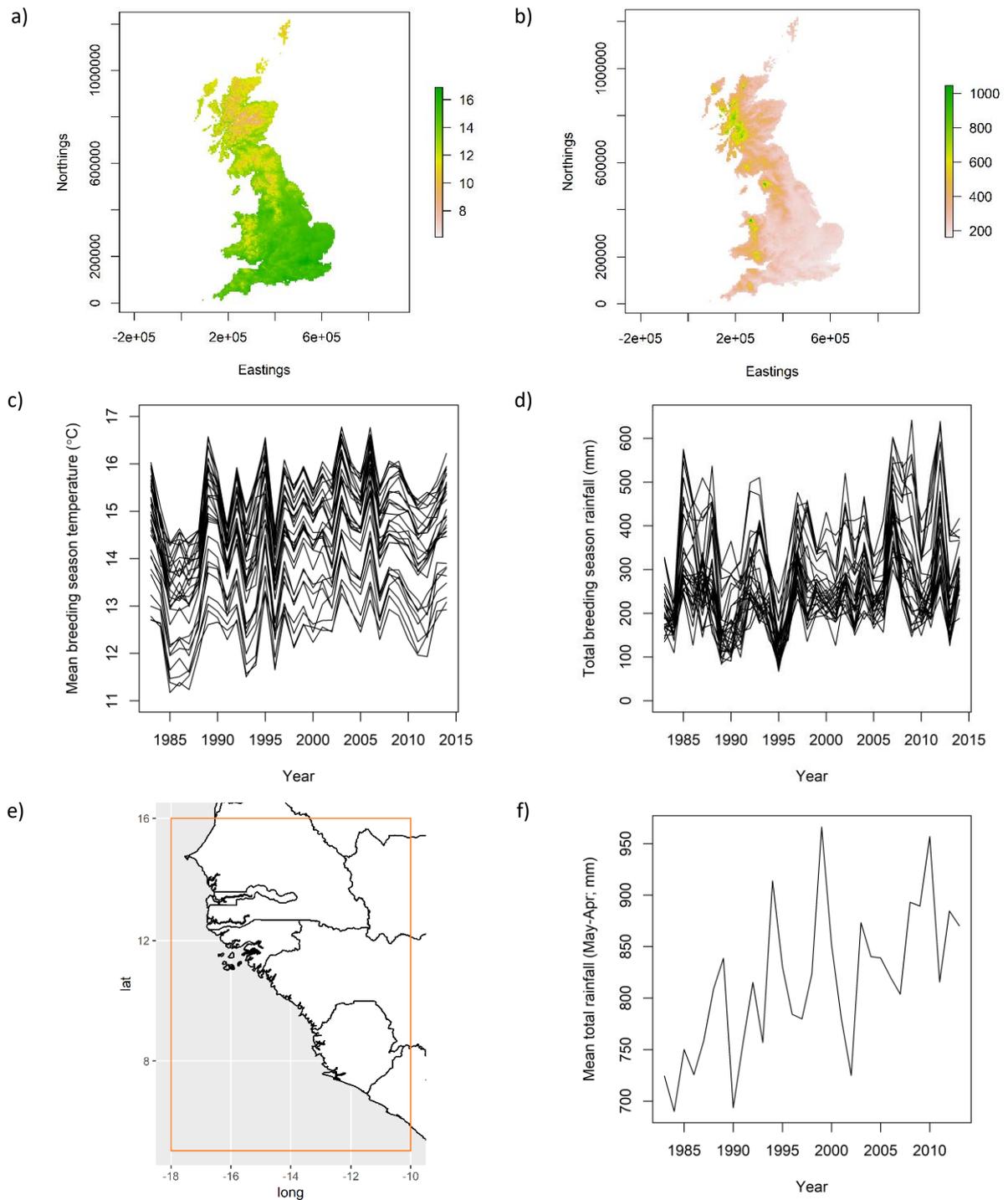


Figure 4.3. Climate data used in analyses. a) Mean breeding season temperature in Britain, 1983-2014. b) Mean total breeding season rainfall in Britain, 1983-2014. Change over study period (1983-2014) in: (c) mean breeding season temperature; and (d) total breeding season rainfall. Lines link annual values for each 100 km x 100 km grid cell containing data-contributing CES or NRS sites in c) and d). e) Extent (rectangle) in West Africa from within which rainfall data extracted (Senegal in NW, Liberia in SE). f) Mean (May-Apr) total rainfall across West African region in (c), 1983-2013.

4.3.2 Overall modelling approach

I estimated reed warbler demographic parameters over the period 1983-2014 in separate analyses and in an IPM (4.3.4). Survival and population size were modelled from capture histories and counts

in models with a hierarchical structure (as for occupancy in Chapter 2; also see 1.5): an observation error component and a latent ecological process component. Details of the Bayesian modelling are given in 2.3.1.2. As in Chapter 2, a separate model was run for each covariate (year, temperature and rainfall). All covariates were scaled to mean 0 and standard deviation 1 to ease model running (Kéry and Schaub 2011) and to allow comparison of slopes between covariates.

The demographic parameters, and their slopes with each covariate, are assumed to be spatially autocorrelated (e.g. Du Feu & McMeeking 2004). This means that data from closely-located sites are likely to be non-independent. This was modelled using spatial random effects (as for occupancy; see 2.3.1.1): this allowed estimation of the different parameters, and their slope with covariates, for each grid cell across Britain (e.g. Saracco et al. 2010). Furthermore, one might expect demographic parameters to follow a hump-shaped distribution from one edge of a species' range to the other (e.g. Eglinton et al. 2015). Thus as a range edge is approached, one might expect a non-linear decline in a demographic parameter approaching the range edge. Therefore, although the fitted global and cell-wise slopes were linear, the flexible modelling approach permitted the data to suggest deviations from linear relationships with covariates across the British range as a whole.

Some parameters – clutch size, egg survival, chick survival and adult survival – could be directly estimated from data. For these, an individual model was run for each parameter (4.3.3). These sub-models were then combined with population size data into an integrated analysis (4.3.4). I detail the specifics of the demographic parameter sub-models and their integrated analysis below.

4.3.3 Demographic parameter sub-models

4.3.3.1 Likelihood of clutch size data

The data used for clutch size were the minimum clutch size from nest records for which the maximum contents was the same as the maximum clutch size, leaving 5,505 records. Being a non-negative integer, it was assumed that the clutch size of a nest c is Poisson distributed with rate κ (equation 4.1). On the scale of the link function, target parameters (in this case, clutch size) in all demographic parameter sub-models varied around a global intercept with: a spatial random intercept for each grid cell; a global slope with the covariate; a spatial random offset to the global slope for each grid cell; an annual random residual. For example, for the clutch size sub-model, the log of clutch size κ is determined by a global intercept α_1 , a spatial random intercept β_1 , a global slope γ_1 , a spatial random offset to the slope δ_1 , and an annual random residual ε_1 (equation 4.2). Random effects β and δ were

spatially discretised by 100km x 100km grid cell (identity $gridid$). For nest i in year j (N.B. each nest was observed in one year only),

$$c_{i,j} \sim Pois(\kappa_{gridid_{i,j}}) \quad Eq. 4.1$$

$$\log(\kappa_{gridid_{i,j}}) = \alpha_1 + \beta_1_{gridid_i} + (\gamma_1 + \delta_1_{gridid_i})covariate_{i,j} + \epsilon_{1j} \quad Eq. 4.2$$

4.3.3.2 Likelihood of egg survival data

Nest records were used to estimate egg survival if the nest had been visited more than once during the egg stage, and if the hatching success was known, leaving 4,428 records. Hatching was deemed successful if the maximum number of days the nest was observed with chicks was greater than zero, or if the nest failed at chick stage, or if the nest was successful, or if any young were observed. Being a binary variable, it was assumed that the observed hatching success se of the nest was a Bernoulli distributed variable, the parameter of which was the daily egg survival ϕ_1 raised to the maximum number of days te for which the nest was observed during the clutch phase (Mayfield 1961; equation 4.3). The logit of ϕ_1 varied with covariates (equation 4.4), as for clutch size. For nest i in year j ,

$$se_{i,j} \sim Bern(\phi_1_{gridid_{i,j}}^{te_i}) \quad Eq. 4.3$$

$$\text{logit}(\phi_1_{gridid_{i,j}}) = \alpha_2 + \beta_2_{gridid_i} + (\gamma_2 + \delta_2_{gridid_i})covariate_{i,j} + \epsilon_{2j} \quad Eq. 4.4$$

4.3.3.3 Likelihood of chick survival data

Nest records were used to estimate brood survival if the nest had been visited more than once during the chick stage, if the nests were known to have hatched (see 4.3.3.2), and if the fledging success was known, leaving 4,264 records. Being a binary variable, it was assumed that the observed fledging success sc of the nest was Bernoulli-distributed, the parameter of which was the daily brood survival ϕ_2 raised to the maximum number of days tc for which the nest was observed (equation 4.5). The logit of ϕ_2 varied with covariates, as above (equation 4.6). For nest i in year j ,

$$sc_{i,j} \sim Bern(\phi_2_{gridid_{i,j}}^{tc_i}) \quad Eq. 4.5$$

$$\text{logit}(\phi_2_{gridid_{i,j}}) = \alpha_3 + \beta_3_{gridid_i} + (\gamma_3 + \delta_3_{gridid_i})covariate_{i,j} + \epsilon_{3j} \quad Eq. 4.6$$

4.3.3.4 Likelihood of adult capture histories

Adult survival was estimated from CES capture histories. Captures from sites at which fewer than 20 individuals were ever caught were removed. The minimum required length of capture histories for

survival analysis is three years: thus all sites with fewer than three years' data were removed. This left 43,461 individual capture histories from 139 sites.

The observed presence of an individual y depends on its true presence Z , its capture probability p and its true residency η (equation 4.7). It was assumed that each individual survives from one year to the next with probability ϕ_3 , and that once an individual dies it remains dead (equation 4.8). Having binary outcomes, both y and Z were assumed to be Bernoulli-distributed variables. Adult survival probability ϕ_3 varies with covariates as above (equation 4.9). In the analysis for rainfall, an additional term λ_4 was included for the slope of the relationship of survival with rainfall in the wintering grounds in Africa. For individual i in year j ,

$$y_{i,j} \sim \text{Bern}(\text{site}p_{\text{site}_i} Z_{i,j} R_i) \quad \text{Eq. 4.7}$$

$$Z_{i,j} \sim \text{Bern}(\phi_3^{\text{gridid}_{i,j}} Z_{i,j-1}) \quad \text{Eq. 4.8}$$

$$\text{logit}(\phi_3^{\text{gridid}_{i,j}}) = \alpha_4 + \beta_4^{\text{gridid}_i} + (\gamma_4 + \delta_4^{\text{gridid}_i}) \text{covariate}_{i,j} + \varepsilon_{4j} \quad \text{Eq. 4.9}$$

Capture probability can vary markedly between sites. The logit of the capture probability p at a given site was determined by a global capture probability $\text{mean}p$ and a random offset for each site ζ (equation 4.10). Values of $\text{mean}p$ were drawn from a normal distribution with mean 0 and standard deviation 32; a reasonably uninformative prior. The precision of the random effect ζ needed a slightly more informative prior for the model to run successfully; values for this quantity were drawn from a gamma distribution with shape 1 and rate 0.1. The capture probability $\text{site}p$ at a CES site in a given year was p multiplied by the proportion e of 12 visits that were operated at that site in that year (equation 4.11). For site i in year j ,

$$\text{logit}(p_i) = \text{mean}p + \zeta_i \quad \text{Eq. 4.10}$$

$$\text{site}p_{i,j} = p_i e_{i,j} \quad \text{Eq. 4.11}$$

Transient reed warblers mix with residents on the breeding grounds (Thaxter *et al.* 2006; Johnston *et al.* 2016). I therefore incorporated transience into the analysis, in order to avoid underestimating survival. No term was included to allow movement between sites. Thus it was assumed that the only way individuals can become impossible to capture at the site at which they were first captured is by dying. Individuals caught more than once in their first year of capture were classed as 'resident'. That is, it is assumed that an individual cannot be caught on more than one visit in a year unless it is truly resident. This observed residency res depends on the true residency of an individual η , the probability

of capturing an individual on two or more visits pt , and the number of visits ef made in their first year of capture (equation 4.12). I assumed that the true residency η of an individual depends on a global residency probability π (equation 4.13). Having binary outcomes, both res and η were assumed to be Bernoulli-distributed variables. For individual i ,

$$res_i \sim Bern(\eta_i p t_i e f_i) \quad Eq. 4.12$$

$$\eta_i \sim Bern(\pi) \quad Eq. 4.13$$

Saracco et al. (2012) model the probability of capturing an individual on two or more visits as a latent parameter ρ (rho). In order to minimise the number of latent parameters, I calculated this probability pt from the (already estimated) capture probability p . The complement of p is the complement of the per-visit capture probability pv , raised to the power of 12 (for 12 CES visits; equation 4.14). For site i ,

$$1 - p_i = (1 - pv_i)^{12} \quad Eq. 4.14$$

thus

$$pv_i = 1 - (1 - p_i)^{\frac{1}{12}} \quad Eq. 4.15$$

The probability of capturing an individual on more than two occasions is calculated by taking the probability of capturing an individual just once (the probability mass function of the binomial distribution),

$$\binom{12}{1} pv_i (1 - pv_i)^{11} \quad Eq. 4.16$$

and the probability of capturing an individual zero times $(1-p)$, and subtracting these from unity.

$$pt_i = 1 - (1 - p_i) - 12(pv_i(1 - pv_i)^{11}) \quad Eq. 4.17$$

thus

$$pt_i = p_i - 12(pv_i(1 - pv_i)^{11}) \quad Eq. 4.18$$

4.3.3.5 Inference and model fit

The prior distributions used for global intercepts and slopes were reasonably vague compared to prior belief (Table 4.1; more detailed explanation of approach to selection of prior values given in 2.3.1.2). As for the analyses of occupancy, preliminary analysis showed that the global intercept could be given

a reasonably vague prior, and so was assumed to be drawn from a normal distribution with mean 0 and precision 0.001. The values of the slope parameters were likewise assumed to be drawn from a normal distribution with mean 0; preliminary analysis showed that these needed more informative priors, and so were given precision 0.1. Vague priors for the precisions of the random effects generated traps and errors; more informative priors were given for those quantities (Table 4.1). As for analyses of occupancy (see 2.3.1.3), values of the precision of the random effects had to be drawn from positively-skewed positive real numbers, and were therefore drawn from gamma distributions.

Models were fitted in WinBUGS from R (R Core Team 2018), using the package R2WinBUGS (Sturtz et al. 2005). To run the models for long enough to satisfactorily converge while keeping runtime length reasonable (see 2.3.1.2), each demographic parameter sub-model was updated 10,000 times, of which a burn-in set of 5,000 was discarded. One in six updates were retained to form the posterior sample, in order to avoid autocorrelation in the MCMC chain. As for the analyses of occupancy, model fit was assessed by examining the between-chain and within-chain variance by eye, and using the statistic \hat{R} .

Table 4.1. Priors for terms in linear predictor for each target parameter, for demographic parameter sub-models in separate analyses. Parameters of the normal distribution given as mean and precision.

Target parameter	Global intercept	Global slope	Precision of grid cell intercept random effect	Precision of grid cell slope random effect	Precision of global annual random effect
κ	N(0, 0.001)	N(0, 0.1)	Gamma(10,1)	Gamma(10,1)	Gamma(10,1)
φ_1	N(0, 0.001)	N(0, 0.1)	Gamma(10,1)	Gamma(10,1)	Gamma(10,1)
φ_2	N(0, 0.001)	N(0, 0.1)	Gamma(10,1)	Gamma(10,1)	Gamma(10,1)
φ_3	N(0, 0.001)	N(0, 0.1)	Gamma(10,1)	Gamma(10,1)	Gamma(10,1)

4.3.4 Integrated population model

4.3.4.1 IPMs: introduction

It is rare that we have parallel datasets with which to estimate each of a species' demographic parameters in detail. However, we can take advantage of the fact that the size of a population at any time step is determined by births, deaths, immigration and emigration. The ramification of the population size through time itself therefore provides additional information on demography. IPMs combine population size and demographic data to allow estimation of parameters for which no explicit data exist (Robinson et al. 2014).

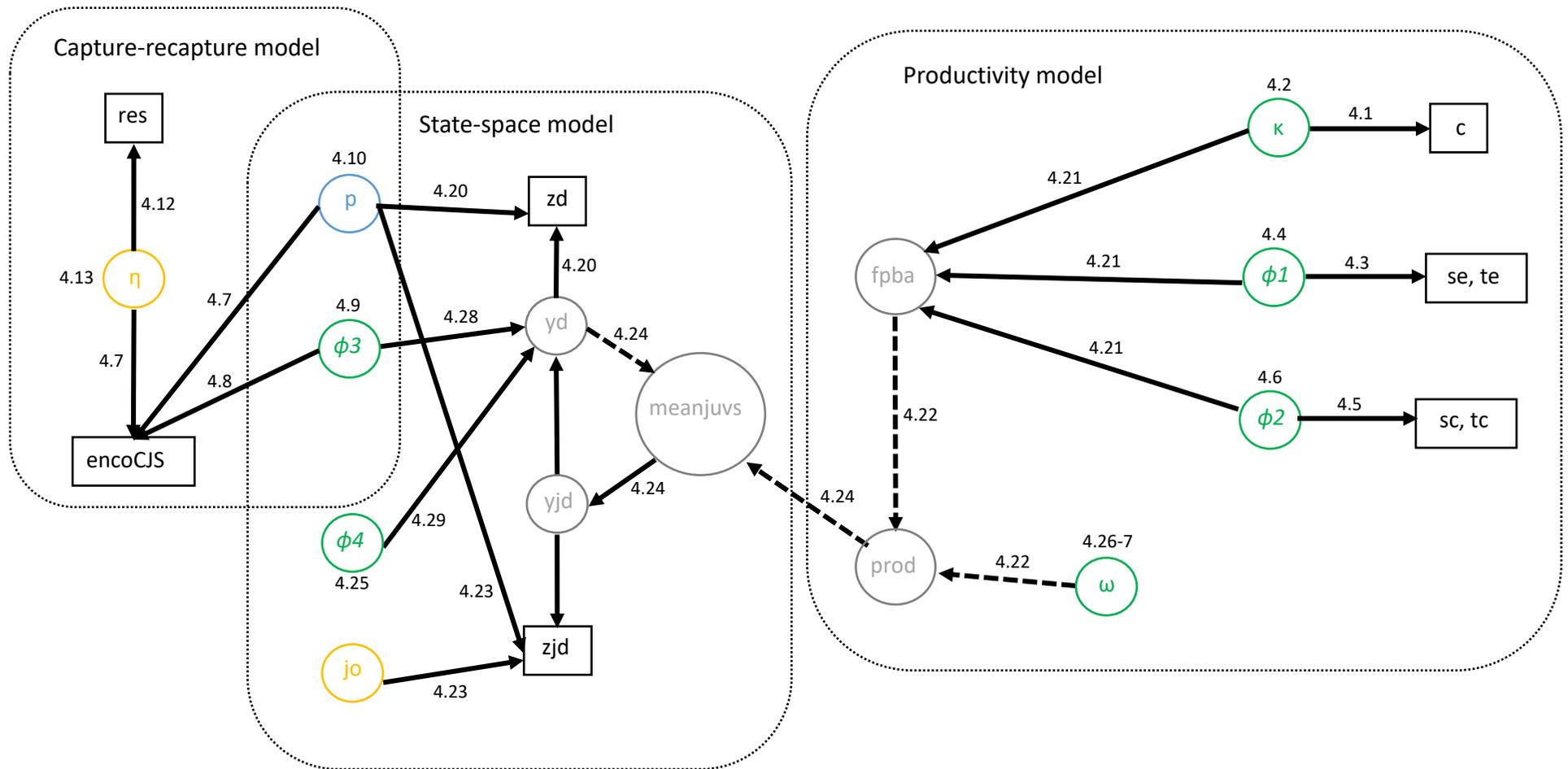


Figure 4.4. Directed acyclic graph of spatio-temporal integrated population model for reed warbler in Britain. The notation for the nodes matches the text notation. Solid arrows depict stochastic dependencies and dashed arrows depict deterministic dependencies. Data are depicted within rectangles and unknown quantities are depicted within circles. Estimated parameters are coloured and non-estimated parameters are grey. The permitted variation in an estimated parameter is shown by colour: orange = global intercept; blue = global intercept and fixed per-site intercept; green = global intercept, random spatial intercept, global slope with covariate, random spatial slope with covariate and random annual residual. The equation numbers in the text are given adjacent to the corresponding nodes or dependencies. The IPM is run once for each of the three covariates: time, temperature and rainfall.

Here, I estimated reed warbler demographic parameters using an IPM for the reed warbler population in Britain. This required defining the likelihood of population size data given true population size, and defining how demographic rates produce changes in population size (Kéry & Schaub 2011). The joint likelihood for the whole IPM was then the product of the individual likelihoods of the seven contributing datasets. The schematic in Figure 4.4 describes how the demographic parameter sub-models were combined with an additional state-space sub-model for population size in an IPM. As for the separate analyses (4.3.3), I assumed that processes at the site- or nest-scale are determined by demographic parameters which vary at the grid cell (100 km x 100 km) scale.

4.3.4.2 Likelihood of adult capture totals

Adult survival probability ϕ_3 and capture probability p were modelled from their respective datasets (*encoCJS* and *res*, given residency parameter η). True adult population size yd was modelled, given capture probability p , from adult capture totals zd (equation 4.20). In practice, the site-wise p was multiplied by whether the site was operated in that year ed (equation 4.19). As the result of several trials with binary outcomes, zd was assumed to be binomially-distributed. For site i and year j ,

$$ps_{i,j} = p_i ed_{i,j} \quad \text{Eq. 4.19}$$

$$zd_{i,j} \sim \text{Binom}(yd_{i,j}, ps_{i,j}) \quad \text{Eq. 4.20}$$

4.3.4.3 Likelihood of juvenile captures and dependency of population size on demographic rates

Clutch size κ , egg survival ϕ_1 and brood survival ϕ_2 were modelled from their respective datasets (*c*, *se*, *te*, *sc*, *tc*). Clutch κ , egg survival ϕ_1 and brood survival ϕ_2 (the latter two raised to the length of the incubation *inc* and chick period *bro* respectively; 10.5 and 11 used here) were multiplied together to give the number of fledglings per breeding attempt *fpba* (equation 4.21). This was multiplied by a latent parameter ω , to give the per-pair productivity *prod* (equation 4.22). For grid cell i and year j ,

$$fpba_{i,j} = \kappa_{i,j} \phi_{1,i,j}^{inc} \phi_{2,i,j}^{bro} \quad \text{Eq. 4.21}$$

$$prod_{i,j} = fpba_{i,j} \omega_{i,j} \quad \text{Eq. 4.22}$$

The true number of juveniles yjd was estimated by multiplying the number of breeding females in the population (half of the true adult population size yd) by per-pair productivity *prod* (equation 4.24). The observed number of juvenile captures zjd is proposed to be generated by the true number of juveniles present yjd , given the juvenile capture probability (the adult capture probability p multiplied by an offset j_0 ; equation 4.23). As the result of several trials with binary outcomes, zjd was assumed

to be binomially-distributed; as a non-negative integer, yjd was assumed to arise from the Poisson distribution. Juvenile capture probability was expected to be lower than adult capture probability, because juveniles are present for a lower proportion of the breeding season than adults, by definition. Being between 0 and 1, values of jo were drawn from a Uniform distribution with minimum 0.01 and maximum 0.99 (using parameters 0 and 1 caused numerical problems in the model). For site i and year j ,

$$zjd_{i,j} \sim Binom(yjd_{i,j}, ps_{i,j}jo) \quad Eq. 4.23$$

$$yjd_{i,j} \sim Pois(prod_{gridid_{i,j}} \frac{yd_{i,j}}{2}) \quad Eq. 4.24$$

Juveniles survive to the following year with probability $\phi4$. As for the other target parameters (κ , $\phi1$, $\phi2$ and $\phi3$), the latent parameters ω and $\phi4$ were allowed to vary with covariates in the same way (equations 4.25-4.27). For grid cell i and year j ,

$$logit(\phi4_{i,j}) = \alpha5 + \beta5_i + (\gamma5 + \delta5_i)covariate_{i,j} + \varepsilon5_j \quad Eq. 4.25$$

and

$$\omega_{i,j} \sim LogNormal(\mu_{i,j}, \theta) \quad Eq. 4.26$$

$$\mu_{i,j} = \alpha6 + \beta6_i + (\gamma6 + \delta6_i)covariate_{i,j} + \varepsilon6_j \quad Eq. 4.27$$

The latent parameter ω was assumed to be a non-negative real number, with small values more likely than large values, so was assumed to arise from the log-normal distribution (a gamma distribution was also trialled but caused the model to fail). Values of ω outside of the interval [0.0001, 100] were censored to prevent traps from unrealistic parameter space being explored (see 4.2.4.5). Adults survive to the following year with probability $\phi3$ (equation 4.28). Surviving adults Ns and recruiting immature birds $Nrec$ are combined to make a given year's adult population (equations 4.29 & 4.30). As the result of several trials with binary outcomes, both Ns and $Nrec$ were assumed to be binomially-distributed. For site i and year j ,

$$Ns_{i,j} \sim Binom(yd_{i,j-1}, \phi3_{gridid_{i,j}}) \quad Eq. 4.28$$

$$Nrec_{i,j} \sim Binom(yjd_{i,j-1}, \phi4_{gridid_{i,j}}) \quad Eq. 4.29$$

$$yd_{i,j} = Ns_{i,j} + Nrec_{i,j} \quad Eq. 4.30$$

4.3.4.4 Omitted IPM structure

Some known aspects of reed warbler's life history were omitted from the IPM. This was either due to lack of data, or to keep the model to a manageable size. Here I identify some key sources of unmodelled variation in the IPM.

IPMs describe the flow of individuals over time between 'pools' (e.g. egg to chick, fledgling to fully-grown juvenile). The flow of individuals is subject to key operations between pools: perhaps new individuals being created, being multiplied (e.g. by double-brooding), or being reduced by mortality. It is desirable to estimate these operations: demographic parameters. Sometimes not enough data exist at the key points of a species' life-cycle to isolate every important demographic parameter.

The latent parameter ω , not corresponding neatly to a particular demographic process in reed warbler, can be thought of as a scaling parameter (Robinson et al. 2014; Stenglein et al. 2014). As such it accounts for unmodelled variation between the number of fledglings per breeding attempt per pair, and the total number of fledglings per pair. There are likely to be two main demographic contributions to ω . Firstly, reed warblers make repeat breeding attempts throughout a season, even if they have already been successful, sometimes fledging three consecutive broods (Batey & Leech 2018). Secondly, the immediate period after fledging is a high mortality period in most passerines.

Both of these demographic processes are of interest and potentially contribute importantly to variation in productivity. Extensive work went into estimating season length from the temporal distribution of first egg dates, from NRS data. A further model was created to calculate mean attempt length from nest failure rates. Mean attempt length and season length could then be combined to estimate the number of breeding attempts. However, nest recorders varied in when they stopped searching for nests, and this date was fairly repeatable among years. Attempts to account for this variation were not adequate, and so this attempt to partition ω was not robust and was omitted from the full IPM.

4.3.4.5 IPM inference and model fit

IPMs were fitted as for the demographic parameter sub-models, except the IPMs were updated for longer (50,000 iterations with 40,000 iterations' burn-in) because convergence was much slower. Priors for some quantities had to be very informative for the model to even run (Table 4.2). With so many parameters, simultaneous extreme values in several parameters at the same time could generate very large or very small numbers. For example, a vague prior for ω could mean that the

chains explored annual productivity values of more than 10,000 juveniles per pair. WinBUGS trap messages are not always easily interpreted, but from inspecting the state of parameters at the final iteration before crashing, it appeared that in some such situations WinBUGS was encountering numerical overflow from having to divide by values very close to zero. Several other issues were encountered in development of the IPM. These were typically solved by careful selection of and experimentation with the family and parameters of the distributions of the priors, the family of the distribution of the stochastic nodes, mathematically realistic initial values for the chains, and the number of iterations and length of burn-in.

Therefore, the specific prior parameter values used in the IPM (Table 4.2) were the result of adjustment of each prior over an iterative debugging process. The global intercepts in the IPM needed to be more informative, and so κ , ϕ_1 , ϕ_2 and ϕ_3 were given prior means close to those estimated from the demographic parameter sub-models. The means used for the priors for the global intercepts for ϕ_4 and ω were arrived at through trial and error. The prior precisions used for the global intercepts were all higher than those used in the demographic parameter sub-models, to avoid exploration of nonsensical parameter space. The global slopes for each parameter in the IPM were still given priors with mean 0, but the precision needed to be increased relative to those in the demographic parameter sub-models. In general, the random effects in the IPM had to be given more precise prior values than in the demographic parameter sub-models.

Debugging was slow because of the high runtime; the debugging process was made faster by parallelising the task so each chain ran on a different core. This brought the runtime down to five-six days for 50,000 iterations. IPMs are typically run for tens/hundreds of thousands of iterations (Kéry and Schaub 2011); the version (structure and priors) of the IPM presented was the only version that comfortably updated for 50,000 iterations without failing. To my knowledge this is the first IPM to incorporate space more formally than as a simple covariate, and the first IPM to simultaneously incorporate environmental covariates across demographic processes.

Table 4.2. Priors for terms in linear predictor for each target parameter in IPM.

Target parameter	Global intercept	Global slope	Precision of grid cell intercept random effect	Precision of grid cell slope random effect	Precision of global annual random effect
κ	N(1, 0.7)	N(0, 0.3)	Gamma(10,1)	Gamma(10,1)	Gamma(10,1)
ϕ_1	N(4.2, 0.3)	N(0, 0.3)	Gamma(10,1)	Gamma(10,1)	Gamma(100,1)
ϕ_2	N(5, 0.3)	N(0, 0.3)	Gamma(10,1)	Gamma(10,1)	Gamma(100,1)
ω	N(0.2, 0.2)	N(0, 0.1)	Gamma(100,0.5)	Gamma(100,0.5)	Gamma(100,0.5)
ϕ_4	N(0, 1.3)	N(0, 0.3)	Gamma(10,1)	Gamma(10,1)	Gamma(10,1)
ϕ_3	N(0, 1.3)	N(0, 0.3)	Gamma(10,1)	Gamma(10,1)	Gamma(10,1)

4.4 Results

4.4.1 Separate analysis

In the separate analyses, R-hat was less than 1.1 for all parameters in all models. This, and visual inspection of the MCMC chains, suggested that all parameters had converged satisfactorily. The models for egg survival needed running for twice as long as the other models (20,000 iterations with 10,000 discarded as ‘burn-in’) to achieve satisfactory convergence.

Table 4.3. Intercept estimates of occupancy and demographic parameters, and estimates of nuisance variables, from models with time as a covariate.

Parameter	Estimate (95% credible interval)
Clutch size κ	3.824 (2.705, 5.305)
Daily egg survival ϕ_1	0.985 (0.982, 0.989)
Daily chick survival ϕ_2	0.993 (0.991, 0.994)
Adult survival ϕ_3	0.441 (0.403, 0.478)
Capture probability p	0.696 (0.662, 0.732)
Residency π	0.643 (0.627, 0.656)

Clutch size was slightly higher in the south and west of the range and lowest in the east (Figure 4.5a). For all covariates, the credible interval of the slope of the relationship of clutch size with that covariate overlapped with zero (Figure 4.6). There were non-significant trends for clutch size to slightly increase over time and with temperature, and to slightly decrease with rainfall (Figure 4.6). There was spatial variation in these relationships, but no clear systematic pattern (Figures 4.7b, 4.8b, & 4.9b).

Daily egg survival very slightly increased from the south to north of the range (Figure 4.5b). Egg survival increased considerably over time (Figures 4.6 & 4.7c), and the improvement in egg survival was slightly higher in the south than in the north of the range (Figure 4.7d). Egg survival had a stronger positive relationship with temperature than with time (Figures 4.6 & 4.8c), and this positive relationship was considerably stronger in the east of the range than elsewhere (Figure 4.8d). Rainfall and egg survival were negatively related (Figures 4.6 & 4.9c), although the slope of the relationship was shallower than between temperature and egg survival (Figure 4.6). Notably, egg survival was particularly low in 2012 (as was chick survival), the wettest summer in the UK since 1912 (Figure 4.7c). An increase in rainfall had a slightly stronger negative effect on egg survival in the south and east of the range than elsewhere (Figure 4.9d).

Daily chick survival was higher than daily egg survival (Table 4.3), and was slightly higher in the north and east of the range (Figure 4.5c). Chick survival had a very strong positive relationship with temperature. This relationship was considerably stronger than the relationships with time (positive) and rainfall (negative); the credible intervals of the global slopes of both marginally overlapped with

zero (Figure 4.6). There was very little spatial variation in the relationship between chick survival and temperature (Figures 4.8e and 4.8f). Chick survival increased more over time in north-east England than elsewhere (Figure 4.7f). There was no systematic spatial pattern in the relationship between chick survival and rainfall (Figure 4.9f).

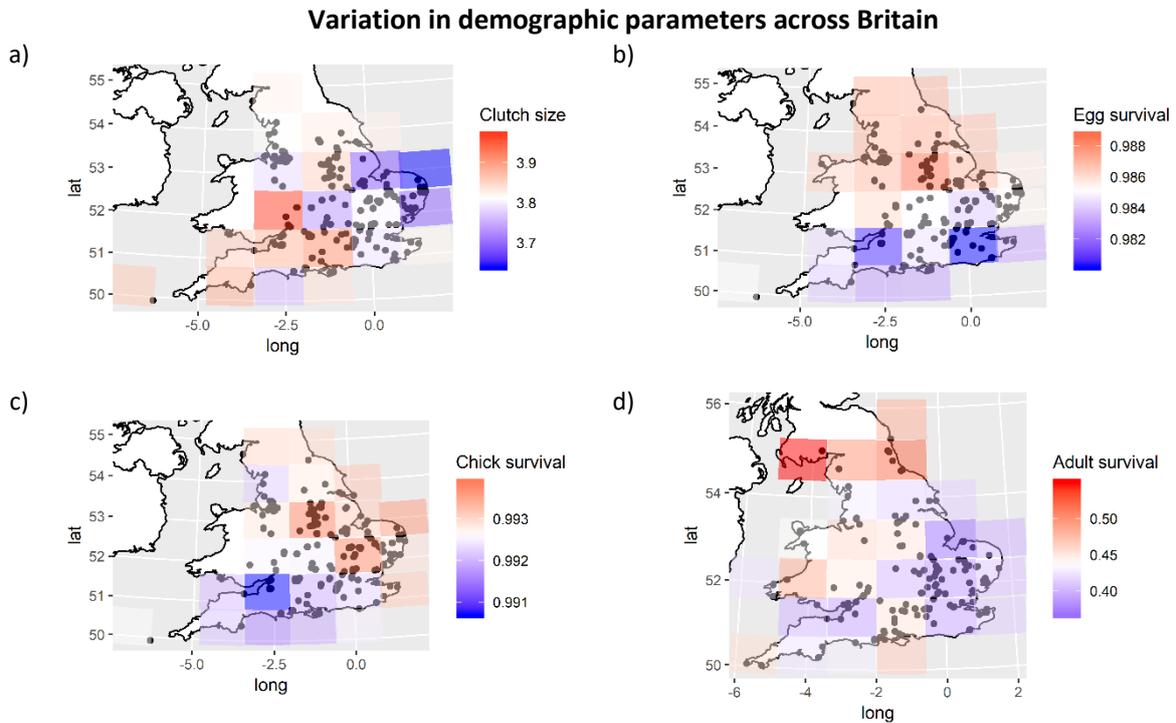


Figure 4.5. Maps of modelled demographic parameters at middle of 1983-2014 study period.

Annual fledglings per breeding attempt $fpba$ was computed post-hoc from annual estimates of clutch size, egg survival and chick survival, according to equation 4.21. The relationship between annual fledglings per breeding attempt and temperature and rainfall was likewise computed from estimates of the equivalent relationships for the above parameters. Because fledglings per breeding attempt was computed post-hoc, uncertainty is not known for estimates of fledglings per breeding attempt, nor its relationships with covariates. Fledglings per breeding attempt was higher in the north and west of the range than in the south and east (Figure 4.10a). The relationship between fledglings per breeding attempt and temperature appeared to be stronger than with the other covariates (Figure 4.10d). There was no clear systematic spatial variation in the relationship between fledglings per breeding attempt and temperature and rainfall (Figures 4.10e & 4.10g), but fledglings per breeding attempt seemed to increase more in the north than in the south of the range (Figure 4.10c).

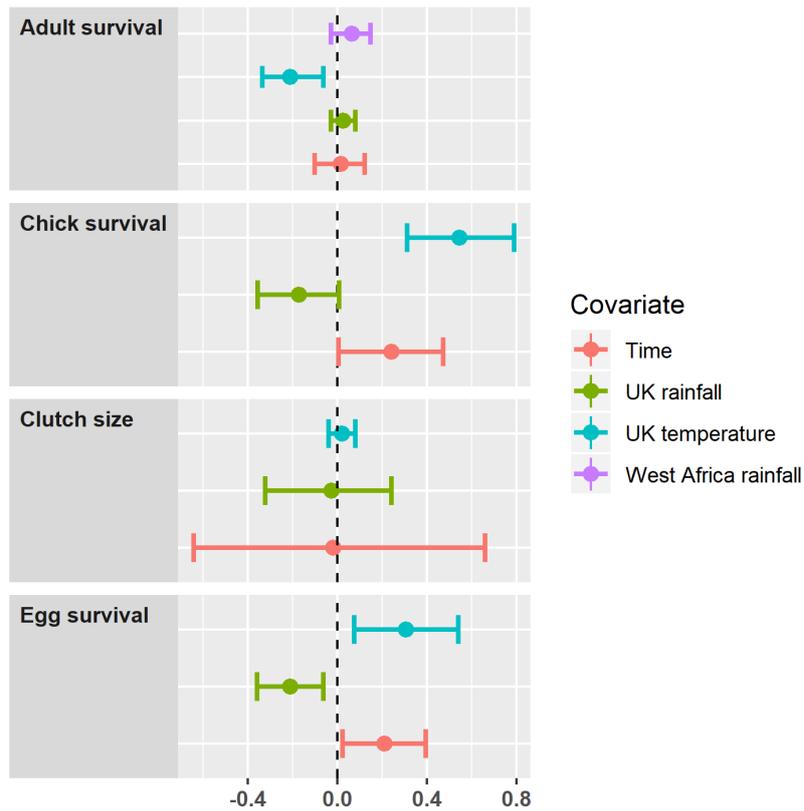


Figure 4.6. Slope estimate (& 95% CI) against scaled covariate for each demographic parameter.

Adult survival was considerably higher in the north of the range (Figure 4.5d). There was no relationship between adult survival and time, Britain rainfall or West African rainfall, although there was a slight indication for all three to be positive (Figure 4.6). Adult survival had a strong negative relationship with temperature (Figures 4.6 and 4.8g). This negative relationship was stronger in the north and west of the range (Figure 4.8h).

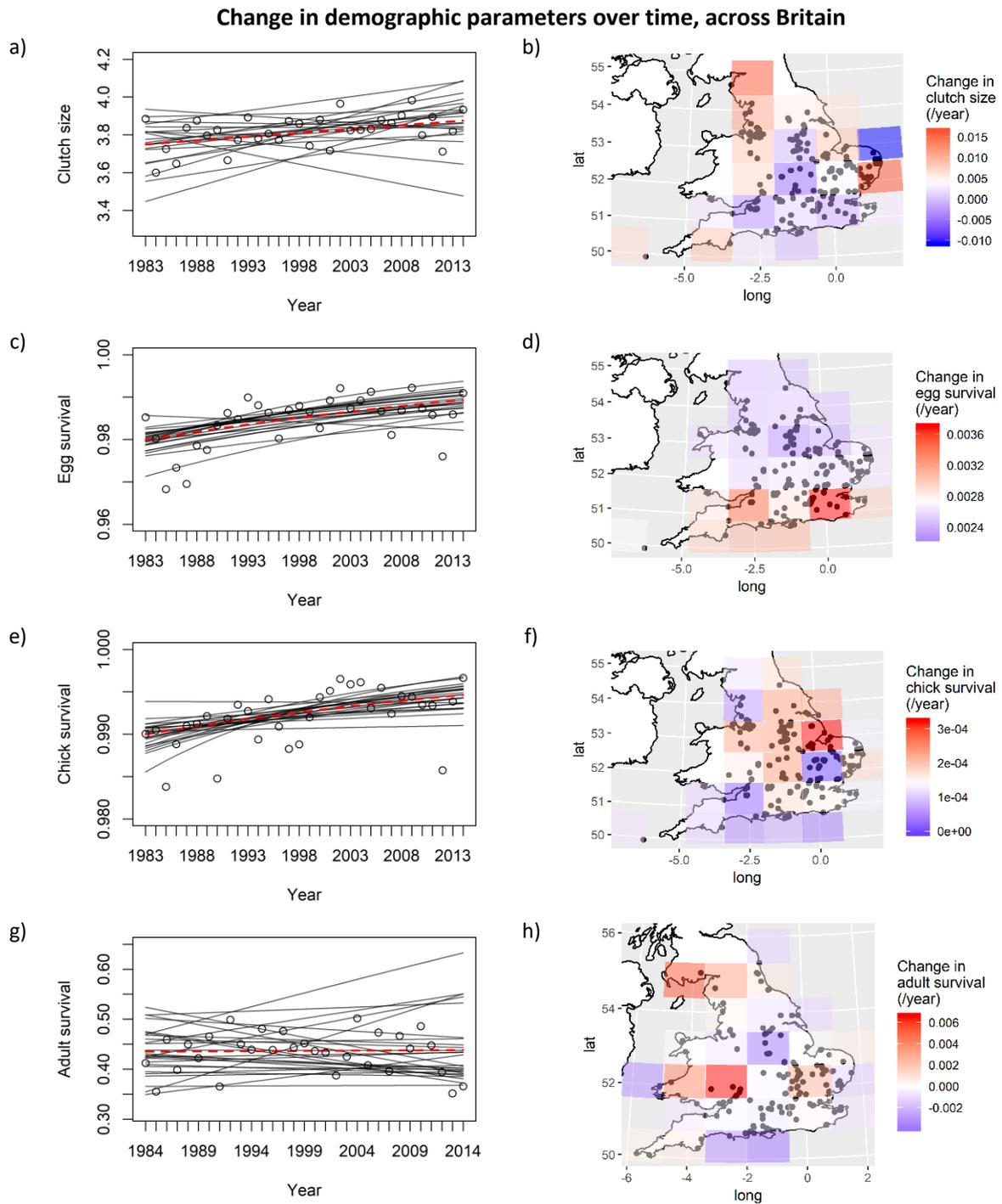


Figure 4.7. Fitted relationships of reed warbler demographic parameters against time. (a), (c), (e), (g): red dashed line is global slope, black lines are slopes for grid cells, points are annual global estimates. (b), (d), (f), (h): 'change' is difference in fitted parameter between value at middle of study period and one year later, ignoring annual residuals.

Relationships of demographic parameters with temperature, across Britain

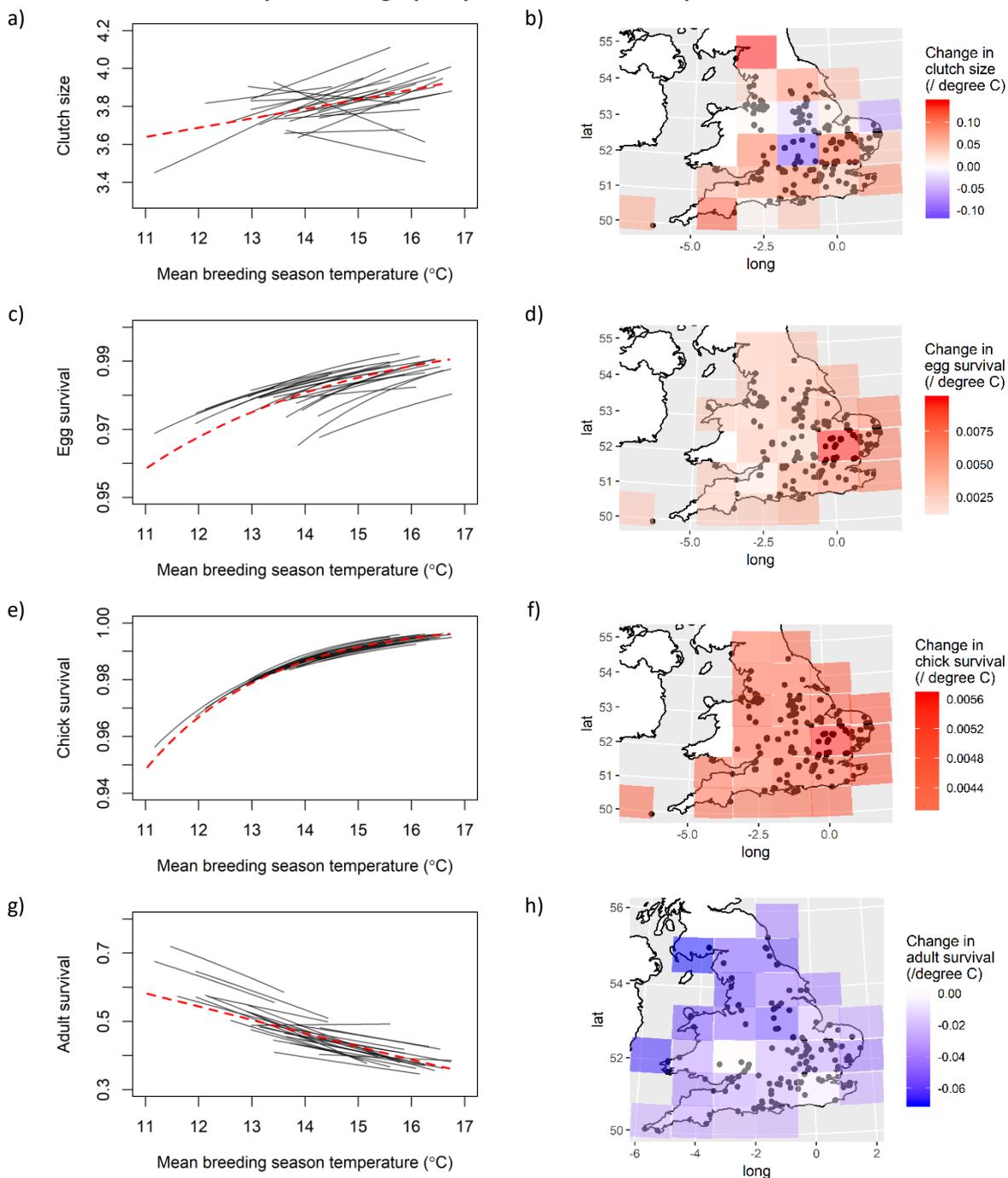


Figure 4.8. Fitted relationships of reed warbler demographic parameters against mean breeding season temperature. (a), (c), (e), (g): red dashed line is global slope, black lines are slopes for grid cells. Fitted line for each grid cell is only plotted within range of temperature recorded in that grid cell. (b), (d), (f), (h): 'change' is difference in fitted parameter between mean mean breeding season temperature (mean taken across all squares, all years) and 1°C higher.

Relationships of demographic parameters with rainfall, across Britain

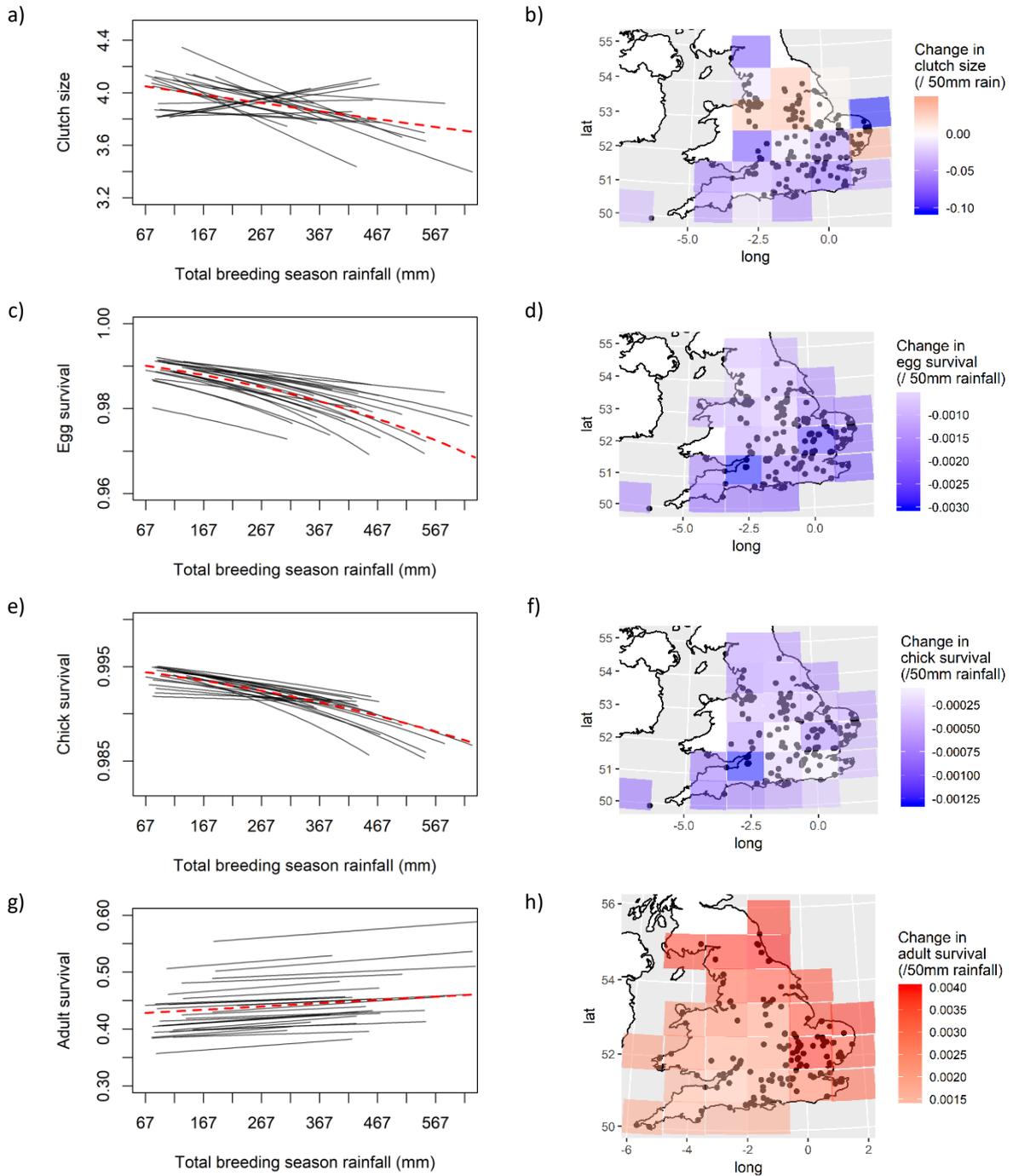


Figure 4.9. Fitted relationships of reed warbler demographic parameters against rainfall. (a), (c), (e), (g): red dashed line is global slope, black lines are slopes for grid cells. Fitted line for each grid cell is only plotted within range of rainfall recorded in that grid cell. (b), (d), (f), (h): ‘change’ is difference in fitted parameter between mean total rainfall (mean taken across all squares, all years) and 50 mm total rainfall higher.

Effects of covariates on fledglings/breeding attempt

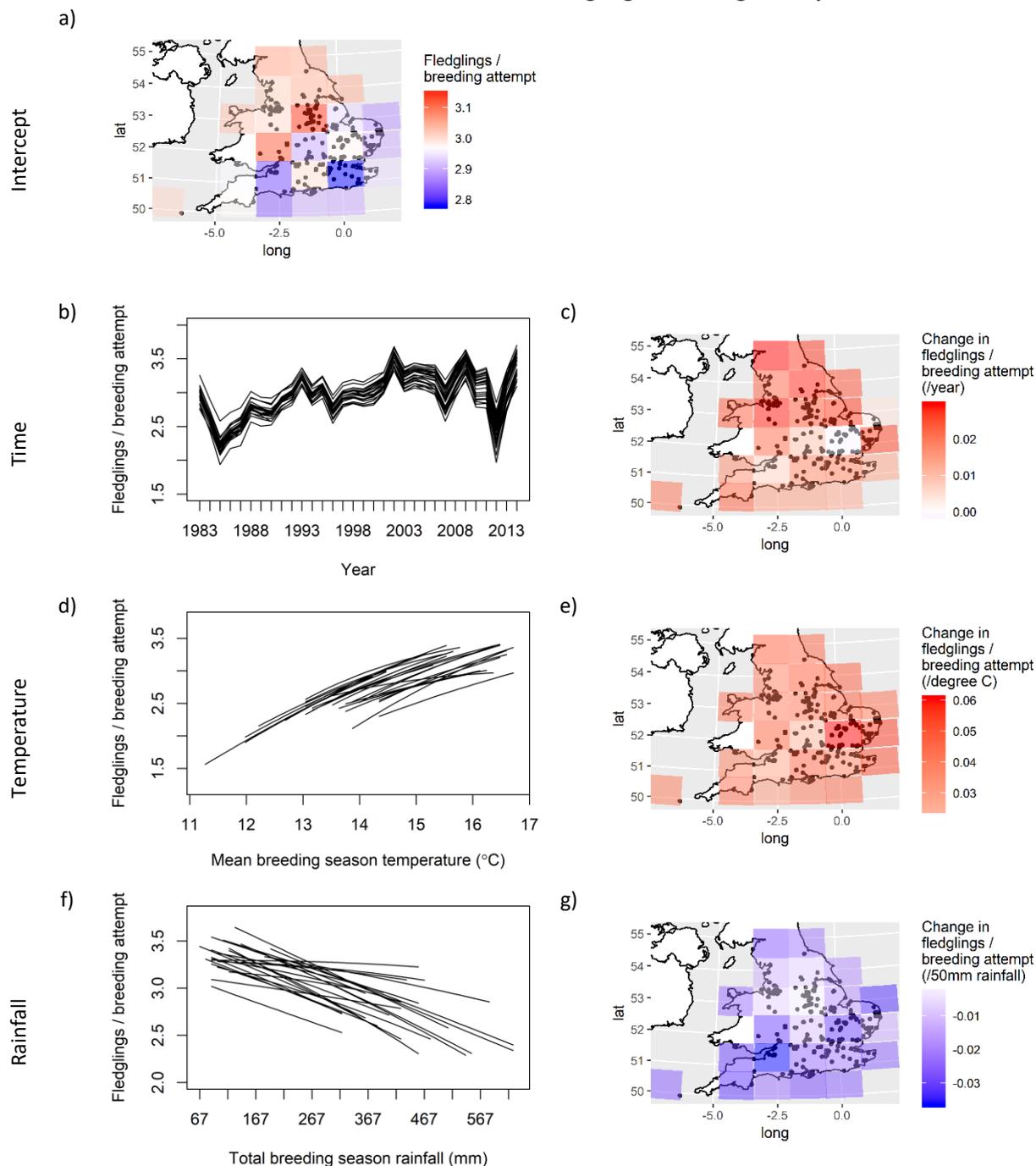


Figure 4.10. Fledglings per breeding attempt. Values computed post-hoc from clutch size, egg survival and chick survival annual estimates and their relationships with covariates. (a) Map of fledglings per breeding attempt at middle of study period. (b) Annual grid cell estimates. (c), (e), (g) For each grid cell, linear model fitted to annual post-hoc estimates; 'change' is change in parameter predicted from linear model over one year (c), over an increase of 1°C mean breeding season temperature (e), or over an increase of 50 mm total rainfall. (d), (f) Relationship with temperature and rainfall.

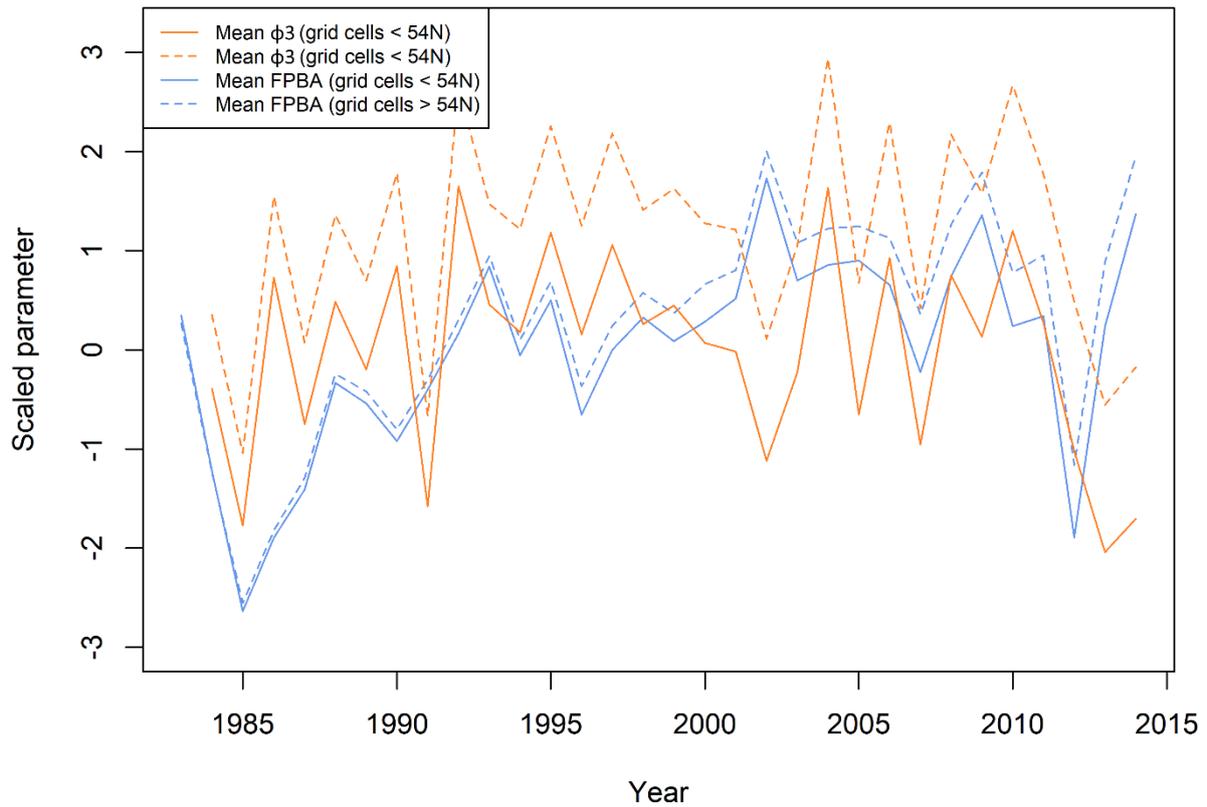


Figure 4.11. Modelled annual adult survival and fledglings per breeding attempt (FBPA). Solid line is mean estimated value for all grid cells south of 54°N containing data-contributing sites for that parameter; dashed line is mean estimated value for all grid cells north of 54°N containing data-contributing sites for that parameter. Values scaled to mean 0 and standard deviation 1 for both parameters; values for northern set of grid cells for a given parameter scaled using mean and standard deviation of values for southern set of grid cells for same parameter.

The exact annual location of the range edge in the years 1983-2014 is poorly known (Chapter 2). This makes it difficult to compare the changes in parameters between the range core and the area colonised after 1983. Based on the description of range change in Chapter 2 (Figures 2.5, 2.6), 54°N was selected as an approximate delineation between the range core and the colonised area. Annual adult survival and fledglings per breeding attempt were computed to the north and south of this line, taking the mean of all data-contributing grid cells in each region (Figure 4.11). Adult survival was always higher in the colonised area, and slightly increased, relative to the range core. Fledglings per breeding adult slightly increased in the colonised area relative to the range core over time. There was no clear indication that at the start of the period, adult survival or fledglings per breeding attempt were lower in the newly colonised area than in the range core.

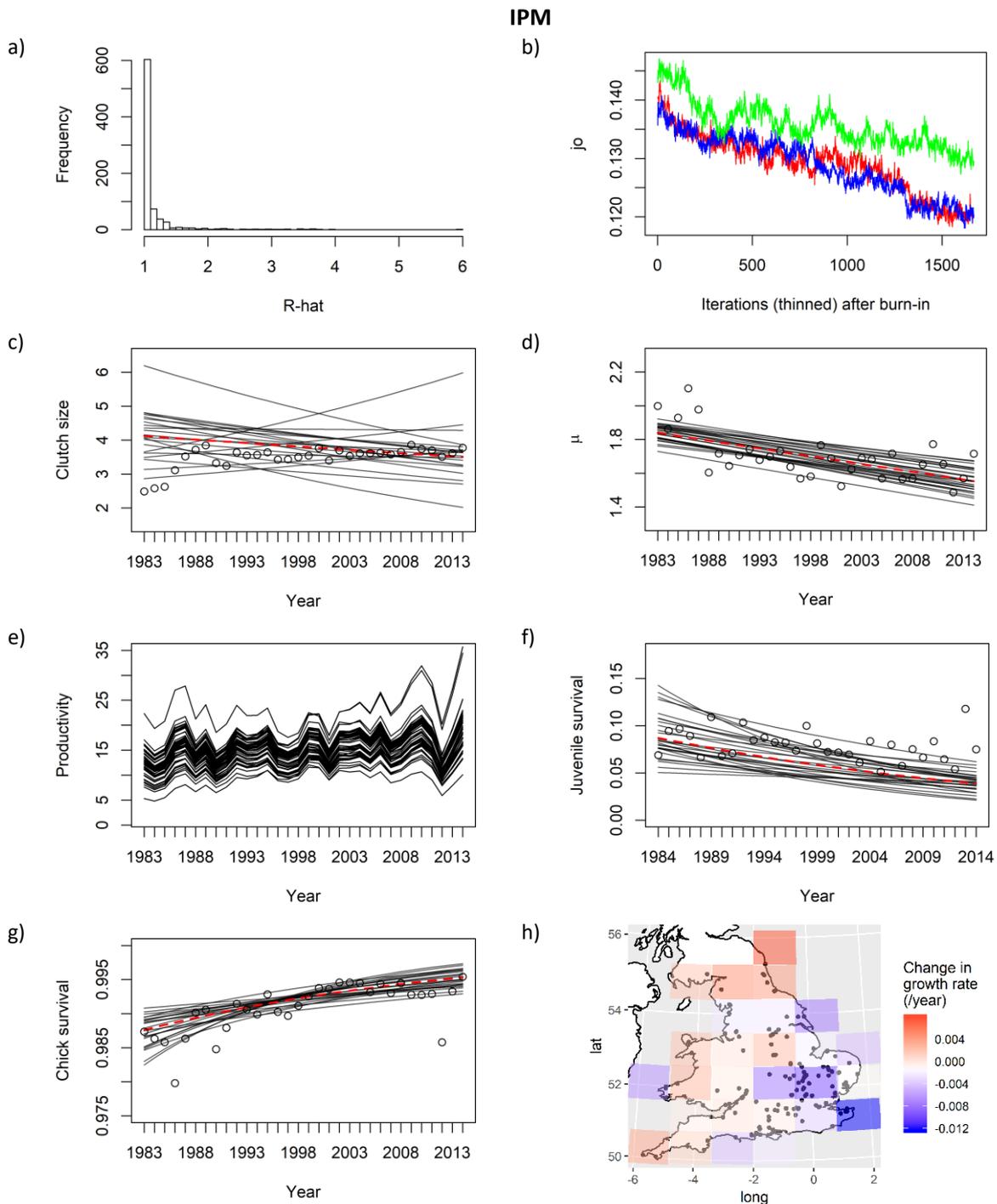


Figure 4.12. Selected output from IPM of reed warbler in Britain, with time as covariate. Outputs are provided to present signs of internal conflict in the model (a-g), and an example map of change in population growth rate over time (h).

4.4.2 Integrated analysis

The IPMs did not converge properly. The IPM with time as a covariate is used as an example here, but the issues were similar in the IPMs for temperature and rainfall. In the IPM with time as a covariate, 25% of parameters had a value of R-hat of greater than 1.1, indicating that the variation between chains was greater than the variation within chains (Figure 4.12a). The chains for some parameters,

such as the juvenile offset to adult survival probability jo and the productivity scaling parameter ω , were clearly not stationary (Figure 4.12b). There were further indications of internal conflict within the IPM: for example, the model found clutch size to gradually increase over the years; however, the estimated slope was given as negative, while the estimated annual residuals in early years were highly negative to reconcile the negative slope with the increasing clutch size (Figure 4.12c). For some parameters, the estimated values were extreme or nonsensical. For example, values of ω (Figure 4.12d) led to estimates of annual productivity of up to 35 juveniles per pair (Figure 4.12e). This was the apparent cause of very low values of juvenile survival (Figure 4.12f). It is unlikely that this would have been resolved with further iterations, because ω was still continuing to rise when iterations ceased. Interestingly, some parameters were relatively unaffected by the internal conflict: for example, the annual values of chick survival estimated by the IPM (Figure 4.12g) were similar to those estimated in the separate analysis (Figure 4.7e). However, the extent of the lack of fit in the IPM is unknown; therefore the apparent indication that population growth rate increased more in the colonised area (Figure 4.12h) is not robust.

4.5 Discussion

4.5.1 Reed warbler demographic parameters and relationships with time and climate

Reed warbler egg survival and chick survival both increased over time. Both parameters were even more strongly positively related to temperature than to year. This suggests that climate warming has driven an increase in nest survival in reed warbler in Britain. Egg survival had a negative relationship with rainfall, but this was weaker than the relationship between egg survival and temperature, and so the relationship with rainfall could be an indirect one arising out of a positive relationship with temperature. This positive relationship between nest survival and breeding season temperature is consistent with that found elsewhere in Europe (Schaefer et al. 2006; Halupka et al. 2008), and consistent with the identification of weather as the most important cause of nest failure in the UK (Bibby 1978), unlike elsewhere in Europe (Schulze-Hagen et al. 1996). There are multiple possible mechanisms for this relationship, for example: chicks can starve in cold, wet weather (Dyrz 1981); nest predation can be higher when food supply is low (Vafidis et al. 2016). Alternatively, phenotypic plasticity makes up an important component of species' response to climate (Barshis et al. 2013): perhaps adults provisioned their chicks less when food supply was low, in order to maintain their own condition. Unlike Schaefer et al. (2006), but like Halupka et al. (2008) and Vafidis et al. (2016), I did not find a positive relationship between temperature and clutch size.

Reed warbler adult survival decreased with the previous breeding season's temperature, especially in the north and west of the range in Britain. This relationship was much stronger than the relationship between adult survival and time, suggesting that the relationship with temperature was genuine, rather than arising from covariance with a latent variable that followed a trend over time. This negative relationship is surprising, especially for a species at the cool edge of its range. No other study has found effects of breeding season climate on reed warbler survival (see 1.4.3.3). It is relatively rare for the survival of bird species of temperate regions to be influenced by breeding season conditions rather than non-breeding season conditions (Robinson et al. 2007). It is possible that breeding season droughts caused by higher temperatures directly cause higher mortality in adult reed warblers. Droughts could also place adults in a poorer condition for autumn migration, causing higher mortality during that period, which is the highest mortality period for this species (Procházka et al. 2017). Alternatively, it could be that this is an indirect relationship with temperature through breeding success. If nest survival is relatively high, then adults spend more time during the season in the laying, incubation and chick period than if nest survival is low. Mortality is higher in this period in reed warbler than during the nest building and fledging period (Wierucka et al. 2016).

It is also difficult to explain the steeper negative relationship between adult survival and temperature at lower temperatures; perhaps this is due to local adaptation to cooler conditions in range edge populations. Although the same relationship was not found in reed warbler, in Bulgaria great reed warblers had a lower haemoparasite prevalence in a colder high altitude marsh than in a low altitude marsh (Shurulinkov & Chakarov 2006). This relationship was presumed to be due to lower Diptera presence at lower temperatures to transmit infections. It is therefore possible that reed warblers at the cold edge of their range sustain lower parasite loads and therefore have higher survival as a result. Interestingly, this negative relationship between survival and temperature did not result in a decline in survival over the study period as the climate warmed.

Like Halupka et al. (2017), I found no effect of winter rainfall in the humid zone on adult reed warbler survival. The strongest relationships between reed warbler survival and African climate have been positive relationships with Sahel rainfall (Salewski et al. 2013; Ockendon et al. 2014; Johnston et al. 2016), even though reed warblers winter to the south of the Sahel, suggesting that the effects of rainfall there arise from stopover site condition. Halupka et al. (2017) suggested that reed warbler's use of mangroves make it more resilient to drought (although see Dieye et al. 2013). However, no studies have delineated the exact wintering range of reed warbler, and so rainfall data averaged over broad areas of west Africa (as used in all studies to date) probably include much data from outside

reed warbler's wintering range. This alone could cause a true relationship between reed warbler survival and wintering range climate to go undetected.

Although climate strongly influenced demographic parameters, especially nest survival, there was considerable spatial and temporal variation in demographic parameters that (informally) did not fit with spatial and temporal climate gradients (Figures 4.5 & 4.6). This suggests that other factors, such as biotic interactions or density-dependence, exert significant influence on reed warbler demographic parameters in Britain. I was not able to investigate this here.

It is regrettable that the IPMs did not fit, thus preventing estimation of further demographic parameters and population growth rate, and their relationships with time, space and climate. A key assumption of IPMs is that the structure of the state equations and the observation process are described correctly (Schaub & Abadi 2011). Based on the parameters which were not stationary in the MCMC chains, it seems that the likelihood for the number of juvenile captures is not correctly described. It could be that juvenile captures contain a large proportion of staging birds on migration. Indeed, estimated values of *omega* were high on the south coast of England (not shown), where juveniles can aggregate in late summer (Insley & Boswell 1978). This would make the number of juvenile captures difficult to reconcile with the estimated number of adults and estimated fledglings per breeding attempt. Individuals may not have fallen neatly into the pools and operations assumed by the IPM, in other ways. For example, it was assumed that juvenile reed warblers caught on CES had already passed through the main period of high post-fledging mortality (3.5.1), and all mortality thereafter was juvenile over-wintering survival (potentially with a different rate); this may not have been the case, and the proportion of juveniles captured on CES while still in the high post-fledging mortality period could have varied. As with any IPM, there is also additional unknown omitted structure that could be causing the internal conflict (see 4.3.4.4).

4.5.2 Role of demography in reed warbler's range dynamics in Britain

None of reed warbler's clutch size, egg survival, chick survival or adult survival declined to the range limit. Indeed, egg survival, chick survival and adult survival were even higher in the north than the south of the range, and clutch size was intermediate in the north. This suggests that none of these parameters are involved in causing the range limit in this species in Britain. My results therefore do not provide support for the hypothesis that reed warbler's range is limited by deaths exceeding births in the un-colonised area. However, I was not able to estimate the rest of reed warbler's demographic parameters, and so I still cannot rule out this hypothesis.

Fledglings per breeding attempt has increased across reed warbler's range, in Britain particularly in the area where most colonisation has taken place. This appears to have been caused by climate-driven increases in nest survival. However, given that fledglings per breeding attempt do not appear to have been limiting range, the increase in this parameter cannot have caused the range expansion specifically by increasing potential population growth rate in the un-colonised area. Instead, an increase in fledglings per breeding attempt could have increased population growth rate short of the range edge. This increase in population growth rate could have increased the emigration rate, and therefore the rate of the expansion that was already underway. Interestingly, this increase in fledglings per breeding attempt between 1983 and 2014 was over a period when reed warbler's range centroid moved more rapidly (1988-91 to 2008-11; Chapter 2).

Ultimately, however, it is not certain that this increase in fledglings per breeding attempt has actually led to an increase in productivity, nor in population growth rate. It may be that the number of breeding attempts, or juvenile post-fledging survival, have declined over the same period. Also, elsewhere along reed warbler's range edge in Europe, productivity is only weakly related to population growth rate (Meller et al. 2018). The precise role of demography in range limitation and change in reed warbler in Britain will only be known when the full cycle of demographic processes can be estimated.

4.6 Conclusion

To my knowledge, this is the first time that a species' demographic parameters, and their relationships with time and climate, have been estimated at such high spatial resolution. I found that an increase in reed warbler egg survival and chick survival in Britain between 1983 and 2014 may have been driven by an increase in temperature. Egg survival and chick survival were positively related to breeding season temperature, while adult survival was negatively related to the previous breeding season's temperature. None of clutch size, egg survival, chick survival or adult survival declined to the range limit, suggesting that demography does not limit reed warbler's range in Britain; however, not all key aspects of demography were estimated. Likewise, an increase in fledglings per breeding attempt may have increased reed warbler's rate of range spread, but it is unclear how strongly fledglings per breeding attempt is related to population growth rate.

5. Sentinel-2 multitemporal imagery for estimating distribution of common reed

Phragmites australis in Britain

5.1 Abstract

Reed, one of the mostly widely distributed wetland plants globally, is important as a wildlife habitat, for ecosystem services, and as a resource for humans. Reed has a dynamic geographical range and has recently expanded outside of its native range, modifying ecosystems. However, like most wetland plant communities, reedbed has rarely been mapped at large geographical scales, thus restricting the information available to ecologists and resource managers. Using Sentinel-2 data and machine learning in open-source software, I produce the first remotely-sensed reedbed map of Britain. A random forest was trained on 79.2 ha of reedbed and 2,719.2 ha of non-reedbed habitat, using free online imagery. Accuracy was high within the training area (AUC = 0.9983-0.9997) but much lower in the validation area (AUC = 0.6708), where there were many false positives (user's accuracy of 6.6%). Using the known commission and omission error, I estimate that 3684.5 ha of Britain is reedbed. A similar workflow carried out in Google Earth Engine, using nearly an order of magnitude more images, gave a lower commission error but a disproportionately higher omission error. I discuss challenges for mapping rare vegetation types over large geographical areas, and present potential solutions. It is likely that reflectance error, the number of confusion habitats and systematic variation in temporal reflectance function place upper limits on the size of a geographical area that can be classified accurately with such a workflow.

5.2 Introduction

Global wetland area is declining at a high rate; however, quantitative estimates of regional or even national change in wetland area are scarce and geographically biased (Davidson 2014), with studies often focussing on individual wetlands. To inform policy, there is a clear need for wetland inventories on a larger geographical scale (Hu et al. 2017).

Reed, a large grass, is one of the most widely distributed wetland plants globally (Packer et al. 2017). Due to its highly competitive ability in specific environmental conditions, it often forms common wetland communities in which it is monodominant or dominant. Partly because of its wide geographical distribution and propensity to form monocultures, reed is globally important for biodiversity, ecosystem function, nutrient cycling, and to humans. Some species (e.g. Eurasian bittern *Botaurus stellaris*) are entirely or almost entirely restricted to reedbeds. Reed colonises open water,

and has very high primary productivity and a slow rate of decay: it thus expedites ecological succession from open water to land. Reedbed plays a complex role as a greenhouse gas source and sink (Brix et al. 2001). In the last century, reed has colonised areas outside of its native range (e.g. tidal wetlands of North America - Chambers et al. 1999). A large body of research has developed into its invasion ecology, resulting in calls for its formalisation as a model species for studying invasions (Meyerson et al. 2016). As a habitat and as a material, humans have found a wide range of historical and current uses for reed (Köbbing et al. 2013): for example, reedbeds are used for water treatment, and reed is used for biofuel and for thatch. Due to negative effects, particularly on agriculture, large amounts of money have been spent on eradicating it outside of its native range (Martin & Blossey 2013).

As a globally-distributed (except Antarctica) species, reed has proved highly adaptable (Packer et al. 2017) and is not under threat (IUCN category Least Concern; Lansdown 2017). However, it has a dynamic geographical range (e.g. Van Der Putten 1997), and is often a conservation priority at national scales. In order to understand its range dynamics and to target its conservation, it is important to map reed distribution at larger scales and develop technologies and workflows for applied ecologists and resource managers to continue to do so.

Remote sensing uses variation in reflectance of electromagnetic radiation from the Sun to distinguish objects on the Earth's surface. Plant species vary in electromagnetically distinctive characteristics (e.g. leaf morphology, leaf water content, and the variety and concentration of photosynthetic pigments), which themselves vary through time, and thus can often be distinguished by remote sensing. Remote sensing is particularly useful for the mapping of wetland vegetation, because of its difficult accessibility. Furthermore, the training of classification algorithms is aided by reed's frequent monodominance. Consequently, remote sensing (and aerial photography) has been an asset to the mapping of reedbed for several decades (e.g. Butera 1983). Research questions have been varied: addressing the distribution (e.g. Silva et al. 2008), change in distribution (e.g. Arzandeh & Wang 2003), or biophysical characteristics of reedbeds (e.g. Onojeghuo & Blackburn 2016b).

As for other wetland types, few studies have mapped reedbed at scales larger than individual wetlands, with none to my knowledge mapping this wetland type at the national scale. In Britain, reed is an important component of a variety of plant communities (Packer et al. 2017). Although reedbed is known to be declining in extent on the near European continent, there is no published estimate of reedbed extent, or change in extent, in Britain. In this study I aim to map the current extent of reedbed in Britain, using remotely-sensed data. In doing this, I aim to provide an easily-implemented method

which can be repeated in the future, in order to estimate the change in distribution of this species over time. I use this reedbed map of Britain to run my IBM of the British reed warbler population within (Methods in Appendix; preliminary results in 6.2).

5.3. Methods

5.3.1. Study area, scale and species

I aimed to map all communities where reed is dominant or monodominant (hereafter 'reedbed') in Britain, at 10 m x 10 m scale. There was a wide variety of non-reedbed land cover types in the study area, and so it would not be possible to distinguish presence of reed at the sub-pixel scale through linear unmixing (partitioning the spectral signature of a mixed pixel), e.g.: the edge of an area of reedbed; an area where reed is present but not dominant or monodominant; or a sub-10 m x 10 m area of reedbed. Reed typically spreads by rhizome or stolon (Packer et al. 2017), and so I assumed that the last of these scenarios would be less prevalent than for a typically seed-dispersed species.

5.3.2 Data

I acquired remotely-sensed imagery from the Multi-Spectral Instrument of the Sentinel-2A satellite. Sentinel-2A is one of two satellites in the Sentinel-2 mission, between them collecting high spatial, spectral and temporal resolution images of global terrestrial surfaces (Drusch et al. 2012). These data are available free of charge, on multiple mirrors, typically within hours of capture. Sentinel-2 represents the latest manifestation in the recent trend (Pettorelli et al. 2014) for the increasing relevance of remote sensing for acquisition of spatial environmental information.

Images for all 100 km x 100 km tiles overlapping any of the land surface of Britain (except Rockall), captured during the period 1st October 2015 – 30th April 2017, were downloaded. The long study period was selected because much of Britain frequently experiences cloudy weather, and therefore many passes were required in order to achieve enough non-cloud coverage for the whole study area. All Level-1C Sentinel-2A images, from all 13 channels of the onboard Multi-Sensory Instrument (MSI), in these spatial and temporal ranges, with a given cloud cover of $\leq 5\%$, were downloaded. Tiles of the GDEM digital elevation model (DEM) from the ASTER satellite (1 arc-second resolution) were also downloaded for the study area.

5.3.3 Pre-processing

Atmospheric correction of satellite data was image-based, and achieved by means of a simple dark-object subtraction, implemented in QGIS (QGIS Development Team 2017) using the Semi-Automatic Classification Plugin (Congedo 2016). Reed does not occur below the low tide mark in Britain, and so all sea outside of the low tide mark was masked out for all tiles.

A random forest classification model was created to identify cloud. Random forest is an ensemble approach to classification, constructing many decision trees during training and then taking the mode of those trees during prediction, to avoid overfitting. A random forest (500 trees, three variables tried at each split) was trained (using all 13 bands) on known cloud/non-cloud for one pass of one scene (30UYD on the military grid) (*randomForest* package in R; Liaw & Wiener 2002). Training areas of cloud and non-cloud for this pass were identified by eye. This model had an out-of-bag error rate (mean prediction error for withheld data in a bootstrap sample) estimate of 1.1%. Cloud presence/absence was then predicted using this model across all other scenes, and all predicted cloud pixels were masked out of all images.

I found, as have others (e.g. Skakun et al. 2017), that multi-temporal Sentinel-2A images can be mis-registered with respect to each other by up to three pixels at 10 m x 10 m resolution, and need co-registering in order to compare by-pixel reflectances over time. Images were co-registered using the *coregisterImages* function in the package *RStoolbox* in R (Leutner & Horning 2017). This function (modified here to allow rasters including NA values) makes several candidate linear x/y shifts to a slave image, and selects the shift which maximises the mutual information of the slave image and a master image.

The accuracy of the co-registration function was inspected manually. Although the mis-registration was typically eliminated, for some images the function only marginally reduced the mis-registration, or made no improvement at all. Thus it is probably inevitable that my reflectances are slightly spatially smoothed when summarised over time, and my map probably misses some true narrow reedbeds. The co-registration function failed when the non-NA content of the slave rasters was below 3%, and especially below 1% (e.g. if the tile had been mostly sea, cloud, or was the intersection of the edge of a swathe with a scene). Thus, four scenes for which the non-NA content of the non-master tile never reached above 3% were removed from analysis. Significantly, these scenes contained small areas of land (Scilly Isles, St Kilda, part of Bressay, and a very small area of Cape Wrath) which were not covered by other scenes. This therefore reduces the study area below the full extent of Britain.

5.3.4 Multi-temporal images

At a given time of the year, reed has broadly similar reflectance to other vegetation (e.g. Gilmore et al. 2008). However, across the seasons, reed has a seasonal pattern in reflectance and vegetation indices which is more distinct (e.g. Villa et al. 2013). Thus by using data from more than one season, one can reduce the classification uncertainty for reed: Onojeghuo & Blackburn (2010) found that a reedbed map based on both a summer and winter pass was of higher accuracy than one based on just a single pass.

Ideally I would estimate the temporal reflectance function for reed for each band, and use that to predict reed presence/absence. However, it was not possible to train my cloud classification model to recognise cloud shadow, and so cloud shadows were removed by taking the median reflectance of several cloud-free images. Furthermore, my study was carried out over 11 degrees of latitude. Reed greening is known to vary in date by up to a month over relatively small geographical distances (<5 miles: e.g. Haslam 1972). Villa et al. (2013) found the temporal function of various vegetation indexes to vary considerably with reedbeds' biophysical characteristics. Thus any true reed reflectance function is likely to have considerable variation across my study area.

Instead, to avoid green-brown transitions, I split the year into just two 'seasons': 'summer' (June – September) and winter (November – April). Due to the climatic situation of the study area, and the short study period, few cloud-free images were available for some scenes, otherwise a three- or four-season resolution would have been used: for example, purple inflorescences emerge in late summer, which have a different reflectance from reed leaves. Reed's growth cycle in Britain is completed between April and September (Haslam 1972). The date by which the reedbed becomes dominated by green growth varies latitudinally (pers. obs.), with some southern English reedbeds becoming green in the first weeks of May, while some northern Scottish reedbeds remain brown until the first week of June; likewise some northern reedbeds become brown early in October, while some southern reedbeds stay green until late October. To reduce confusion for the classification model, all data from May and October were removed. Future analyses with more cloud-free and cloud shadow-free data could include latitude as a factor in a temporal reflectance function. The median reflectance was taken for each pixel of each scene for each season respectively.

5.3.5 Training, classification and prediction

173 training polygons (29 reed, 144 non-reed) with a total area of 2,798.4 ha (79.2 ha reed, 2719.2 ha non-reed) were identified from personal knowledge, Google Maps and Google Street View imagery.

These polygons were located on three different scenes (Figure 5.1) to train the model on reedbed across a range of latitude and longitude, and on a variety of non-reed potential confusion habitats. The edges of training polygons were located away from reed/non-reed boundaries in order to avoid errors arising from any remaining mis-registration. Training the classification model using free online imagery avoids one of the two field data collection campaigns associated with remote sensing land cover classification, and the associated financial and time costs. However I acknowledge that some of the training data may not have been monotypic stands of reed: this is a potential source of error in the model.

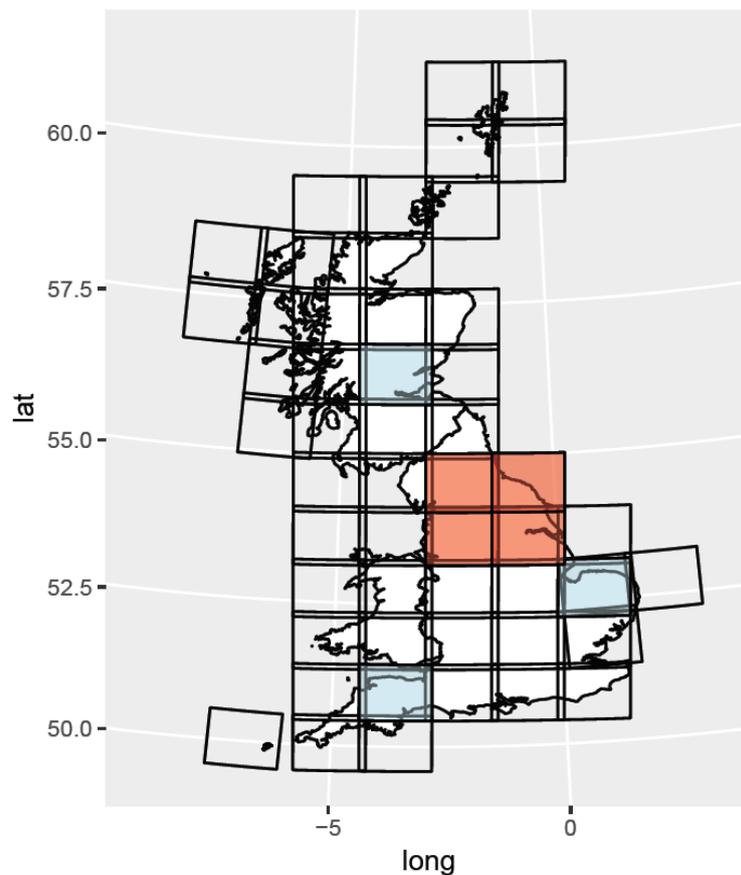


Figure 5.1. Map of scenes contributing to combined dataset, training scenes (blue) and validation scenes (red).

A random forest (500 trees, three variables tried at each split) was trained on known reed/non-reed. The median reflectance (by season) for each of the 13 MSI bands, and two associated vegetation indices, were stacked to form the training data. The model was trained at points sampled at random from within the polygons: 100 points from each polygon; points in the same pixel as another point were then discarded. Differences and ratios, such as NDVI, are often found to improve classification methods solely using reflectances. Using band ratios or indices, rather than raw bands, can avoid noise from natural absolute variation in irradiance over multiple dates (Singh 1989). Various vegetation indices have proved useful in mapping reedbed in previous studies (e.g. Davranche et al. 2010; Villa et

al. 2013), but no single index has proved useful across all survey areas. My combined dataset consisted of seven indices, band ratios and standardised bands (Table 5.1) for each season, and the difference in SAVI and NDWI between seasons.

Table 5.1. Members of the combined dataset.

Quantity	Formula
Enhanced vegetation index (EVI)	$2.5 * ((B8 - B4) / (B8 + (6 * B4) - (7.5 * B2) + 1))$
Green-blue ratio (GB)	$B3 / B2$
Normalised difference vegetation index (NDVI)	$(B8 - B4) / (B8 + B4)$
Normalised difference water index (NDWI)	$(B3 - B8) / (B3 + B8)$
Red-green ratio (RG)	$B4 / B3$
Soil-adjusted vegetation index (SAVI)	$(1.5 * (B8 - B4)) / (B8 + B4 + 0.5)$
Standardised blue band (SBB)	$B4 / (B2 + B3 + B4 + B8)$

Other studies have found important rules with which to discriminate reed from confusion species in their study system. Davranche et al. (2010) found the difference in near-infrared (NIR) of SPOT-5 between March (just before the greening) and June (at the peak of reed growth) was an important criterion for their classification tree. Gilmore et al. (2008) found the NDVI and NIR/red ratio in late summer to be important for classification. However, the rules with which to discriminate land cover types are context-specific: the distinctiveness of a particular bandwidth at a particular point in time depends on the local confusion species, and on the local reflectance function for the study species. Furthermore, my study encompasses a much wider range of confusion species than these studies, because mine covers a much larger geographical area. Onojeghuo & Blackburn (2010, 2016a) found that incorporating texture information improved reedbed classification accuracy. However, their study used much finer resolution data (2.4 m x 2.4 m pixels) to map large reedbeds. I sought to map reedbeds down to the size of one Sentinel 2-A pixel (10 m x 10 m) – often the full extent of a reedbed - and thus texture measures were unlikely to improve my classification accuracy and were omitted.

Using the trained classification model, reed presence probability was predicted across Britain for each scene using the equivalent combined dataset. The probability threshold which maximised the kappa coefficient (Cohen’s kappa, a measure of inter-rater reliability) was calculated for the model: where the probability was above this threshold, reed presence was ‘1’; when below the threshold, reed presence was ‘0’. An iterative process of focussed training and re-prediction to improve visual accuracy was carried out until no improvements could be made to the model.

These predicted maps were aggregated (coarsened – taking the mean) to 100 m x 100 m scale, before being re-projected to WGS 84 UTM zone 30 and mosaicked (joined together side-by-side – taking the

mean where scenes overlapped) together. Slope was calculated from the DEM, and the slope map and DEM were re-projected to the same datum and scale as the predicted reed map. Any cells with a slope of more than 10° or an altitude of more than 470 m (maximum altitude of reed in Britain: Packer et al. 2017) were given a predicted reed presence of '0'.

5.3.6 Validation

Covering 11 degrees of latitude, it was judged unfeasible with available resources to validate the map across the entire study area. The map was validated across four Sentinel scenes in northern England (Figure 5.1). The validation area was selected to maximise geographical distance from the training polygons, to be central in the study area, and to minimise travel costs. Reedbed is a rare habitat nationally, and thus sampling a random selection of pixels will find too few cells with non-zero probability of reedbed occurrence to accurately estimate either commission error (rate of false positives) or omission error (rate of false negatives). Fieldwork was therefore targeted disproportionately towards cells with non-zero probability of reedbed occurrence.

To estimate commission error, 40 hectares were selected from each sub-scene, with 10 randomly selected from within each of the following ranges of predicted proportion (p) of reedbed cover from the predicted map: $p = 0$; $0 < p \leq 0.33$; $0.33 < p \leq 0.66$; $0.66 < p \leq 1$. To minimise travel costs, these were selected from the quarter of the scene with the highest non-zero probability of reedbed occurrence. Each of these hectares was visited, the boundaries delimited (by comparing a satellite map with the cell overlaid with landmarks), and both reedbed (total area of contiguous reed) cover and reed cover (total area of any reed) of the hectare were estimated to the nearest 10%. Then, in each hectare, six 10 m x 10 m cells had previously been randomly selected: where available, three predicted reedbed and three predicted non-reedbed. These 10 m x 10 m cells were visited and reedbed (defined as $\geq 1 \text{ m}^2$ contiguous reed) and reed presence were recorded. Commission error was quantified in two ways. At the hectare-scale, predicted and observed cover were regressed, and the coefficient of determination (R^2) was taken. At the 10 m x 10 m-level, predicted and observed presences were compared, to give an AUC (a performance metric of a classifier across all discrimination threshold values) for each for both reedbed cover and reed cover. Validation fieldwork was carried out from 6th October 2017 to 2nd November 2017.

All data availability query, download, classification, raster manipulation and random selection was carried out in R (R Core Team 2018); pre-processing was carried out in R and QGIS. Due to the large

number of tiles used, some pre-processing tasks and all predictions were distributed over nodes in a small compute cluster and carried out in parallel.

5.3.7 Workflow in Google Earth Engine

Since the previous workflow was carried out, Google Earth Engine ('GEE'; Gorelick et al. 2016) has become widely used. Google Earth Engine uses cloud services to massively scale up computational capability for geospatial analysis, presenting two key advantages over my workflow carried out on a local machine and compute cluster (hereafter 'HPC workflow', after 'high-performance computing'): much greater data storage capacity, and much greater processing speed.

Clearly, carrying out an analysis in GEE provides a product faster. Additionally however, the proportion of data Sentinel-2 data that could be incorporated in my HPC workflow was limited by storage capacity. For example, hard drive space on the local machine limited the number of Level-1C images that could be stored, and so only images with a given cloud cover of $\leq 5\%$ were downloaded. This means that certain scenes only had a small number of cloud-free passes for a given season, and so the temporal resolution of the data on which the random forest could be trained was limited. I therefore repeated the HPC workflow with GEE: to attempt to generate a more accurate reedbed map, and to assess the impact of relaxing data constraints on geospatial analysis.

I used all Sentinel-2 data, from satellites S-2A and S-2B, from the initiation of the Sentinel-2 program on 28th June 2015 until the date of analysis (27th July 2019). Temporal resolution was increased from two periods to four: February-March; June-July; August-September; November-December. The combined dataset comprised NDWI, EVI, SAVI, RG, GB, NDVI and SB4 (inter-seasonal differences in SAVI and NDWI were not used, because there were more seasons). There was the opportunity to further improve the number of passes used and the temporal resolution. GEE imposes user memory limits for tasks, and so there was a trade-off between maximising the number of variables, further increasing the number of images (by relaxing the maximum acceptable cloud cover to $\leq 25\%$) and further increasing the temporal resolution (to eight periods: February, March, June, July, August, September, November and December). One classification model was run for each of these data maximisation approaches, and the accuracy of the resulting map was assessed (see validation process below).

As far as possible, the GEE workflow was kept as similar as possible to the HPC workflow. However, GEE has both extra functionality and reduced flexibility compared to R, and so some aspects were

different. Pixels were sampled within polygons (rather than points within polygons), and so it was not possible to balance sampling between categories. It was not straightforward to buffer a raster land mask in GEE, so I used the British shoreline rather than the shoreline plus 100 m buffer – therefore some coastal reedbeds may be missed. The GEE facility to predict probabilities with random forest was not working at the time of analysis, and so presence/absence was predicted. I used GEE's cloud and cirrus removal tools. Because I varied the number of variables between the three approaches, I set the random forest to the default setting of number of variables per split: the square root of the number of variables.

During preliminary analyses, Sentinel-1 synthetic aperture radar data were also included, but did not improve the accuracy of the classification. This was potentially due to the high noise even after processing: inspection of the processed data revealed greater variation in backscatter within than between habitat types.

The validation fieldwork had already taken place before the GEE workflow was carried out. The validation data were used to assess the accuracy of the GEE reedbed map. The GEE reedbed maps and the validation data are both at 10 m x 10 m resolution, but they have slightly different origins and projections. To assess accuracy at the hectare scale, the GEE reedbed map was projected onto the validation map, and predicted reedbed cover was regressed against observed reedbed cover. To assess accuracy at the 10 m x 10 m cell scale, the centre points of the 10 m x 10 m validation cells were re-projected onto the GEE reedbed map, and the predicted and observed presences were compared. Finally, as presence/absence was predicted (rather than probabilities), AUC could not be calculated for the GEE reedbed map.

5.4 Results

5.4.1 HPC workflow

5.4.1.1 Structure of random forests

For the HPC workflow, visual inspection of candidate random forests showed that balanced and unbalanced random forests, and random forests with slightly different training areas, had similar areas of true positives and slightly different areas of false positives. Thus, in order to reduce the area of false positives, two different random forests ('RF1' and 'RF2') were used for the final model, and the map was created using the minimum predicted reedbed probability of the two random forests, for each pixel.

The three most informative variables in RF1 were winter RG, summer EVI and winter NDWI (Figure 5.2). The three most informative variables in RF2 (considerably more informative than the others) were winter RG, winter NDWI and winter GB. Kappa was maximised at a probability of 0.585 – this was used as the threshold for classifying 10 m x 10 m pixels.

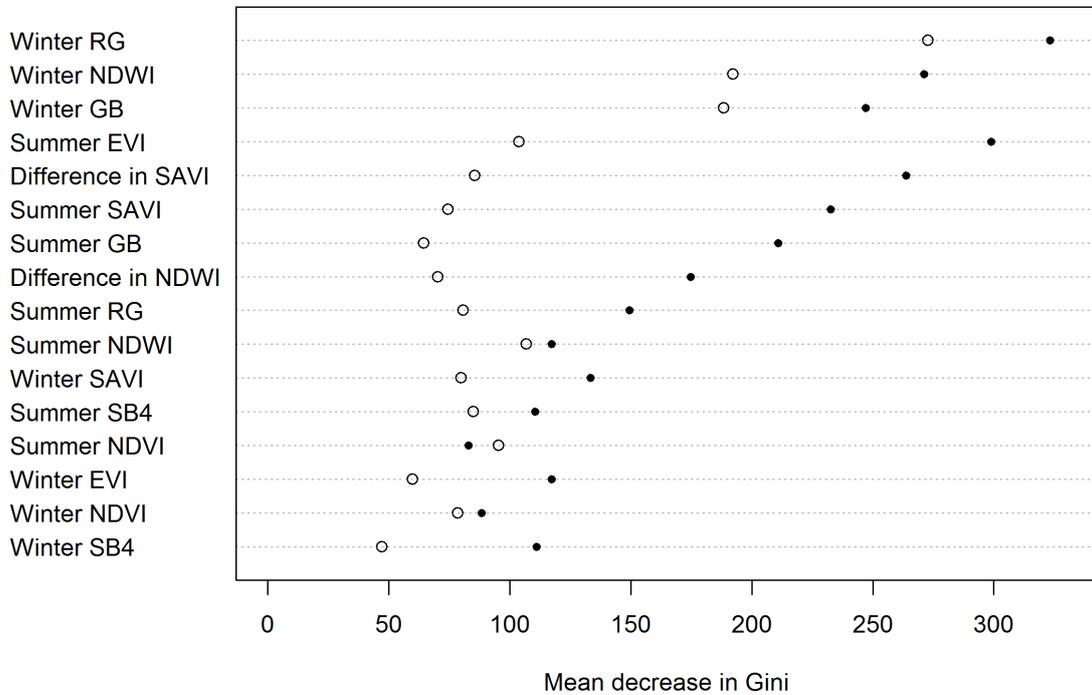


Figure 5.2. Importance of variables in the two random forests contributing to the final map (filled circles = RF1; open circles = RF2), HPC workflow. A higher decrease in Gini denotes a greater variable importance.

5.4.1.2. Accuracy of HPC reedbed map

Files from 541 passes were acceptable for use after pre-processing (mean 10.82 passes per scene, range 3-22). Each scene had at least one winter and one summer pass. The random forests were predicted over indices derived from these data. An example of the predicted 10 m x 10 m map, before aggregation and mosaicking, is given in Figure 5.3.

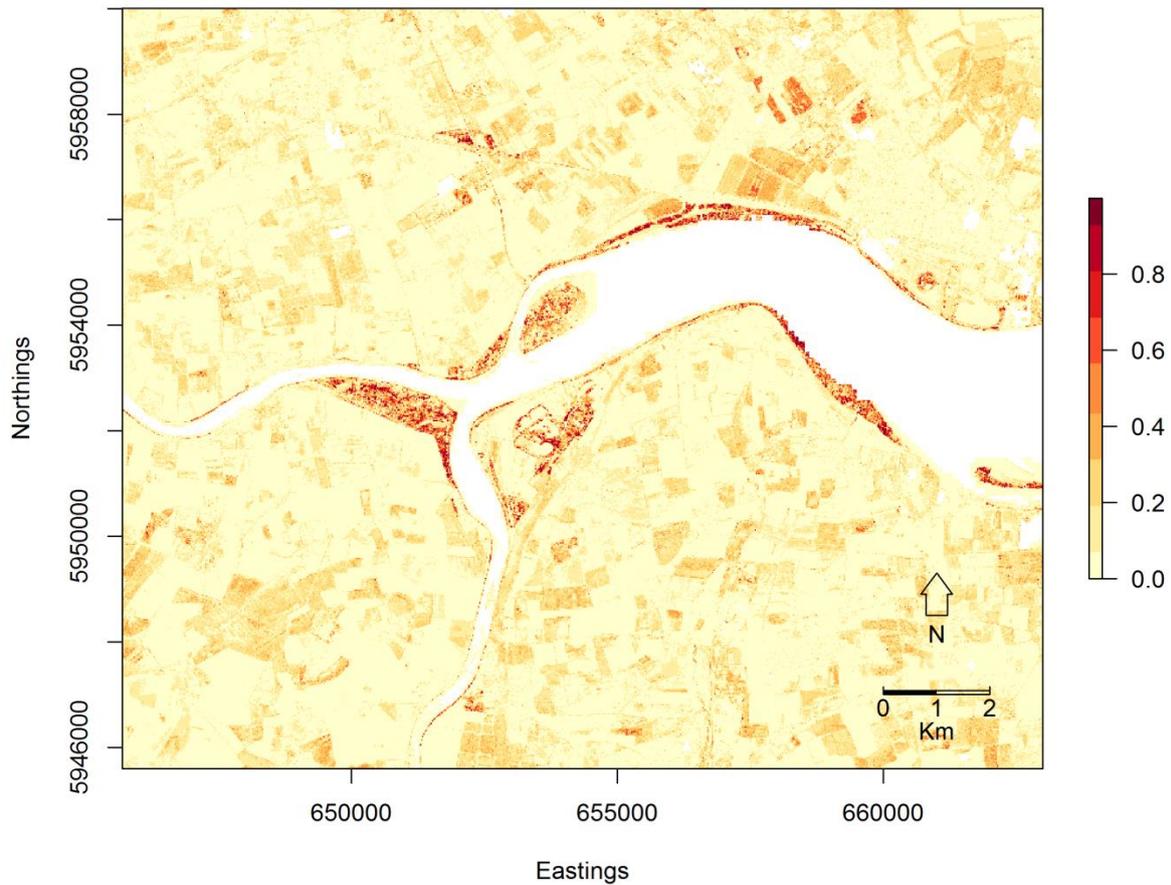


Figure 5.3. Predicted reedbed map (colour = predicted probability of reedbed presence at 10 m x 10 m scale; white = NA) of the upper Humber estuary, Britain, HPC workflow.

When tested against the training data, the classification model had near-perfect discrimination: the two random forests used respectively had AUC values of 0.9997 (RF1) and 0.9983 (RF2) against the final map (Figure 5.4, black and red lines). For one validation scene, only eight squares had a predicted probability of $0.66 < p \leq 1$. Two validation squares from other scenes were not safely accessible, leaving 154 validation squares visited in total. When tested against the validation data, the classification model had much lower discrimination: the combined model had an AUC of 0.6708 (Figure 5.4, blue line). The overall accuracy of the map at the 10 m x 10 m scale was 65.1%, but the commission error for reedbed was very high: the majority of predicted reedbed was not reedbed (Table 5.2a).

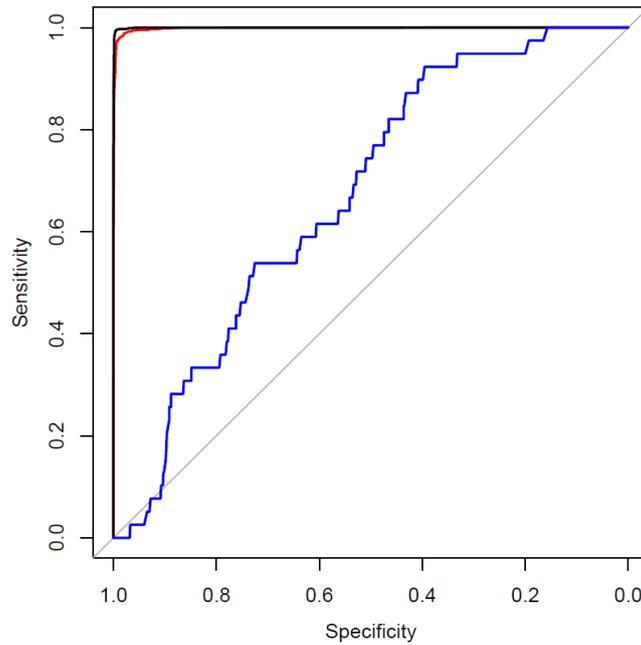


Figure 5.4. Receiver operating characteristic (ROC) curve for 10 m x 10 m pixels, HPC workflow: black, map against RF1 training data; red, map against RF2 training data; blue, map against validation data. The ROC describes the diagnostic ability of a classifier across all discrimination thresholds; the AUC ('area under the curve') is the total area under the ROC.

The commission error for reedbed remained very high at the 100 m x 100 m scale (Table 5.2b), although slightly lower than at the 10 m x 10 m scale. The confusion matrix was the same regardless of whether the 100 m x 100 m map had been aggregated by mean or by sum. The class frequency of predicted reed is deliberately over-represented in my sample (see Methods), and so overall accuracy and omission error are not presented for the 100 m x 100 m scale map, because they would be respectively over- and under-estimated.

Table 5.2. Confusion matrix for reedbed map at: a) 10m x 10m scale; b) 100 m x 100 m scale (proportional reedbed cover converted to binary presence/absence), HPC workflow.

		a) 10m x 10m scale		
		Predicted		
		Reed	Not reed	Omission error
Observed	Reed	21	18	46.1%
	Not reed	297	588	33.5%
	Commission error	93.4%	3.0%	
		b) 100m x 100m scale		
		Predicted		
		Reed	Not reed	
Observed	Reed	11	2	
	Not reed	103	38	
	Commission error	90.3%	5.0%	

There was no relationship between predicted and observed reedbed cover at the 100 m x 100 m scale (Figure 5.5a). False positives were non-randomly spread among habitat types (Chi-square test, $p < 0.0001$; Table 5.3). Arable and other open habitat comprised 61.7% of the sample squares but 73.8% of the false positives.

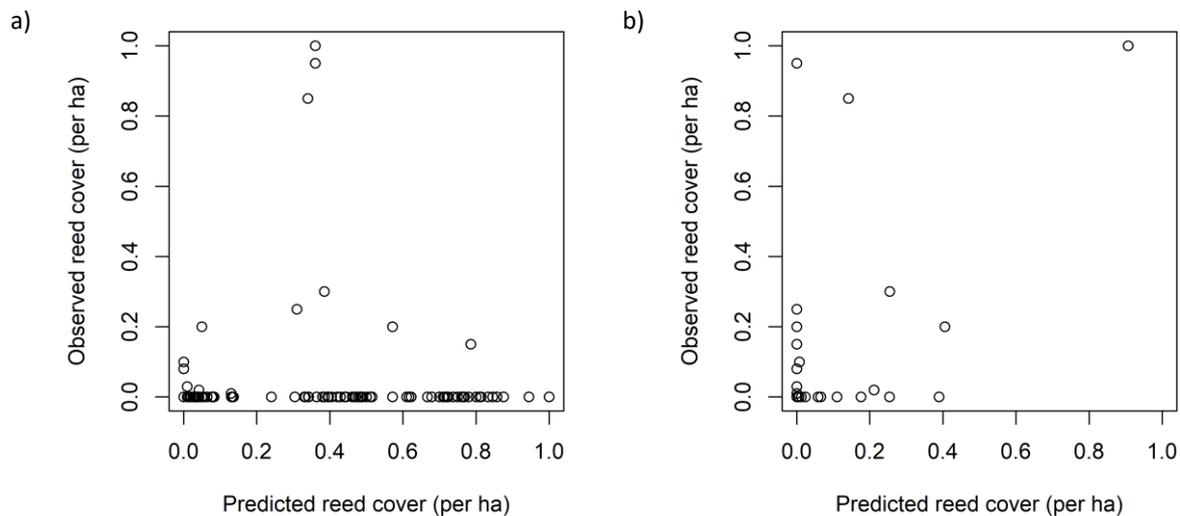


Figure 5.5. Relationship between predicted and observed 100m x 100m pixel reedbed cover: a) HPC workflow, b) GEE workflow.

Table 5.3. Confusion habitats, HPC workflow.

Non-reed habitat	Negatives and true positives	False positives	Proportion of habitat false positives
Arable	8	51	0.864
Conifer	0	2	1.000
Deciduous woodland	4	4	0.500
Freshwater	3	2	0.400
Grass farmland	18	14	0.438
Mixed woodland	0	3	1.000
Not recorded	0	1	1.000
Other open habitat	11	25	0.694
Urban	6	1	0.143

5.4.1.3 Distribution of reedbed

The distribution of reedbed in Britain estimated using the HPC workflow is presented in Figure 5.6. The total area predicted to be covered by reedbed, including known error, is 25,790.5 ha. Assuming 93.4% commission error and 46.1% omission error, I estimate that 3,684.5 ha of Britain is covered by reedbed.

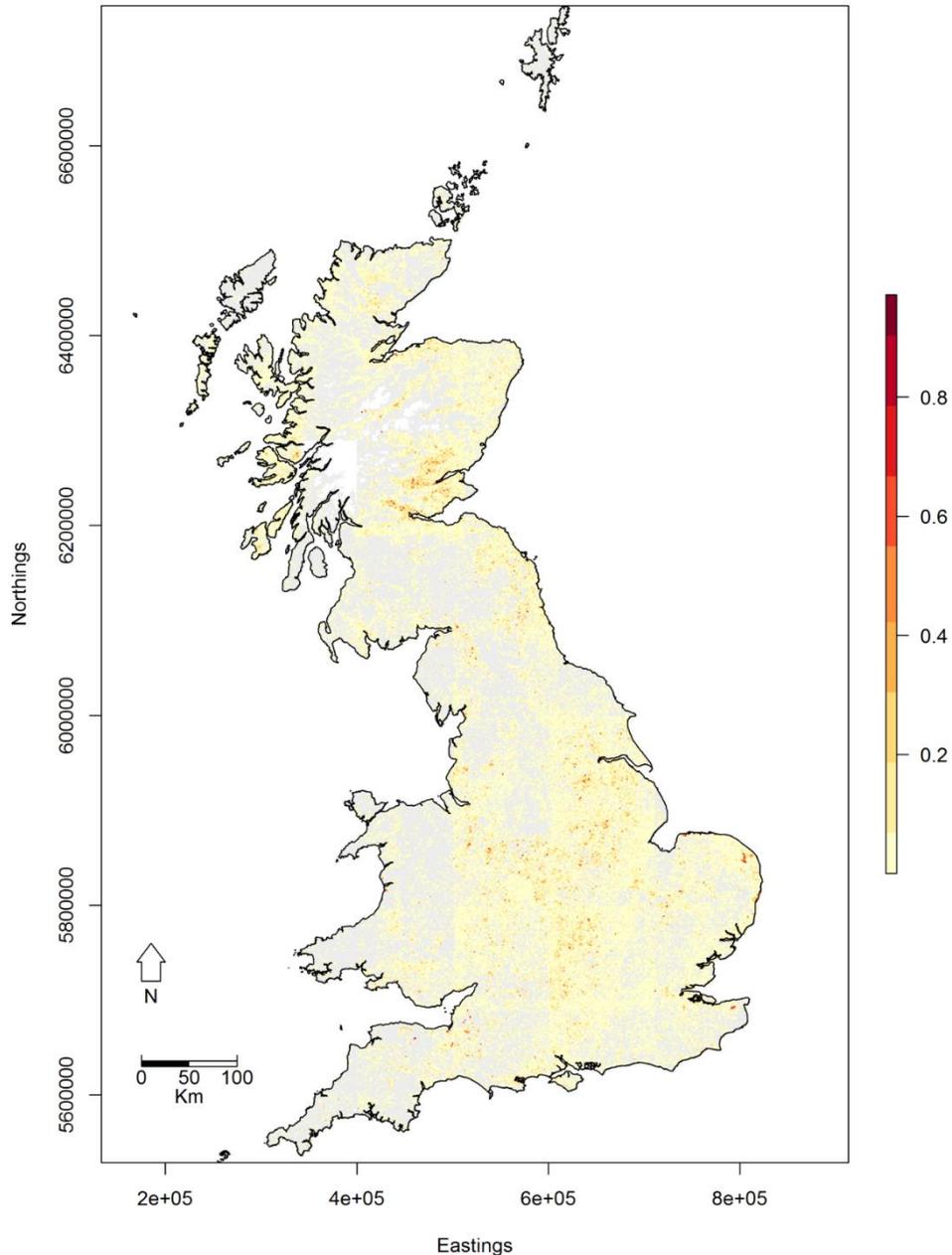


Figure 5.6. Predicted reedbed map (colour = maximum per-hectare cover at 1 km² scale; grey = 0; white = NA) of Britain, HPC workflow.

5.4.2 GEE workflow

It was not possible to balance sampling between categories in the GEE workflow. Therefore only one, unbalanced, random forest was run for each set of criteria. Of the three data-maximisation approaches carried out (maximising number of variables, number of images or temporal resolution), maximising the number of variables gave both the lowest commission error and the lowest omission error: this approach was used. 5,184 images were used, 9.6 times as many as used in the HPC workflow.

Table 5.4. Confusion matrix for reedbed map at: a) 10m x 10m scale; b) 100 m x 100 m scale (proportional reedbed cover converted to binary presence/absence), GEE workflow.

a) 10m x 10m scale				
		Predicted		
		Reed	Not reed	Omission error
Observed	Reed	10	29	74.4%
	Not reed	17	868	1.9%
	Commission error	63.0%	3.2%	
b) 100m x 100m scale				
		Predicted		
		Reed	Not reed	
Observed	Reed	6	7	
	Not reed	10	131	
	Commission error	62.5%	5.1%	

At the 10 m x 10 m scale, the best reed map produced by the GEE workflow had an overall accuracy of 93.8%. This is higher than the overall accuracy of the HPC workflow 10 m x 10 m reed map, but would be very similar to the overall accuracy of a map classifying all the validation points as non-reed (94.1%). The commission error (63.0%) was still high (Table 5.4a), but considerably lower than that of the HPC workflow reed map (Table 5.2a). However, the omission error was considerably higher than that of the HPC workflow reed map: nearly three-quarters of observed reed was predicted not to be reed (Table 5.4a). The increase in omission error is proportionately larger than the reduction in commission error.

At the 100 m x 100 m scale (Table 5.4b), the best reed map produced by the GEE workflow had a similar accuracy to the 10 m x 10 m scale map (Table 5.4a). There was a weak positive relationship ($R^2 = 32.5\%$) between predicted and observed reed cover (Figure 5.5b), although this is again likely to be due to the largely correct identification of non-reed, and the high true class frequency of non-reed.

5.5 Discussion

I demonstrate that remotely sensed data can be used to predict the presence of a wetland habitat, with better-than-random accuracy, hundreds of kilometres from the training area. My estimate (3,684.5 ha) is the first published estimate of reedbed extent in Britain. However, my map was far from perfect. Remote sensing studies focussing on training and predicting within individual wetlands have had much higher accuracy in identifying reedbed than my study (e.g. Davranche et al. 2010): my map had very high commission error, and relatively high omission error in comparison. I argue that this loss of accuracy mostly stems from the much larger geographical area covered by my study. Repeating my workflow in Google Earth Engine with almost an order of magnitude more data did not

improve the accuracy, but it helped us rule out some of the possible causes of the low accuracy: I discuss these issues and potential solutions below.

The first classification issue arising from the large geographical area relates to the relative frequency of reedbed and other habitats within it. Reedbed mapping has been successful on small geographical scales, but some of this success is likely to arise from the restricted set of potential confusion habitats. My study area, spanning 11 degrees of latitude, covers a very wide range of semi-natural and man-made habitats: much of Britain is dedicated to cultivation of grasses *Poaceae* for arable and animal agriculture. This provides a larger set of habitats with similar reflectance profiles to reed than in a single wetland. These confusion habitats can potentially be incorrectly classed as reedbed, increasing the commission error. Also, including these confusion habitats in training data as non-reed potentially makes reedbed less distinctive, causing omission error.

A similar issue arises from the low frequency of reedbed within my study area. Here, reedbed is very rare relative to its confusion habitats. In this situation, even with a very low type I error rate the total area of incorrect commissions should dwarf the total area of correct commissions. Even though many false positives were indeed arable, my total predicted reed area of Britain is just 0.05% of the size of the total arable area of Britain (6,213,777 ha: Morton et al. 2011). When the target habitat is rare, even a low relative false positive rate can increase the absolute commission error to make the map almost unusable.

There is error in reflectance data, presumably due to instrument error, variation in solar radiation, or error in pre-processing functions such as cloud removal. This becomes more of an issue when the study area comprises multiple scenes. This was evidenced in my study by the presence of satellite swath boundaries and scene boundaries in the geographical distribution of predicted reedbed (e.g. Figure 5.6). Massively increasing the number of passes in the dataset (in order to bring the estimated median reflectance or reflectance-derived measure closer to the true median) with Google Earth Engine did not resolve this. The relativity of optical remotely-sensed data therefore limits the possibility for predicting outside the swath in which a classification model has been trained.

There are several potential causes of true reedbeds being missed by my classification method. The first of these causes relates to the uniqueness of reedbed's temporal reflectance function. There is systematic variation in reedbed's temporal reflectance function across my study area (Packer et al. 2017). I deliberately ignored months within which I know that reedbed is at a different stage of growth

at different latitudes; however, there may be additional important systematic variation in reflectance outside of these months. This potentially makes reedbed's temporal reflectance function so variable as to overlap with that of other habitats, preventing a classification algorithm from discriminating between them. This seems to be a particularly important issue for reedbed in my study area, because increasing the temporal resolution of the data (using Google Earth Engine) did not improve the accuracy of the map. This issue could theoretically be resolved by incorporating non-optical data, such as synthetic aperture radar (SAR), hyperspectral data or LiDAR; other studies have found that (at least at small geographical scales) reedbed has a unique LiDAR signature. However, including SAR data from the Sentinel-1 did not improve the Google Earth Engine map, and no freely available hyperspectral or LiDAR products exist for the whole of Britain.

Reedbed is an ephemeral habitat, rapidly succeeding other habitats and being succeeded, and some true reedbeds may have become established only after the start of the satellite imagery used. This source of error could have been reduced by using data from a shorter time frame, but that would have reduced the size of the total dataset, potentially reducing the accuracy in other ways.

Patches of reedbed filling less than a full 10 m x 10 m Sentinel-2 pixel could not be detected by my technique. Reed typically grows in well-lit environments, but will also grow in partial shade (Packer et al. 2017): remotely-sensed optical data cannot be used to detect shaded vegetation. Some small areas had to be discarded for my co-registration technique, or did not have any cloud-free passes: any reedbed in these pixels could not have been detected. Furthermore, there was some (unknown) error in my co-registration technique, meaning that some 10 m x 10 m areas were incorrectly attributed the reflectance of an adjacent 10 m x 10 m area. Finally, some areas (e.g. large areas of Argyll) did not have enough cloud-free scenes within the study period to create a map; this was improved (not shown) in the Google Earth Engine workflow with its longer study period.

Commission errors are non-randomly distributed across true vegetation types, with high commission error in arable land use: the utility of my map could be improved by masking such confusion habitats out with agricultural maps, although this may eliminate some reedbeds which exist in agricultural drains alongside fields.

5.6 Conclusion

My study demonstrated that it is possible to map wetland habitat without a field training data collection campaign, exclusively using open source software and free satellite data. Although

repeating my workflow in Google Earth Engine did not improve the accuracy, it brought the total analysis time down from several weeks to less than a day, and eliminated the need for large data storage capacity. However, some sources of error remain which are not easily solved with a 'big data' approach. It is likely that such a workflow as mine will improve in classification accuracy in the future as reflectance error is reduced – both on the satellite and with more advanced pre-processing techniques. The number of confusion habitats and systematic variation in temporal vegetation reflectance functions probably place upper limits on the size of a geographical area that can be classified accurately with such a workflow.

Although the reedbed map was of low accuracy, it was better than random and the only existing reedbed map of Britain. Much of the inaccuracy arose from confusion habitats, particularly arable farmland; therefore to use the reedbed map in the IBM (preliminary results presented in 6.2) I masked it using an existing map of arable farmland (described in the Appendix).

6. General discussion

6.1 Introduction

In this chapter I synthesise results from the analyses carried out in this thesis, and from preliminary results from analysis of the IBM (6.2), to draw conclusions as to the mechanisms underlying reed warbler's range dynamics in Britain (6.3). I then go on to explore potential implications of my work for the fields of range dynamics and climate change adaptation (6.4). Finally, I review the limitations of my study and make recommendations for future research (6.5), both specifically for understanding recent range change in reed warbler in Britain, and for understanding the role of dispersal in range change across species.

6.2 Individual-based model of reed warbler in Britain: preliminary results

6.2.1 Introduction

In ecology, advances in understanding ecological systems are traditionally made through inductive reasoning from observations. Simulations are mostly used to test that understanding against observed data or make predictions. A rarer use of simulations in ecology is to explore the dynamics of systems. In recent years, spatial simulation models of populations have been increasingly used in studying range dynamics, neatly complementing inferences drawn from data (e.g. Fraser et al. 2015). One class of simulation models used in simulating range dynamics is IBMs. IBMs simulate populations as being composed of individuals, each of which is given a set of state variables (e.g. spatial location, age) and a set of behaviours (e.g. dispersal ability, number of eggs produced per year). IBMs are well suited to simulating range dynamics because they incorporate both population dynamics and dispersal, and can improve realism by allowing for individual variation in key traits, and for stochastic processes to occur at the individual level (Bocedi et al. 2014).

Species differ in their range dynamics due to extrinsic factors such as history, local geography and circumstance – but also due to their intrinsic traits. The behaviour of large systems emerges from the rules by which the agents within the system operate. In the same way, species' range dynamics emerge from the way individuals of those species breed, disperse and die. Differences in range dynamics between species therefore may partly (ignoring extrinsic factors like spatial variation in habitat loss) arise from differences in the rules and parameters describing individuals' breeding, dispersal and demography. For example, a species with high productivity might be limited in its rate of range expansion by its low dispersal propensity or distance. In such a species, relatively small changes in dispersal parameters should cause a relatively large change in the rate of range expansion.

We can better understand how species' range dynamics emerge from their ecology by experimenting with simulated populations (Grimm and Railsback 2005).

In order to better understand the role of dispersal in reed warbler's recent range change in Britain, I developed an IBM of the reed warbler population in Britain. This model was structured and parameterised according to the reed warbler literature and my own analyses of reed warbler dispersal (Chapter 3) and demography (Chapter 4). I ran the IBM in the reedbed map I made of Britain (Chapter 5), and I present in this section some preliminary results from analyses of the behaviour and patterns of the simulated British reed warbler population.

During its recent range expansion, reed warbler was in some ways unable to track its climate space as it moved polewards, and even after a slower rate of warming the species was unable to regain the climate space it occupied in the late 20th century (Chapter 2). This is not surprising, given that only 5.3% of individuals disperse northwards fast enough to match the highest rate of shift in climate space (Chapter 3). However, it is not intuitive whether reed warbler's ability to track its climate space would be improved by a slight change in dispersal (e.g. greater dispersal distance) or in demography (e.g. higher survival probability). In my first analysis of the IBM, I estimate the sensitivity of reed warbler's range size to changes in dispersal and demography, with a view to ascertaining which process plays the greater role in reed warbler range change and limitation.

Next, reed warbler has multiple relationships with climate that are relevant to range limitation. Firstly, reed warbler occupancy is strongly positively related to breeding season temperature in the current year (Chapter 2). Secondly, reed warbler egg survival and chick survival are positively related to breeding season temperature, while adult survival is negatively related to breeding season temperature. In isolation, the positive relationships with climate for occupancy and nest survival could each limit reed warbler's range, but it is not clear what relative role they would have (in terms of the position of the range limit). Conversely, the negative relationship between adult survival and temperature might allow reed warbler to spread further north than it would if no such relationship existed, but it is not intuitive to what extent this might change a range limit set up by occupancy or nest survival. To explore the role of each relationship between a demographic or dispersal parameter in setting up the range limit, in my second analysis of the IBM I simulate the range size and the location of the range limit under five scenarios: one with no parameter linked to temperature, one each with settlement probability (positive), nest survival (positive) or adult survival (negative) linked to temperature, and one with all three parameters linked to temperature.

Foppen et al. (2000) simulated reed warblers in a system of reedbed patches using an IBM, to understand source-sink dynamics in a metapopulation. As far as I am aware, the IBM presented in this chapter is the second IBM used to simulate reed warbler populations. As is appropriate for its purpose, this IBM includes more detail and operates at a larger spatial and temporal scale than the IBM used by Foppen et al. (2000). I present results from the two analyses in Section 6.2.2; the details of the IBM, and methods for analysis, are given in the Appendix. The conclusions are preliminary, because more exploration of the simulations is required for confidence that the results are realistic.

6.2.2 Results

6.2.2.1 General performance of the IBM

Preliminary simulations of the reed warbler population of Britain were somewhat realistic in terms of total range extent, with the population on a given simulation neither fully colonizing all available reedbed, nor frequently going extinct. Simulated population sizes were of a similar order of magnitude to the current British reed warbler population. As in real populations (Borowiec 1992), some males remain unpaired for the whole season. Even without any relationship between climate and demography or dispersal, the rate of colonisation of northern Britain was relatively slow, sometimes taking hundreds of years: the range typically had not reached equilibrium by the end of the simulation.

6.2.2.2 Sensitivity of range size to demography and dispersal

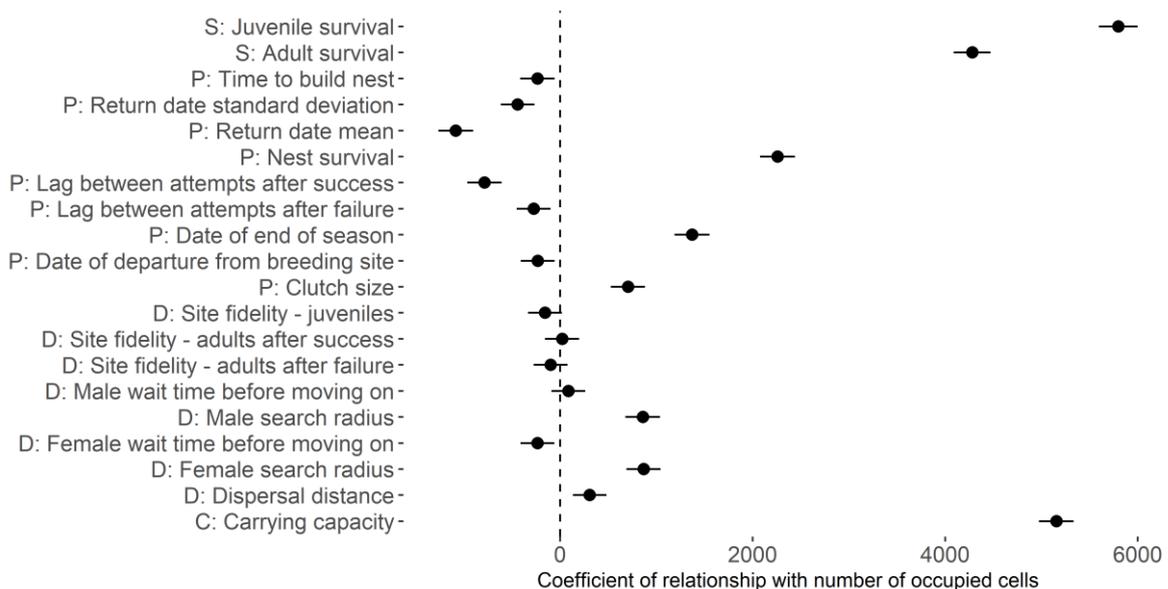


Figure 6.1. Coefficients (mean and standard error from 1000 IBM runs; see Appendix) of relationships between demographic parameters and range size.

70.2% of variation in range size was explained by variation in demographic and dispersal parameters, when no parameter was linked to climate (Figure 6.1). Juvenile survival, adult survival and carrying capacity all had very strong positive effects on total range size. The next most important parameters were nest survival and the parameters for the start and end of the season. The remaining parameters were more minor in influence. Within dispersal parameters, search radius (both sexes) had a larger effect on range size than did dispersal distance or either sex's wait time before moving on.

6.2.2.3 Role of individual parameters in range limit and size

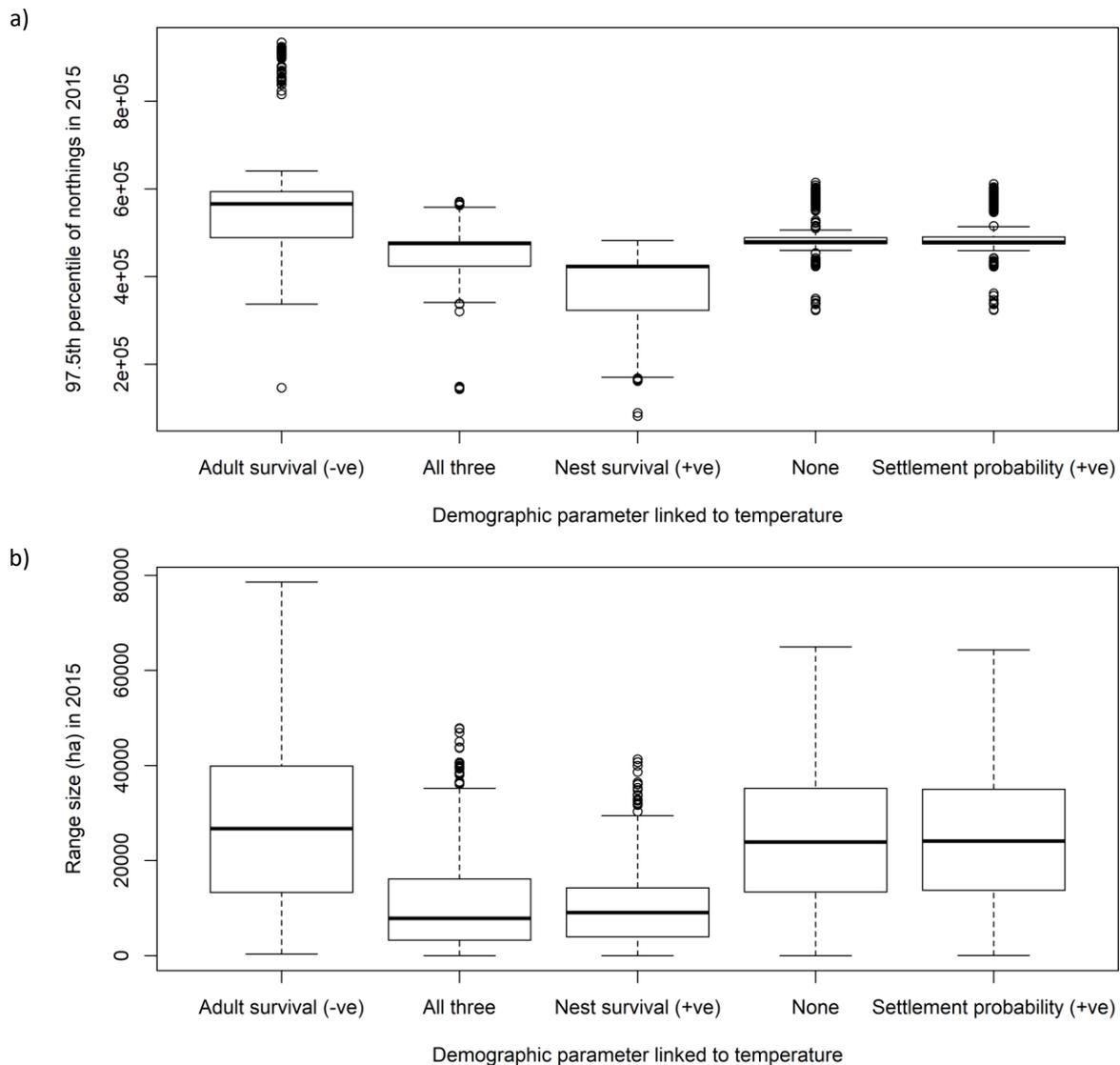


Figure 6.2. Effect of demographic climate link on (a) northern range limit and (b) range size. Boxplots show spread of each summary variable in final year of 1000 runs, run separately for each climate link (see Appendix).

The identity of the demographic or dispersal parameter linked to climate had an important effect on range and population size (Figure 6.2); more so for the northern range limit (linear model; $F_{4, 4359} = 766.6$, $p < 0.001$, $R^2 = 0.412$) than for range size (linear model; $F_{4, 4361} = 332.6$, $p < 0.001$, $R^2 = 0.233$).

Climate-linked settlement probability made little difference to summary statistics. A positive relationship between temperature and nest survival suppressed range size and drove the northern range limit south. A negative relationship between temperature and adult survival made little difference to range size, but drove the northern range limit north. Without a climate link to adult survival or nest survival, there was little variation between runs in the northern range limit.

6.2.3 Discussion

The demographic and dispersal parameters with the largest effect (all positive) on simulated reed warbler range size were juvenile survival, adult survival and carrying capacity. Overall, dispersal parameters were relatively unimportant in determining range size in comparison to survival, productivity and carrying capacity. This suggests that while few reed warblers disperse fast enough to match the recent rate of shift of climate space (Chapters 2 & 3), the rate of reed warbler range spread could be increased more readily by minor changes in demography than minor changes in dispersal. This is consistent with other studies which have found abundance trend to be more important than dispersal ability in determining range size trend (Mair et al. 2014).

Survival and productivity have different effects on metapopulation persistence and spatial dynamics (Howe & Davis 1991). I found that survival parameters had a stronger relationship with range size than did productivity. This is in common with Julliard (2004), who found that reed warbler population growth rate is more sensitive to survival than productivity (also see Johnston et al. 2016; Meller et al. 2018). There was variation in the sensitivity of range size to the different dispersal parameters. Range size was more sensitive to male or female search radius than to dispersal distance, which is surprising given that the spatial scale of the latter is much larger. Simulated reed warbler populations expanded slightly more and had a much more northerly range limit when adult survival was negatively linked to climate. This suggests that reed warbler's population expansion has to some extent been enabled by this relationship.

The simulated reed warbler population had a much more southerly range limit when nest survival was positively linked to temperature than when settlement probability was positively linked to temperature. A positive relationship between settlement probability and climate made no clear difference to the range size or the location of the range limit. This could mean that demography has a stronger influence on the range limit than does settlement probability; alternatively the same pattern could arise from differences between the parameters in the slope used for the relationship with temperature. Another possibility is that the mechanism by which climate is related to settlement

probability in the IBM is unrealistic: in the current formulation, having encountered a climatically unsuitable cell, male reed warblers only search within their local area (square with 500m to 2,000m edge) for a climatically suitable area. On encountering climatically unsuitable habitat, reed warblers might instead move on in steps of greater distance, or in a non-random (e.g. south) direction; this aspect of reed warbler's ecology is poorly known.

The IBM exhibited some realism, but not all the dynamics were necessarily realistic. For example, relatively little of the full extent of available habitat was colonised under any scenario. This could be due to mischaracterisations of the structure of the IBM: some aspects of reed warbler dispersal ecology in particular (e.g. how individuals search for new sites, the role of spatial inaccuracy in migration in dispersal) remain poorly known. Similarly, unrealistic simulations could arise from incorrect parameter values in the IBM, or the range over which parameter values were varied may have been too wide or too narrow for particular parameters. Furthermore, the relationships with climate used in the IBM were linear, which should generate different range dynamics to the logistic relationships estimated from the data in Chapters 2 and 4. Alternatively, unrealistic simulations could be due to inaccuracies in the estimated total extent, location or aggregation of reedbed in the map, or due to the fact that reedbed distribution was assumed to be static over time. Some simulated reed warbler populations in the far north of Britain were settled when adult survival was linked to temperature, suggesting that at relatively low temperatures, nonsensically high values of adult survival (although not above 1) are achieved. Further work to refine and check the IBM, improve the reedbed map, and compare simulated and observed reed warbler distributions (e.g. van der Vaart et al. 2015) are likely to improve its accuracy and utility.

6.3 What is the role of dispersal in recent range change in reed warbler in Britain?

6.3.1 Ecological processes in reed warbler range dynamics

In this study I sought to understand the role of dispersal in reed warbler's range dynamics in Britain. Here I discuss the cause of the range limit, followed by the cause of the range expansion, before exploring the role of dispersal in range dynamics in general.

It has long been proposed that reed warbler is limited by climate in Britain (Sharrock 1976). I found that climate sets up reed warbler's range limit in Britain, probably through settlement probability (Chapter 2). The strong positive relationship I found between reed warbler occupancy and breeding season temperature was also found near reed warbler's cool range edge in Finland (Virkkala et al.

2005). There was little evidence of a demographic contribution to the limit in terms of a relationship between occupancy and the previous year's temperature. The positive relationship I found between occupancy probability and breeding season temperature could be due to late reed phenology in cold locations, given that both reed growth and reed warbler occupancy probability are strongly reduced below 14°C (Vafidis 2014). Alternatively, it may be that invertebrate availability or diversity are too low in cold reedbeds; for example, reed-specialist moth diversity declines to the north and west of Britain (Quinn et al. 1997). However, invertebrate availability or diversity are unlikely to limit reed warbler: reed warblers are opportunistic feeders, with a broad trophic niche, and cold reedbeds beyond reed warbler's range edge do support some insectivorous passerines, including the closely-related sedge warbler (Figure 6.3).

Although egg survival and chick survival were positively related to climate, these components of productivity did not decline to the range edge (Chapter 4). I therefore did not find any evidence that demography plays a role in limiting reed warbler's range in Britain. However, I was not able to explore some crucial aspects of reed warbler's demography, such as the number of breeding attempts (which could vary with season length), and juvenile survival. Nevertheless, across Britain occupancy was much more strongly related to the breeding season temperature of the current year than of the previous year, suggesting that if productivity or juvenile survival decline towards the range edge, the contribution to the range limit of this is only minor. Interestingly, survival was negatively related to temperature (Chapter 4), and preliminary simulations (6.2) suggest this may have allowed reed warbler to maintain a more northerly range limit than would be achieved without such a relationship. In Chapter 1 I characterised two generic causes of range limitation: insufficient immigration into the un-colonised area, and insufficient potential births-to-deaths ratio in the un-colonised area (Figure 1.4). Given the evidence in this thesis, I propose that reed warbler's range is limited in Britain by insufficient immigration into the un-colonised area.

Reed warbler expanded its range in the direction of climate change (Chapter 2). Given that reed warbler did not catch up to the far edge of climate space, it seems that reed warbler's range change can be explained by its range gradually equilibrating with climate space. In terms of the generic causes of range expansion I characterised in 1.4.3.5, I propose therefore that reed warbler's range expanded due to newly-sufficient immigration into the un-colonised area, rather than increased potential births-to-deaths ratio in the un-colonised area.

Reed warbler's range expanded at an unusually high rate relative to other species in Britain (Mason et al. 2015). Only long-distance dispersing reed warblers matched the rate of spread of the range edge (Chapters 2, 3): therefore the rate of reed warbler's range expansion (in terms of the range edge) has been enabled by rare long-distance dispersal. Although reed warbler's natal site fidelity was relatively low (at least within 1km of the natal site), only long-distance dispersing reed warblers matched the rate of range expansion (Chapters 2, 3): therefore the rate of reed warbler's range expansion has been enabled by long-distance dispersal. However, I only sampled from within the range core: the dispersal kernel may be different at the range edge, where a greater proportion of individuals might be highly dispersive (e.g. Dytham 2009). Although the possibility has been suggested that reed warbler's range expansion in Scotland has been caused by Scandinavian birds (Robertson 2001), reed warbler's dispersal kernel is at least sufficient to explain its rate of expansion in terms of a gradual colonisation from England.

Although reed warbler's range edge tracked climate space, the bulk of the population lagged behind (Chapter 2). Emigration rate is modified by demography, in terms of the number of dispersers produced. Preliminary simulations indicate that reed warbler's range size is more sensitive to demography than dispersal (6.2). Perhaps, therefore, at reed warbler's population growth rate, newly-established populations in the un-colonised area take too long to build to a sufficient size that they themselves can contribute significant numbers of dispersers. The two Scottish reedbeds whose colonisation by reed warbler was described in 1.4.2 differed considerably in distance from other reed warbler populations, but not in relative breeding season temperature (not shown here). The more southerly site, close to reed warbler populations in Cumbria, grew in size much more rapidly than the more distant site (Robertson 2001; Bruce 2007). It could be, therefore, that reed warblers are quick to occupy sites in climatically suitable habitat, but the populations then grow only slowly without supplementary immigration.

There were further suggestions of the potential role of demography in reed warbler's range expansion. The range centroid moved only slowly during a period when occupancy thinned out across the range (Chapter 2), perhaps due to a coincident decline in extent of mangrove forests in the wintering range (Dieye et al. 2013) impacting survival. Furthermore, the rate of movement of the range core was much higher during a period over which fledglings per breeding attempt increased (Chapters 2, 4). Although these variations in rate of movement in the range core could not be analysed in relation to detailed demographic data, they are at least consistent with potential demographically-caused changes in emigration rate.

The fragmentedness of reedbed might have influenced the rate of range spread in reed warbler: the simulated reed warbler population was particularly slow to colonise northern Britain, even without any relationships between climate and demographic or dispersal parameters (see 6.2). Landscape heterogeneity can greatly influence the rate of range expansion, even when the capacity exists for long-distance dispersal (Fraser et al. 2015). In northern Scotland, reedbed (Packer et al. 2017) and suitable climatic conditions (Figure 2.4) are particularly fragmented and disparately spread. Therefore if reed warbler's range continues to spread in Britain under forecast continued warming (Harrison et al. 2003; Lowe et al. 2018), the rate of spread may decline, and its progress could be particularly contingent on chance extinction and colonisation events. However, continental migrant reed warblers arrive on the east coast of Scotland in autumn, in locations distant from the range edge. If they return to breed the following year then as northern Scotland becomes more climatically suitable for reed warbler, continental individuals may supplement the rate of colonisation.

6.3.2 Potential evolutionary processes in reed warbler range dynamics

Evolution plays a major and complex role in range dynamics (Thomas et al. 2001). Evolutionary processes set up the range limit: we can think of the range edge as being a symptom of a species' inability to adapt. Evolutionary processes modulate the rate and pattern of range expansion. Although I did not directly study evolutionary processes in reed warbler in this thesis, I speculate on their potential role in reed warbler's range dynamics in Britain below.

The probability of reed warbler occupying a site is strongly related to breeding season temperature. This may be because reed growth is low at low temperatures, and reed warblers infrequently build their nests in pure old reed with no stems from the current year; therefore, by the time new reed has grown up, it is relatively late in the season compared to reed warbler spring and autumn migration dates. If this is the case, then by adapting their nesting ecology, reed warblers could gain the ability to breed in cold wetlands with no new reed growth early in the season. Species closely related to reed warbler have quite different nest-site preferences: for example, Blyth's reed warblers *Acrocephalus dumetorum* build their nests in bushes. Although reed warblers almost always build their nest on reeds, they themselves sometimes build them on other vegetation (Catchpole 1974). For example, in the first year of the fieldwork to study reed warbler dispersal (Chapter 3), the site flooded while many pairs had young broods. The floodwater took weeks to subside, and almost completely submerged a large proportion of reedbeds. Although some reed warbler pairs left the site and did not breed again

that season, some pairs built their nests instead in the forks of grey willow *Salix cinerea* (Figure 6.3, lower panels); many of these pairs fledged young successfully from these tree nests.



Figure 6.3. Upper panel: a reedbed at Kingussie, Highland (UK), beyond reed warbler's range edge in Britain, 2019. Reed growth had not started at this location by the date of the photograph (May 24th), at a time when some reed warblers in southern Britain had already completed their first breeding attempt. Deciduous trees and bushes in and adjacent to the reedbed had been in leaf for some time. The site is one of a set of several reedbeds of multiple hectares in size in an area of <10km²; all are unoccupied by reed warbler, but support insectivorous passerines such as the closely-related sedge warbler. Lower panels: reed warbler nests in grey willow in 2016, Watermill Broad NR, Norfolk (UK).

Given that reed warblers did not build their nests in trees except during the flooding, tree-nesting at this site arose from phenotypic plasticity in nest-site preference, rather than from a proportion of the population having a genetic predisposition for tree-nesting in normal conditions. Therefore if reed warblers avoid breeding in colder locations because of a lack of reed growth in the late spring, while

non-reed vegetation types have leaf growth by then (Figure 6.3, upper panel), then from an evolutionary perspective we can consider the range limit to be set by a genetic predisposition against tree-nesting.

A genetic change in nest-site preference could therefore set a different potential range limit, allowing reed warblers to nest in reedbeds where reed growth begins later in the spring. Similar evolutionary changes in habitat selection have been shown to cause range changes: for example, a recent climate-related range expansion in brown argus *Aricia agestis* was caused by an evolutionary shift in host plant preference (Buckley and Bridle 2014). However, I am not aware of any evidence that such a phenotypic shift in nest-site preference is underway in reed warbler in Britain.

Interestingly, there were slight indications that the negative relationship between breeding season temperature and reed warbler survival was stronger in cooler areas (Figure 4.8g, h). Preliminary results from the IBM suggest that reed warbler's range edge is further north than it would be with no negative relationship between temperature and adult survival. This steepened relationship between temperature and adult survival near the range edge could therefore result from local adaptation to extreme conditions at reed warbler's range edge (close to the coldest temperatures experienced by reed warbler anywhere in its range – Figure 1.6). Similarly, I found that although elements of productivity declined with decreasing temperature (Figure 4.8), they did not decrease towards the range edge; this may likewise arise from local adaptation near the range edge (Figure 4.5). Overall, the role of local adaptation in setting up reed warbler's range edge remains unclear, but could be explored in more detail in future evolutionary research, or by fieldwork to ascertain the mechanism by which occupancy is related to climate (see 6.5).

Similarly, it is unclear whether any adaptive changes have taken place across reed warbler's range to influence the rate of range expansion. During a range expansion, we should expect dispersiveness to increase as it becomes more selectively favourable (e.g. Travis & Dytham 2002; Phillips et al. 2006). Intriguingly, all of the cases of long-distance dispersal in reed warbler took place during a period when the range centroid was moving relatively rapidly. There is therefore the tantalising possibility that reed warbler dispersiveness evolved during its range change, in response to the increased availability of climatically suitable habitat. However, these cases of long-distance dispersal numbered only seven, and are therefore too few to base any robust inference on.

The degree of local adaptation at the range edge is determined partly by gene flow from the range core. Counter-intuitively, population declines could cause range expansion through eco-evolutionary feedbacks (Kirkpatrick & Barton 1997). It was notable that reed warbler's range edge moved the fastest during a period where the range thinned out (Figure 2.4). Reduction of gene flow from the range core to the range edge could have reduced gene swamping at the range edge, allowing greater local adaptation there and potentially causing a range expansion.

Overall, the role of evolutionary processes in reed warbler's range change are unclear, but could be explored in more detail in future research (see 6.5). Nevertheless, the patterns in reed warbler's range expansion do not require evolutionary change for their explanation: reed warbler's range change is consistent with equilibration with its climate space (see 6.3.1).

6.4 Implications

Many studies of the mechanisms of range dynamics have focussed only on a single demographic parameter (Gaston 2009). The main novelty of my study is that it uses information on the patterns of range change, dispersal and several demographic parameters to build up a uniquely holistic understanding of range dynamics in one species (at least in a refined geographical area, over a few decades). The value in my study is therefore in showing what is true, and what can be found out, about the causes of range dynamics for one species; as such I can make no generalisations about what is true across all species. I discuss how future research could ascertain such generalities in 6.5. Here, I explain some additional implications of my study for pure and applied ecology.

Reed warbler has probably been gradually changing its range for tens of thousands of years; I studied its range dynamics over a few decades. Even within this timeframe, and over a small geographical area, I found that the role of dispersal in range change varied over time and between areas (6.3). Also, no relationship has been found elsewhere in reed warbler's range between adult survival and breeding season temperature (Chapter 1); the negative relationship that I found (Chapter 4) may allow reed warbler to occupy cooler areas than if there were no such relationship (see 6.2). Assessments of the causes of range dynamics in a species may therefore be time- and location-specific, and so may soon become out of date, or may not apply outside of the study area (e.g. Gaston 2003).

Next, the role of dispersal and demography is strongly interlinked. Only a small proportion of individuals dispersed far enough to match the rate of annual environmental change (Chapter 3). Although this could be framed as an insufficiency in the mean dispersal distance, preliminary

simulations suggest that reed warbler range size is more sensitive to demographic than dispersal parameters (see 6.2). If the increase in the number of fledglings per breeding attempt over time contributed to an increase in the number of dispersers, then the relative balance between dispersal-limitation and demographic-limitation may have shifted over time (e.g. Nathan et al. 2011). These findings are therefore consistent with studies such as Mair et al. (2014) that emphasise the combined and inter-dependent role of dispersal and demography in range dynamics.

Under climate change, we need to help species track their climate space through geographical space. The inter-dependency of the roles of dispersal and demography in range change mean that we should not necessarily aim to aid a dispersal-limited species to track climate change by focussing solely on its dispersal ability: it may be even more effective to focus on its demography. This may be best achieved through holistic approaches to conservation planning which aim to maximise both abundance and connectivity through ecological networks (such as 'More, bigger, better, more joined up'; Lawton et al. 2010).

The role of demography in reed warbler's range dynamics remains unclear: I was not able to determine whether productivity or juvenile survival decline to the range edge, or whether climate-related changes in these parameters have boosted the rate of range expansion. Therefore, even after applying state of the art statistical tools to an exceptionally data-rich and well-studied species, I still have not completely described the cause of either the range limit or the range expansion. Furthermore, understanding a species' range dynamics requires the study of multiple components of a species' ecology; not single components in isolation (Gaston 2009). Each variable I studied contributed something different to an understanding of reed warbler's range dynamics, but none is sufficient alone. For example, if I had solely modelled the effect of climate on chick survival, I might conclude that chick survival is limiting reed warbler's range. Given that most species are much more data-poor and poorly-studied than reed warbler, there may be upper limits to the understanding we might expect to have of species' range shifts.

SDMs, based solely on spatial relationships between environmental variables and presence/abundance, currently prove insufficient to predict species' range dynamics (Sofaer et al. 2018). This is perhaps because they often do not model dispersal, or because assume that a species is at equilibrium with its climate space, or that all individuals of a species have the same tolerances to climate. It has been hoped that building more biological realism into mechanistic, rather than correlative, SDMs will lead to accurate predictions (e.g. Merow et al. 2014). However, I propose that

it will be rare for us to build up a complete understanding of the mechanisms underlying a species' range dynamics: therefore we should not necessarily expect to be able to predict individual species' range shifts with high confidence, even for a very well-studied species.

This has two key implications for conservation in the Anthropocene. Firstly, as climate change progresses, we need to target our conservation planning not only to where species currently are, but increasingly to where we expect them to be in the future. My findings suggest that it will be exceptional for us to be able to successfully pre-emptively spatially target conservation management accurately for an individual species' future range (e.g. by preparing reserves in a location where we expect a particular species, or set of species, to be present in the future). Secondly, species' predicted range change is a key criterion assessed as part of climate change vulnerability assessment (Thomas et al. 2011). If we do not fully understand an individual species' range dynamics, we should not be able to predict its climate change vulnerability accurately.

6.5 Limitations and future work

Generally my work was successful in allowing me to answer the questions I asked. By drawing on multiple sources of information and methods of analysis it was more robust. Typically the inferences I made from my different analyses were in agreement with each other. However, some analyses were unsuccessful, and I could not investigate some aspects of reed warbler's range dynamics due to constraints to resources or time. I outline some of these limitations below, and discuss potentially valuable avenues for future work.

It was disappointing that the spatial IPM did not work (Chapter 4), as this could have provided key information about spatial variation in demographic parameters. Specifically, it could have allowed estimation of spatial variation in the latent scaling parameter ω (containing number of attempts per pair and juvenile post-fledging survival), juvenile over-wintering survival and population growth rate, and their relationships with climate and time. This would have allowed me to understand more clearly the role of demography in range limitation in reed warbler; for example, whether the ratio of births to deaths declines to the range edge, or declines with decreasing temperature or increasing rainfall. Comparing how the births-to-deaths ratio and settlement probability decline to the range edge could allow evaluation of whether reed warbler's range limit is set up by conservative habitat selection. Describing spatial patterns in the births-to-deaths ratio could allow estimation of where reed warbler's range edge lies relative to the edge of its fundamental niche.

Fitting the IPM in WinBUGS allows great flexibility in customising the model. However, Bayesian models can run slowly or fail to converge if fitted using MCMC, which is currently the only available option for fitting IPMs. Major advances have recently been made in the efficiency and stability of fitting large spatial Bayesian models, using Integrated Nested Laplace Approximation (Rue et al. 2009). If these innovations can be applied to allow a more flexible model structure, then this might solve the challenges I experienced in fitting a spatial IPM. Alternatively, it could be that I specified the model structure incorrectly, poorly describing the ecological and observation processes generating the data and causing internal conflict within the model. Future work to refine the likelihood formulation may therefore allow stable model fitting. Furthermore, leveraging the spatial information associated with species' capture histories (Royle et al. 2014) may allow estimation of spatial variation in immigration and emigration, to evaluate hypotheses for the mechanisms underlying range dynamics in reed warbler in another way.

The mechanism was unclear for the strong relationship I found between occupancy and temperature (Chapter 2). Future fieldwork could discern whether, when reed warblers choose to occupy a site on the basis of temperature, they are responding directly to low temperatures, or to a covariate of temperature such as reed growth.

The low accuracy of the reedbed map (Chapter 5) possibly introduced uncertainty into the IBM (6.2). If a higher accuracy reedbed map could be produced, this could allow a much greater understanding of the rules underlying reed warbler dispersal. For example, reed warbler's dispersal kernel could be compared with the frequency distribution of distances between reedbeds. If these are similar, then it may be that reed warbler's dispersal kernel arises from a rule whereby dispersing individuals settle at the first reedbed they encounter.

Ecological factors in the non-breeding season can influence the population size (Johnston et al. 2016), and potentially therefore the range, of Afro-Palearctic migrants. Winter temperature and habitat availability could both be important for reed warbler in its West African wintering grounds (although reed warbler is catholic in its habitat use on the wintering grounds: Dowsett-Lemaire and Dowsett 1987; Zwarts et al. 2014). In this study, I only incorporated the effect of winter rainfall into my models (Chapter 4). Future work could incorporate extra environmental variation into models as extra covariates.

Although I have highlighted potential evidence of evolutionary processes in reed warbler's range dynamics in Britain (see 6.3.2), I did not study this issue directly. Future work could investigate this issue using genomic analyses or simulations. Genome sequences from contemporary reed warblers could be compared to sequences from museum specimens, to understand genomic changes over the course of the range expansion (e.g. Bi et al. 2013). Comparison with an annotated genome would reveal whether allele frequencies had changed over time in relation to traits relevant to range expansion, such as dispersiveness. Alternatively, allele frequencies for traits could be incorporated into an IBM. Allele frequencies for key traits could be explicitly varied, and the effects on range dynamics assessed. Furthermore, simulations could be allowed to run and the spatial patterns of allele frequencies at the range edge could be assessed, in order to understand the relative role of local adaptation and gene flow in setting up the range limit.

The only environmental covariates I related to reed warbler occupancy and demographic parameters were mean breeding season temperature and total breeding season rainfall (Chapters 2 & 4). I did not study meteorological extremes, which might have an important and different effect on reed warbler occupancy or demographic parameters. For example, reed warbler productivity can be strongly influenced by short periods of very heavy rainfall (pers. obs.). If such rainfall episodes are rare, then they might not influence total breeding season rainfall. Future studies could relate reed warbler occupancy and demographic parameters to measures of meteorological extremes such as days of consecutive rainfall above a certain rainfall rate, or to maximum temperature.

In this thesis, I only studied the dynamics of the reed warbler's cool range edge in a small region of western Europe. The causes of range dynamics may differ in different parts of a species' range (e.g. Hersteinsson and Macdonald 1992); therefore a more complete understanding of the causes of range dynamics in the species would require equivalent study of the other edges of reed warbler's range.

Future IBM studies could simulate species that were limited in range by dispersal or by demography, and investigate whether the two mechanisms for range limitation influence the patterns of the range expansion. This could allow us to infer in a more resource-efficient way whether species are dispersal or demography-limited: from the patterns of their range dynamics alone.

I have described in detail the mechanisms underlying range dynamics in reed warbler. Future work could apply my methods more generally, in order to establish generalities in the mechanisms underlying range dynamics in other species. For example, in some regions, few species are tracking

their climate space (Tayleur et al. 2015). Reed warbler to some extent tracked its climate space, and could therefore be classed as a climate change 'winner' (at least away from the warm edge of its range; Johnston et al. 2016). The dispersal kernel could be estimated from ringing data for a wide variety of bird species, and the proportion of long-distance dispersers could be compared with the temperature of the cool edge of their ranges over time. By investigating covariates of range dynamics in such a way for a large number of species, we could thus establish what facets of their own ecology set apart climate change 'winners' and 'losers'. Another study could investigate whether the range dynamics of species are typically more sensitive to dispersal or demography. This might allow us to establish with more generality whether species can be more effectively helped to track their climate space by promoting their dispersal ability, or by promoting their productivity and survival.

Appendix: Methods for individual-based model of reed warbler *Acrocephalus scirpaceus* in Britain

A.1 Overall approach

There are two main tasks when constructing an IBM: deciding on an appropriate structure, and deciding on appropriate parameter values. The closer the structure and parameter values of the IBM are to representing the true life-cycle of the target species, the more accurate the outputs should be. The life history of reed warbler is very well described and quantified, allowing me to arrive at a structure and parameter values that are reasonably accurate. However, as for most species, the best described aspects of reed warbler's life history are those that are easiest to study. It is important to note that much of reed warbler ecology is known from fairly few sites, and that structure or parameter values may be different at the range edge. For example, much of what we know about how reed warblers establish territories and choose mates comes from one study on a Polish reedbed (Borowiec 1992). There are some aspects of the life of this well studied species that still remain obscure. In particular, we know very little about how reed warblers search for sites, or how they select sites.

I describe the structure and parameter values of the IBM in A.2. Where available, structure or parameter values were drawn from the literature or from understanding of reed warbler's dispersal and demography obtained through analyses in Chapters 3 and 4; otherwise I used plausible structure or parameter values. Although effort has been made to make this IBM as faithful a representation of reed warbler's life history as possible, the IBM is still valuable even if it deviates slightly from this. As presented here, the structure of the IBM still requires fine-tuning and so the results from the simulations (6.2) are preliminary.

There are practical considerations when choosing the structure of an IBM. There must be enough detail for it to represent reality, but it must also run efficiently, especially if running many times to explore parameter space. Fortunately, reed warbler has a relatively small population size in Britain (hundreds of thousands of individuals; Newson et al. 2008), so this trade-off was rarely important.

A.2 Structure of IBM

In the IBM, individuals are subject to certain operations over a yearly cycle (e.g. yearly mortality as adults). The names of the parameters associated with these operations, along with a description and

the range of values used in analyses (see 6.4) are given in Table A.1. Below, I give an overview of the structure of the IBM.

In the IBM, reed warblers return from spending the winter in Africa on a day randomly drawn from a given distribution *returns*: depending on their age and sex. Adult males return first, followed by adult females, followed by juvenile males, followed by juvenile females. There is substantial overlap between the distributions of return dates of the different ages and sexes. Juveniles return to their exact natal site with probability *rts0*. Adult site fidelity is much higher than juvenile site fidelity in reed warbler (Chapter 3). Adults return to their exact breeding site in the previous year with probability *rts1* or *rts2*, depending on whether they failed or succeeded respectively. If birds do not return to their exact natal/breeding site, they make a dispersal movement from an exponential distribution with parameter $1/\text{meanjump}$. This dispersal movement is in a random direction, and occurs until the bird lands in an area with habitat. It is right to characterise reed warblers (at least for juveniles) as having a two-step dispersal movement (decide to leave current site, and then move), because the dispersal kernels at the within-site- and out-of-site scale are discontinuous (Chapter 3). If there is available carrying capacity *cc*, then males search around for an available nest site, with daily search radius *nhd_m*. When females return, they search for an available male, with daily search radius *nhd_f*. Having landed in suitable habitat with non-zero carrying capacity, the male searches around within *nhd_m* for cells with available nest space. The male randomly selects one of these cells, and then chooses a nest location (with exact x and y coordinates) from within this cell. Males and females will wait for *wait_m* and *wait_f* days respectively, and if no breeding attempt has been made by that time, they will move on. Females select a cell with the most singing males, or one at random if they are tied.

When a pair initiate breeding for the first time in the season, they spend *lag0* days nest building before they lay their first clutch. Clutch size is determined by probability *clutch*. Clutches survive through hatching to fledging with daily probability *survn* (here, egg and chick survival are combined into one parameter for simplicity). It takes *ndur* days from the completion of the first clutch to fledging a successful nest. The pair spend *lag1* or *lag2* days preparing for the next breeding attempt, depending on whether the previous attempt failed or succeeded, respectively. There is assumed to be a last Julian day *jcut* of the season on which breeding can be initiated. After this, birds depart on autumn migration on day *leave*.

Juvenile birds survive from fledging to the next breeding season with probability *surv1*, which incorporates a seasonal decline in over-wintering probability, according to the relationship estimated

in Chapter 3 (Figure 3.6b). Adult birds survive from the start of one breeding season to the start of the next breeding season with probability *surv2*.

At each time step, the IBM iterates through vectors of cells and individuals, performing operations on individuals in sequence. In order to avoid spurious effects of order (e.g. always giving certain individuals preference for finding a site first), the order of vectors was shuffled at each time step.

A.3 Running the IBM

The IBM was coded by Dr Phil Platts in C++ according to the specification of reed warbler's life history I provided, and according to further discussions. The IBM was adapted from an existing IBM 'Geneshifter' by Phil Platts and Calvin Dytham, used for simulating butterfly populations in Britain. For testing, the model was compiled using Dev-C++ to be run in Windows.

I ran the IBM in a map of British reedbed (described in Chapter 5). Although this reedbed map is the only existing one for Britain, it was of low accuracy, mostly due to high commission error. Fieldwork revealed many of the false positives in this map to be due to confusion with arable farmland. Therefore I masked the reedbed map with the Arable and Horticulture layer of the CEH Land Cover map (Morton et al. 2014). The masked reedbed map was then aggregated to give proportional reedbed cover for each land hectare in Britain. The IBM was run on this hectare grid. Each grid cell of the map has a value of proportional reedbed cover in the range [0,1], invariant over the spin-up and simulation period; carrying capacity *cc* was multiplied by this coefficient to give the carrying capacity for each grid cell. An example hectare-scale map of simulated reed warbler presence from the end of a run is shown in Figure A.1.

The IBM was run over the period 1961 to 2014. The IBM was initiated in all hectares within hectads occupied by reed warbler during the 1968-1972 Bird Atlas (Balmer et al. 2013). The IBM was looped for a spin-up of 220 years to allow dynamics to stabilise, before simulation from 1983 to 2015 was initiated. The spin-up was confined to hectares from northern England south, to run quickly. The year range of the simulation was selected in order to stay approximately in line with the study period of the rest of the thesis. Running the IBM took several hours, with the time depending on the size of the simulated population. In order to explore the behaviour of the IBM throughout parameter space, individuals runs of the IBM were distributed over nodes of the Viking Research Computing Cluster at

the University of York, and called through a wrapper written in R (R Core Team 2018). In order to do this, the original IBM was re-compiled in Linux.

Climate was incorporated as a layer into the IBM as breeding season temperature, using 5 km x 5 km-scale UKCP09 data (Met Office 2017). Annual breeding season temperature was calculated as the mean temperature over the period May to August, the main months of the breeding season in reed warbler in Britain. During the spin-up period, the climate of the 22 years from 1961 to 1982 was looped sequentially. Therefore, if there were truly a particularly cold or warm year just before the start of the simulation, the spin-up would reflect this.

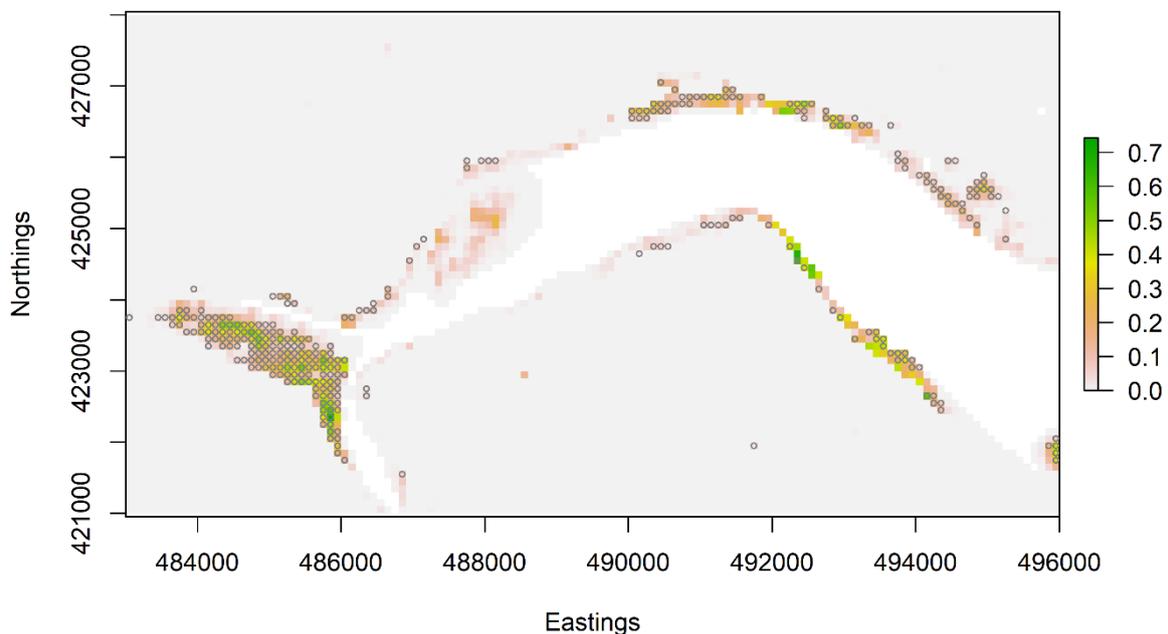


Figure A.1. Simulated reed warbler distribution around Humber Estuary, Britain in 2014 from one sample run. Northings and eastings are in metres. Colour = proportion reedbed, circles = reed warbler presence.

A.4 Data analyses

A.4.1 Sensitivity analysis

The relative influence of demographic and dispersal parameters on reed warbler's range dynamics was investigated by varying the demographic parameters and assessing their influence on range summary statistics. 20 potentially influential parameters were varied across a plausible range of parameter space (Table A.1). Latin hypercube sampling is an ideal method for sampling close to randomly from a distribution with many dimensions. Preliminary analyses suggested that approximately 1,000 samples would be required for the next step; to save time, 20 Latin hypercubes with 50 samples were created using the *lhs* package (Carnell 2019) in R (R Core Team 2018), and combined. This gave 1,000 sets of estimates for all 20 parameters. One IBM run was carried out with

each of the 1,000 parameter combinations. Summary statistics (number of hectares occupied, and 97.5th percentile of northings of occupied hectares, at the end of each run) were calculated for each IBM run. A linear model was then fitted with a given summary statistic as the response variable, and the 20 demographic parameters as the explanatory variables. The influence of each demographic parameter on the summary statistic was assessed according to the coefficient of the slope of its relationship with the summary statistic. The mean and standard error of the coefficients for each parameter over 1,000 runs are presented in 6.2.

A.4.2 Effect of relationship of parameters with climate on range dynamics

In the second analysis, I simulated reed warbler's range size and the location of the range limit under five scenarios: one with no parameter linked to temperature, one each with settlement probability (positive), nest survival (positive) or adult survival (negative) linked to temperature, and one with all three parameters linked to temperature. When a parameter was not linked to temperature, it was fixed at the intercept of that parameter's slope with the mean British temperature.

The relationships with temperature were linearised versions of relationships estimated in analyses from Chapters 2 & 4: $survn = 0.004t + 0.911$; $surv2 = -0.043t + 1.088$; $settle = 0.065t - 0.388$. The slopes of these relationships were checked to make sure that no values of temperature in Britain produced probabilities outside the interval [0,1]. As in Chapter 4, adult survival was linked to the previous year's climate. These climate relationships generated values of nest survival, adult survival and settlement probability for every grid cell in that year. The values of nest survival and adult survival were incorporated directly into the corresponding parameters in the IBM. Settlement probability applies during the male's search for a nest site. When the male is searching for suitable habitat cells for nesting in, a random number is drawn from a uniform distribution within the interval [0,1]. If the climate-generated settlement probability of a cell is below that random number, the male does not attempt to move there.

As in A.4.2, for each scenario the IBM was run 1,000 times. All parameters except settlement probability, nest survival and adult survival were allowed to vary according to their values in the Latin hypercube. Summary statistics (number of hectares occupied, and 97.5th percentile of northings of occupied hectares, at the end of each run) were calculated for each IBM run and are presented in 6.2.

Table A.1. Parameters in reed warbler IBM. ‘Minimum’ and ‘Maximum’ are the range used for each parameter in simulations.

	Parameter	Description	Minimum	Maximum
Settlement & dispersal	returns_m0	Return date distribution (min, max, mean, s.d.) - juvenile males	(100, 220, 150, 5)	(100, 220, 170, 15)
	returns_f0	Return date distribution (min, max, mean, s.d.) - juvenile females	Min, max & mean as returns_m0+7; s.d. as returns_m0	Min, max & mean as returns_m0+7; s.d. as returns_m0
	returns_m1	Return date distribution (min, max, mean, s.d.) - adult males	Min, max & mean as returns_m0-10; s.d. as returns_m0	Min, max & mean as returns_m0-10; s.d. as returns_m0
	returns_f1	Return date distribution (min, max, mean, s.d.) - adult females	Min, max, mean as returns_m0-3; s.d. as returns_m0	Min, max, mean as returns_m0-3; s.d. as returns_m0
	rts0	Probability of returning to last year’s exact site - juveniles	0.05	0.35
	rts1	Probability of returning to last year’s exact site - adults if breeding failed last year	0.6	0.99
	rts2	Probability of returning to last year’s exact site - adults if breeding succeeded last year	0.95	0.99
	cc	Carrying capacity - pairs per m ² of pure habitat (e.g. 0.002 = 20 pairs ha ⁻¹)	0.001	0.003
	meanjump	Mean long distance dispersal (m)	5,000	15,000
	nhd_m	Daily search radius for males looking for nest site (m, implemented as square)	500	2,000
	nhd_f	Daily search radius for females looking for male (m, implemented as square)	500	2,000
	wait_m	Days males will wait until moving, if no breeding attempt has been made in current location	5	15
	wait_f	Days females will wait until moving, if no breeding attempt has been made in current location	1	10
	Breeding	lag0	Days before first clutch (nest building etc)	4
clutch		Clutch size distribution (min, max, mean, s.d.)	(2, 5, 3.5, 0.5)	(2, 5, 4, 0.5)
survn		Probability of daily nest survival	0.975	0.999
lag1		Days before clutch, if previous brood failed	4	7
lag2		Days before clutch, if previous brood succeeded	8	15
jcut		Last Julian day that nesting can be initiated	210	232

	leave	Julian day that birds leave for winter migration	270	300
Survival	surv1	Probability of fledgling/juvenile overwintering survival, given 120 days in UK post-fledging	0.2	0.4
	surv2	Probability of adult overwintering survival	0.4	0.7

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