Demographic mechanisms of avian responses to climate change: long-tailed tits *Aegithalos caudatus* as a case study

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General summary

Understanding ecological responses to climate change is a great challenge for ecologists today. Altered phenology, survival and productivity are influencing population size amongst numerous taxa, with consequences for species distributions locally and globally. Understanding the effects of weather on demography is therefore crucial for improving predictions of future range shifts, yet such knowledge is currently lacking.

I address these issues using the long-tailed tit *Aegithalos caudatus* as a case study. I investigate trends in the phenology, survival and productivity of a resident breeding population in central England over the past two decades, in response to temperature and precipitation over the entire annual cycle. I use these historical associations to explore the mechanisms responsible for the two-fold increase in the UK long-tailed tit population over the past 48 years, and to estimate future demographic trends.

I find that increasing adult survival in response to warming during spring and autumn is probably contributing to the population increase, and should continue to do so over the coming decades. In contrast, juvenile recruitment is unlikely to increase, despite positive effects of warmer May temperatures, due to the opposing negative impacts of warmer March temperatures and the strong density dependence of recruitment I observe. I show that breeding seasons are shortening, because the faster rate of warming during April compared to March is driving a greater advance in the timing of breeding termination compared to initiation. Earlier termination may be linked to an advance in the timing of peak caterpillar abundance, which I show to be an important food source for breeding long-tailed tits. If breeding seasons continue to contract, I indicate that fledgling production could be reduced in this population. Ultimately, the consequences of climate change for passerines will depend on the precise timing and extent of alterations in weather patterns and community dynamics.

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Chapter 1. General introduction

1.1 Climate change impacts on passerine birds

Current climate change is now indisputable and severe (Stocker *et al.* 2013). Across the globe, mean air temperature has increased by approximately 0.89ºC since 1900 and is expected to continue rising over the next century (Stocker *et al.* 2013); in the UK the most recent two decades have been the warmest since instrumental records began over 240 years ago (Met Office 2014). Precipitation patterns show less consistent change over the past century, but overall annual precipitation is expected to increase at mid to high latitudes over the coming decades, particularly during winter months (Stocker *et al.* 2013). Extreme weather events are also occurring more frequently across the globe, a trend which is expected to continue over the coming century (Stocker *et al.* 2013). Such drastic climatic changes are likely to affect ecosystems in a plethora of ways, particularly as they come at a time when species face numerous other human-induced pressures such as habitat loss and land-use change (Thomas *et al.* 2004).

Understanding ecological responses to climate change is one of the greatest challenges facing ecologists today (Walther *et al.* 2002; Parmesan & Yohe 2003; Buckley *et al.* 2010). Recent range shifts are well documented across a very wide range of taxa, indicating changes at both the local scale, through elevational and microclimatic shifts, and the regional to global scales, through latitudinal shifts (Thomas & Lennon 1999; Parmesan & Yohe 2003; Willis *et al.* 2009; Buckley *et al.* 2010; Midgley *et al.* 2010). Such range shifts are expected to arise not through differential dispersal of individuals, but rather through local changes in population size, as a result of alterations in population productivity and survival rates (Ådahl, Lundberg & Jonzén 2006; Huntley *et al.* 2007). Understanding the effects of weather on demographic rates is therefore crucial for improving the predictive capacity of models of future range shifts (Robinson, Baillie & Crick 2007; Buckley *et al.* 2010; Bykova *et al.* 2012; Fennell *et al.* 2013), which is an essential step in mitigating against the negative ecological consequences of climate change (Parmesan *et al.* 2011; Bellard *et al.* 2012).

Passerine birds are one group of animals that are responding strongly to climate change, and have become an important model for studying the effects of climate change on populations and communities (Walther *et al.* 2002; Charmantier *et al.* 2008; Sæther & Engen 2010). Some recent population declines have already been attributed to climate change, with many more declines expected over the coming decades (Beale *et al.* 2006; Balmer *et al.* 2013). Meanwhile, other species are expected to show local increases in population size (Huntley *et al.* 2007; Balmer *et al.* 2013). Various demographic mechanisms could be driving such changes in population size, yet knowledge in this area is severely lacking (Miller-Rushing *et al.* 2010; Sæther & Engen 2010; van de Pol *et al.* 2010), despite mounting evidence of changing phenology, productivity and survival in numerous passerine species (Crick *et al.* 1997; Root *et al.* 2003; Leech & Crick 2004; Sæther & Engen 2010). The aim of this thesis is to consider a subset of the various demographic responses to climate change that may be particularly important in influencing population size amongst temperate woodland passerines.

1.2 Mechanisms of climatic impact

Establishing the mechanistic basis for climatic impacts on passerine population size is vital for developing predictive models that can inform conservation management (Buckley *et al.* 2010; Pearce-Higgins & Gill 2010; Bykova *et al.* 2012; Fennell *et al.* 2013). Developing such understanding consists of two elements. First, the demographic drivers of population change must be determined, by assessing the effects of climate on survival and productivity (Robinson, Baillie & Crick 2007; van de Pol *et al.* 2010). Second, the proximate mechanisms linking demography and population change should be identified (Pearce-Higgins & Gill 2010). However, whilst the need to incorporate demographic and proximate mechanisms into predictive models is increasingly recognised, research addressing these issues remains rare.

Weather can influence survival and productivity through numerous processes (Newton 1998). Broadly, these can be split into direct effects on thermoregulation, and indirect effects on key factors such as food availability, predation, and disease (Pearce-Higgins & Gill 2010). Indirect effects may be mediated through changes in phenology, i.e. the timing of recurrent life-cycle events, because phenology is a key determinant of species interactions (van Asch & Visser 2007), as well as being essential for maintaining coherency of the multiple stages of an individual's life cycle (Carey 2009). In the following sections, I will briefly review the ways in which climate can influence population size via several key mechanisms linked to phenology, productivity and survival, focussing in particular on passerine birds breeding in temperate woodlands.

1.2.1 Mechanisms acting via phenology

Changes in the timing of life-cycle events are amongst the most widely-documented ecological consequences of climate change (Root *et al.* 2003; Carey 2009; Miller-Rushing *et al.* 2010). For instance, spring events are advancing in response to warming, including tree budburst, insect larval emergence, and bird egg-laying (e.g. Crick *et al.* 1997; van Asch & Visser 2007; Charmantier *et al.* 2008; Vitasse *et al.* 2009). However, different species often show contrasting climatic responses, and patterns of climatic change are not equal throughout the year (Buse *et al.* 1999; Walther *et al.* 2002; Visser & Both 2005; van Asch & Visser 2007). Consequently, as well as disrupting the timing of events within the life cycle of individual species (Husby, Kruuk & Visser 2009; Møller 2010), phenological change can disrupt species interactions (Walther *et al.* 2002; van Asch & Visser 2007). There is increasing evidence that phenology could be an important mediator of population change (Both *et al.* 2006; Visser, Holleman & Gienapp 2006; Goodenough, Hart & Stafford 2010; Jones & Cresswell 2010), with species exhibiting larger phenological shifts being typically more resilient to the negative impacts of climate change than those exhibiting more limited phenological flexibility (Møller, Rubolini & Lehikoinen 2008; Jones & Cresswell 2010).

A particularly well-studied example of recent phenological change is the earlier onset of breeding in temperate bird populations in years with warmer spring conditions (Crick *et al.* 1997; Thomas *et al.* 2001; Charmantier *et al.* 2008; Both *et al.* 2009). Earlier onset of breeding could bring about a lengthening of the breeding season, potentially increasing productivity by increasing the number of breeding attempts (Crick & Sparks 1999; Møller 2010). However, the divergent nature of climatic change between different parts of the year means that in some species, earlier onset of breeding may be combined with an even more marked advance in the timing of breeding termination, leading to a shortening of the breeding season (Dawson 2005; Møller 2010). Such an effect could reduce productivity by limiting re-nesting opportunities following nest predation events, as well as limiting double-brooding in multi-brooded species (Husby, Kruuk & Visser 2009).

Alongside altered breeding season length, the main way in which phenological change is expected to influence passerine productivity is via disruptions to the synchrony of breeding with the brief temporal peak in food abundance, i.e. trophic mismatch (Buse *et al.* 1999; Møller, Rubolini & Lehikoinen 2008; Visser 2008; Carey 2009; Bauer *et al.* 2010). For most insectivorous temperate woodland passerines, caterpillars form an important part of the nestling diet (e.g. Perrins 1965, 1991; Charmantier *et al.* 2008). The sharp temporal peak in caterpillar abundance occurs earlier in warmer springs (Visser, Holleman & Gienapp 2006; Smith *et al.*

2011) and maintaining synchrony with this peak has been suggested to improve productivity (Tremblay *et al.* 2003; Visser, Holleman & Gienapp 2006) and adult survival (Thomas *et al.* 2001). However, although trophic mismatch has been suggested as a mechanism for population decline in some migratory passerines (Both *et al.* 2006), it is not clear whether trophic mismatch is a widespread phenomenon. Moreover, the consequences of trophic mismatch for productivity and population size remain largely unknown (Stevenson & Bryant 2000; Both 2010; Vatka, Orrell & Rytkönen 2011; Burger *et al.* 2012; Reed, Jenouvrier & Visser 2013). Previous studies have shown contrasting results in different populations (Buse *et al.* 1999; Visser, Holleman & Gienapp 2006; Both *et al.* 2006). Thus, there is a need for further study in a wider range of species, habitats and populations.

1.2.2 Mechanisms acting via adult survival

Weather conditions influence the survival of adult passerines primarily through influencing thermoregulation and food availability (Perrins 1965; Newton 1998; Leech & Crick 2007). Thus in temperate species, survival rates are typically reduced by cold temperatures (Lahti *et al.* 1998; Peach, Siriwardena & Gregory 1999; Perdeck, Visser & van Balen 2000; Doherty & Grubb 2002) and increased precipitation (Altwegg *et al.* 2003), as well as perhaps the interaction between the two (Robinson, Baillie & Crick 2007). In contrast, summer heat stress effects may become an important determinant of survival under future climatic conditions, even in temperate regions (Jiguet *et al.* 2006; Grosbois *et al.* 2006; Santisteban *et al.* 2012).

In northern latitudes, winter has typically been considered the period during which weather influences the survival of resident passerines most markedly, particularly in small-bodied species (Lack 1954; Peach, Siriwardena & Gregory 1999; Sæther, Sutherland & Engen 2004). However, very few studies have assessed the effects of weather throughout the year, despite recognition that such year-round effects could be important (Grosbois *et al.* 2006; Sæther & Engen 2010; Santisteban *et al.* 2012; Salewski, Hochachka & Fiedler 2013). For instance, inclement weather during the breeding season could increase parental investment (Newton 1998, and references therein; Bradbury *et al.* 2003), thus increasing adult mortality following the breeding season. Furthermore, there have been very few long-term (>7 years) assessments of adult passerine survival in temperate areas (but see Robinson *et al.* 2004; Grosbois *et al.* 2006), with most studies focussing on seabirds in northern latitudes (Grosbois *et al.* 2008). The current and future impacts of weather on passerine survival therefore remain elusive.

1.2.3 Mechanisms acting via productivity

In temperate passerines, spring temperature and precipitation have been shown to influence the production (quality and quantity) of eggs and fledglings via both direct mechanisms (e.g. Nager & van Noordwijk 1992; Dawson, Lawrie & O'Brien 2005) and indirect effects on food availability and predation rates (e.g. Rotenberry & Wiens 1991; Morrison & Bolger 2002; Collister & Wilson 2007; Adamík & Král 2008; Sofaer *et al.* 2013). However, food availability and predation rates can also fluctuate independently of climate (Leech & Crick 2007). Thus, whilst weather may impact the productivity of individual breeding attempts, such effects may be of limited importance in determining annual productivity at the population level if demography is largely controlled by non-climatic factors such as predation. It is therefore unclear if weather is a key mechanism of population control in the majority of passerines (Reed, Jenouvrier & Visser 2013).

Aside from the studies of phenological mismatch discussed in section 1.2.1, there have been rather few investigations of passerine productivity in response to recent climate change, with most estimates of weather effects on productivity being based on experimental (e.g. Nager & van Noordwijk 1992; Dawson, Lawrie & O'Brien 2005) or short-term studies (<8 years; e.g. Rotenberry & Wiens 1991; Morrison & Bolger 2002; Collister & Wilson 2007; Sofaer *et al.* 2013). From the long-term studies that do exist, general patterns of climatic effects on productivity are not evident. For instance, whilst two separate studies of pied flycatchers *Ficedula hypoleuca* demonstrated increasing clutch size in response to spring warming over a period of 22 to 25 years (Järvinen 1989; Winkel & Hudde 1997), only the latter observed a corresponding increase in the number of fledglings produced. This further highlights the fact that mechanistic links between weather and individual productivity outcomes are not necessarily indicative of effects on productivity at the population level.

1.3 Predicting future change

Ultimately, research into the effects of weather on population demography aims to inform predictions of future ecological effects of climate change over the coming decades. However, in order to maximise the utility of such predictive models, a number of issues need to be considered concerning their potential limitations. These encompass aspects relating to species biology and life history, methodological limitations, and climatic uncertainty. In the following sections I briefly highlight some issues of particular concern.

1.3.1 Density dependence

Demographic rates are known to be density-dependent in many passerine populations (Newton 1998), potentially limiting the impacts of weather on population size over the longer term (Robinson, Baillie & Crick 2007). For instance, species often show reduced productivity, survival and recruitment at higher population densities due to increased competition for food and nest sites, and increased predation rates on nests and fledglings (Krebs 1971; Robinson, Baillie & Crick 2007; Norman & Peach 2013). The extent of density dependence is highly variable between populations (Newton 1998), and consideration of such regulatory mechanisms is vital for improving the reliability of future predictions of population size in response to climate (van de Pol *et al.* 2010).

1.3.2 Genetic adaptation

The ultimate consequences of climate change for species demography and population size will depend on the capacity of populations to adapt to future climatic change, yet current understanding of the genetic basis for phenological and demographic change is poor (Garant, Sheldon & Gustafsson 2004; Møller & Merilä 2004; Visser 2008; Reed, Jenouvrier & Visser 2013). Some demographic traits are known to show a considerable heritable component, including lay date in woodland passerines (Sheldon, Kruuk & Merilä 2003). Directional change in environmental conditions could therefore bring about microevolution as a result of changing selection pressures (Charmantier *et al.* 2008; Salewski, Hochachka & Fiedler 2010; Visser *et al.* 2010). Microevolution could also increase the phenotypic plasticity of a population, since the degree of plasticity exhibited by an individual is in part genetically determined (Nussey *et al.* 2005; Charmantier *et al.* 2008). Such phenotypic plasticity enables individuals to respond to fluctuating environments (Charmantier 2008; Reed *et al.* 2009) and could therefore become increasingly important under future climates, with increasing interannual variability of weather conditions being expected (Stocker *et al.* 2013). Such genetic change could therefore enable populations to cope with climate change over the long term more successfully than predictive models may suggest.

1.3.3 Interacting mechanisms

Whilst there may be some general patterns of species responses to climate change, differences in life history and ecological traits mean that numerous demographic drivers and mechanisms are likely to be important, including non-climatic factors such as land use change (Reif *et al.* 2008; Pearce-Higgins & Gill 2010; Parmesan *et al.* 2011). Importantly, multiple mechanisms are likely to interact even within a species (Martin 2007), and a single climatic driver may have opposing effects on different aspects of an individual's demography. For instance, mean winter temperature has a positive effect on adult survival but a negative effect on fecundity of the Eurasian oystercatcher *Haematopus ostralegus* (van de Pol *et al.* 2010). Also, weather at one time of year can impact demography later in the year (Barbraud & Weimerskirch 2001; Sæther & Engen 2010). In order to understand the impact of weather on population growth rates it is therefore essential to consider the effects of weather throughout the entire year on both survival and productivity (Ådahl, Lundberg & Jonzén 2006; van de Pol *et al.* 2010).

1.3.4 Other considerations

Several other factors warrant mention. First, considerable geographical variation is likely to exist in terms of both the nature of climate change (Stocker *et al.* 2013) and the responses of populations to that change (Walther *et al.* 2002). Second, extreme events can undoubtedly impact species demography within years (Parmesan 2007; Moreno & Møller 2011), but are difficult to incorporate into predictive models; species with long generation times and/or small populations may be particularly likely to experience population declines or local extinctions if extreme events surpass a certain frequency (see Crick 2004). Similarly, unforeseen events may occur that limit the validity of extrapolations from historical associations between weather and demography. For example, climate change could bring about a shift in community dynamics via alterations in habitat structure, causing hitherto unexpected consequences for the population dynamics of other species in the community (Thomas *et al.* 2004). Extrapolation of historical relationships is also limited by the fact that associations between climate variables and demographic responses are not necessarily linear (Doak & Morris 2010; Mysterud *et al.* 2001). Finally, with climatic projections themselves subject to considerable uncertainty (Stocker *et al.* 2013), predictions of ecological responses to climate change should be treated with an appropriate degree of caution (Seavy, Dybala & Snyder 2008).

1.4 Current study

I aim to understand how weather influences the phenology, survival and productivity of UK populations of the long-tailed tit *Aegithalos caudatus* (Fig. 1.1), paying attention to the effects of both temperature and precipitation over the entire annual cycle. I will assess historical trends in demography in response to recent climate change, and develop projections of how demography may change under future climates. The objective of this thesis is to examine several key mechanisms that may explain recent increases in the UK long-tailed tit population, with a view to developing understanding of climatic impacts on passerine birds more generally.

The long-tailed tit is a particularly suitable species for assessing the effects of climate change on demography and population size for a number of reasons. First, it shows greater phenological advance than almost any other UK passerine (Baillie *et al.* 2014; Fig. 1.2). Second, the UK population size of long-tailed tits has been increasing since the 1980s, and is higher now than at any point since national monitoring started in 1966 (Baillie *et al.* 2014; Fig. 1.3). Third, its small body size and mass (around 7-8g in UK populations) is thought to make it particularly vulnerable to mortality in harsh winters (Marchant *et al.* 1990), so overwinter survival could be a key driver of population size. Fourth, predation rates on long-tailed tit nests are very high (Hatchwell *et al.* 1999a) and predation is therefore a major determinant of population-level productivity (Hatchwell *et al.* 2013). Finally, whilst bioclimatic envelope models are associated with a number of potential problems, they do suggest that the long-tailed tit's geographic distribution will respond strongly to future climate change (Huntley *et al.* 2007).

Figure 1.1 Adult long-tailed tit *Aegithalos caudatus* showing colour rings that enable unique identification of individuals.

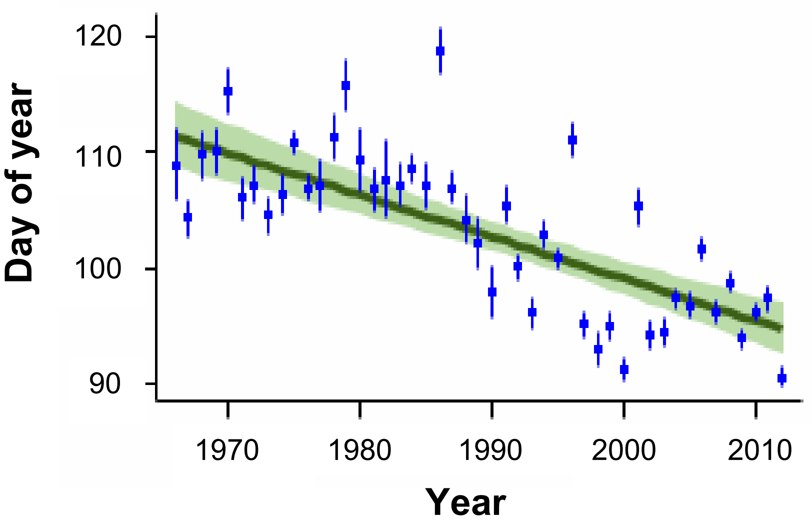

Figure 1.2 Mean average laying date (Julian days ± 1SE) of long-tailed tits across the UK during the period 1966–2012 (mean annual sample size = 53 nests). The plotted line shows the long-term trend in national lay date, indicating an advance of 16 days during 1968–2011. Adapted from Baillie *et al.* (2014).

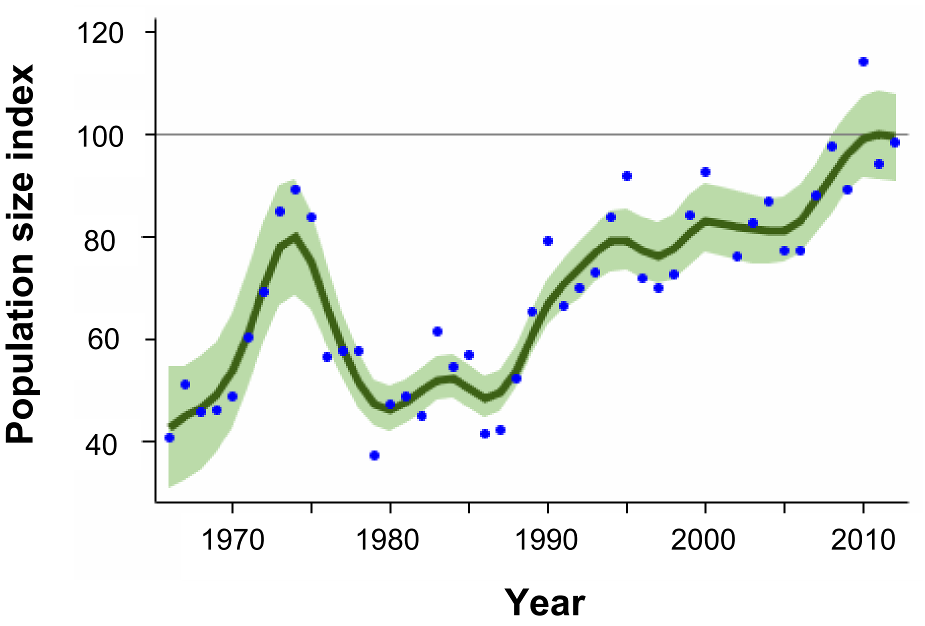

Figure 1.3 Annual UK population size of long-tailed tits during the period 1966–2012. The plotted line shows the smoothed population index, relative to an arbitrary value of 100 in the year 2011, showing 85% confidence intervals (shaded area). Adapted from Baillie *et al.* (2014).

1.4.1 Study species

The long-tailed tit *Aegithalos caudatus* is an insectivorous passerine, resident throughout the UK and present as both resident and migratory populations across much of the Palearctic (Huntley *et al.* 2007). Long-tailed tits are early-season breeders, commencing nest-building in late February to early March, with first attempts hatching in early to mid April and the final attempts hatching in late May. Nests are exceptionally elaborate (Fig. 1.4): the first nests of the season take on average 38 days to build, although later attempts can take just 11 days to complete (McGowan *et al.* 2004). Long-tailed tits are single-brooded, but high rates of nest predation by avian (primarily corvid) and mammalian (primarily mustelid) predators, typically accounting for the failure of around 70% of nesting attempts, mean that many pairs have 2-3 repeat nesting attempts throughout the course of a season (Hatchwell *et al.* 2004).

Figure 2.4 The nest of the long-tailed tit, showing the exceptionally elaborate structure of moss, plant fibres and spiders' silk, coated in flakes of lichen and lined with feathers.

Long-tailed tits are a short-lived (typically 2-3 years), r-selected species with a high level of reproductive investment. Typical clutch size is 8-11 eggs, tending to decline in the latter part of the season (MacColl & Hatchwell 2002). Females start incubating on the final day of laying, and take sole charge of incubation, although males may occasionally bring their partner food (Hatchwell *et al.* 1999b). Eggs hatch after approximately 15 days of incubation, and nestlings are then fed a diet of caterpillars, flying insects and spiders until fledging at approximately 16 days of age. Both parents contribute to parental care of nestlings and fledglings, with provisioning typically continuing for 3-4 weeks after fledging (C. Napper, pers. comm.). Long-tailed tits are almost unique in the UK in that they are facultatively co-operative in their breeding habits: all individuals attempt to breed independently but birds that fail to fledge a brood sometimes assist relatives with the provisioning of nestlings and fledglings, becoming so-called helpers (Russell & Hatchwell 2001). Nestlings from helped broods have increased recruitment compared to unhelped broods, thus helpers gain indirect fitness benefits from their cooperative behaviour (MacColl & Hatchwell 2002, 2004). After the breeding season, all individuals join non-breeding flocks until the following February, with flocks generally comprising close relatives and helpers, as well as unrelated immigrants who are typically females that disperse between flocks in their first year of life (Sharp *et al.* 2008, 2011).

The European breeding population of long-tailed tits is large (exceeding 5 million pairs in 2000) and has been relatively stable overall in recent years (Marchant 1990; BirdLife International 2004). However, there appears to be regional variation in population trends, with populations in central and northern Europe being either stable or increasing, while French and Turkish populations showed slight declines during 1990-2000 (BirdLife International 2004). Future climatic scenarios are predicted to render the southern edge of its current range unsuitable, potentially leading to local extinctions in the Mediterranean and the Balkans (Huntley *et al.* 2007). Phenology and demography also show change. In the UK, the average timing of breeding of the long-tailed tit has advanced by approximately 16 days since 1966, which is more than any other insectivorous passerine in the UK (Baillie *et al.* 2014). In terms of productivity, data from nests across the UK show some evidence for a switch in the prevalence of predation from the egg to the chick stage, and a slight trend towards reduced clutch and brood size, that seems to be driving a slight increase in the number of fledglings per breeding attempt (Baillie *et al.* 2014). However, these demographic trends are based on relatively sparse data (around 40 nests per year across the UK) that are subject to variable observer effort between years (D. Leech, pers. comm.), and knowledge regarding recent demographic change in the long-tailed tit is therefore minimal.

1.4.2 Local study population

A population of long-tailed tits has been studied from 1994 to present in the Rivelin Valley, Sheffield, UK (53º38'N 1º56'W; altitude at centre of site = 168m above sea level, range = 150–270m). The site comprises approximately 2.5km^2 of suitable long-tailed tit breeding habitat in the form of mature woodland (primarily sessile/pedunculate oak *Quercus petraeus/robur* and European beech *Fagus sylvatica*) and scrub (primarily silver birch *Betula pendula* and hawthorn *Crataegus* spp). The remainder is open pasture, with some gardens present along the southern edge and the north-eastern corner. The breeding population size is approximately 25–72 pairs, and has increased since the study started (Meade *et al.* 2010). Almost all individuals (>95%) are ringed with unique combinations of colour rings (Fig. 1.1), either as nestlings hatching within the site, or as adults arriving as new immigrants. Each year, the vast majority of nesting attempts within the site are located by observation and monitored approximately every two days until fledging or nest failure. A very small proportion (estimated to be <5%) of nesting attempts are not found each year, but through monitoring parental activity it is known that the vast majority of these are short-lived attempts that rapidly fail (Sharp *et al.* 2008). In the case of nest failure, the study site is searched intensively for re-nesting attempts.

The majority of nests in the Rivelin population are accessible by humans, being built 1-2m above ground in shrubs, mainly bramble *Rubus spp.*, gorse *Ulex europaeus* and holly *Ilex aquifolium*. However around 10% of nests are inaccessible due to being built very high in trees, primarily silver birch, oak and Scot's pine *Pinus sylvestris*. Therefore data collection protocols differ between accessible and inaccesible nests, being based on direct observation for accessible nests (dates accurate to ± 1 day) and by monitoring parental activity for inaccessible nests (dates accurate to ± 2 days). For all nests, the date on which the first egg of each clutch is laid is recorded, as well as the date of hatching and fledging, or predation. For accessible nests, the mass (± 0.1g) and tarsus length (± 0.1mm) are recorded for all nestlings alive on day 11 of the nestling period (hatch day = day 0) and a blood sample collected by brachial venipuncture (under Home Office licence). Blood samples are used to genetically determine the sex of fledglings (Griffiths *et al.* 1998). All nests are watched for at least one hour every two days throughout the nestling period to record the identity of all carers (parents and helpers), and provisioning rates are recorded throughout each watch for all accessible nests and for the more visible of the inaccessible nests. For provisioning watches conducted during 2011–2013, the composition (caterpillar/non-caterpillar) and size of feeds was also recorded where possible.

The phenology of long-tailed tit food sources was monitored via two methods during 2009–2013: caterpillar phenology was recorded using the frass-fall method of Tinbergen & Dietz

(1994), and flying insect abundance was measured using sticky traps (yellow EasiStick traps measuring 10 x 24cm, Fargro Ltd). Traps were set at four locations covering a range of elevations throughout the study site, in scrubby and mature woodland areas. At each location, frass was collected from two birch and two oak trees, and sticky traps were set at five locations at least 50m apart. In addition, the phenology of budburst was recorded throughout the study site for the period 2010–2013, for approximately 80 individuals of each of five tree species common in the Rivelin site, namely elder *Sambuca nigra*, hawthorn, silver birch, European beech and English oak. Further details of field protocols are given in relevant chapters.

1.4.3 National long-tailed tit data

Data regarding national demography of long-tailed tits were obtained from the British Trust for Ornithology (BTO), which monitors avian demography and population size across the UK under a range of surveys. These surveys are undertaken largely by skilled volunteers, and have been used for numerous applied research purposes, including identification of population declines and species of conservation priority. I obtained data on timing of breeding in long-tailed tits during 1968–2010 from the BTO Nest Record Scheme, which records timing of laying from around 50 nests across the UK annually; individual nest records are geographically patchy, but do comprise nests from a broad range of latitudes within England and Scotland. UK population trends were obtained from the BTO Common Bird Census (1962–2000) and the Breeding Birds Survey (1994–present). Finally, I obtained data from the BTO Constant Effort Site ringing scheme, which offers detailed site-specific data regarding the abundance of juveniles and adults present throughout May to September each year at a range of sites across the UK, with schemes at individual sites commonly running for 10 years or more.

1.4.4 Weather data

Recent local weather data were obtained from the Weston Park Weather Station (Museums Sheffield 2013), located 5km from the centre of the study site and at a similar elevation (53º38'N 1º49'W; 131m above sea level). These data comprised mean temperature and total precipitation on a monthly, daily and hourly basis for the periods 1966–2013, 1994–2013 and 2009–2013 respectively. Local weather data were also collected within the Rivelin study site at twenty points distributed throughout the study site during three years of the study (2010–2012). These data were recorded at 4-hour intervals using miniature data loggers mounted in a white solar radiation shield (DS1921G-F5 thermochron i-buttons). National temperature data were obtained for the period 1968–2010 from the HadCET database (Parker, Legg & Folland 1992) and projected future (2010–2100) absolute climatic variables were extracted from UK Climate Projections 2009 for the 25 x 25km grid square including the Rivelin Valley close to its centre.

1.5 Aims and thesis structure

The overall aim of this thesis is to determine how weather impacts long-tailed tit demography, by investigating temporal changes in weather at a local and national scale and the relationship between these changes and long-tailed tit phenology, survival and reproduction. The thesis is structured as follows. In chapter two, I examine timing of breeding in response to monthly weather, to explore the suggestion that earlier laying in warmer springs leads to an increase in breeding season length, which could increase productivity. In chapter three, I investigate the factors influencing annual adult survival rates of long-tailed tits, to test the hypothesis that increasing winter temperatures are leading to a corresponding increase in over-winter survival. In chapter four, I investigate the relationship between productivity of individual breeding pairs in relation to the weather experienced during each stage of the nesting cycle, as well as the effects of monthly conditions and predation on annual mean population productivity. In chapter five, I provide an investigation of the trophic mismatch hypothesis, exploring the similarity of phenological responses to temperature shown by long-tailed tits and their caterpillar food sources, and the impact of mismatch on reproductive parameters. Finally, in chapter six I synthesise the evidence for the various mechanisms contributing to population change in long-tailed tits, providing an indication of how populations may change in the future.

Chapter 2. Phenology of breeding

This chapter is published as:

Gullett P., Hatchwell B.J., Robinson R.A. & Evans K.L. (2013) Phenological indices of avian reproduction: cryptic shifts and prediction across large spatial and temporal scales. *Ecology and Evolution* 3, 1864–1877.

Summary

Climate change-induced shifts in phenology have important demographic consequences, and are frequently used to assess species sensitivity to climate change. Therefore, developing accurate phenological predictions is an important step in modelling species responses to climate change. The ability of such phenological models to predict effects at larger spatial and temporal scales has rarely been assessed. It is also unclear whether the most frequently used phenological index, namely the average date of a phenological event across a population, adequately captures phenological shifts in the distribution of events across the season. We use the long-tailed tit *Aegithalos caudatus* as a case study to explore these issues. We use an intensive 17-year local study to model mean breeding date and test the capacity of this local model to predict phenology at larger spatial and temporal scales. We assess whether local models of breeding initiation, termination and re-nesting reveal phenological shifts and responses to climate not detected by a standard phenological index, i.e. population average lay date. These models take predation timing/intensity into account. The locally-derived model performs well at predicting phenology at the national scale over several decades, at both high and low temperatures. In the local model a trend towards warmer Aprils is associated with a significant advance in termination dates, probably in response to phenological shifts in food supply. This results in a 33% reduction in breeding season length over 17 years – a substantial loss of reproductive opportunity that is not detected by the index of population average lay date. We show that standard phenological indices can fail to detect patterns indicative of negative climatic effects, potentially biasing assessments of species vulnerability to climate change. More positively, we demonstrate the potential of detailed local studies for developing broader-scale predictive models of future phenological shifts.

2.1 Introduction

Phenology plays a key role in regulating species interactions that can determine population dynamics (Miller-Rushing *et al.* 2010). Recent climate change has brought about phenological shifts in a wide range of species (Walther *et al.* 2002; Thackeray *et al.* 2010), with a particularly well-studied example being the earlier onset of breeding in temperate bird populations in years with warmer spring conditions (Thomas *et al.* 2001; Charmantier *et al.* 2008; Both *et al.* 2009). Species exhibiting larger phenological shifts are typically more resilient to the negative impacts of climate change than those exhibiting more limited phenological advance (Møller, Rubolini & Lehikoinen 2008; Jones & Cresswell 2010), and predicting future phenological trends would therefore facilitate assessment of species sensitivity to climate change (Diez *et al.* 2012). Predictive capacity could be limited by non-linearity in climatic responses, local adaptation, and variation in the capacity to exhibit plastic phenological responses (Primack *et al.* 2009; Perfito *et al.* 2012; Porlier *et al.* 2012), but empirical assessments of the ability of phenological models to predict responses at different spatial or temporal scales are very rare (but see Hodgson *et al.* 2011) and urgently needed (Diez *et al.* 2012).

Some of the assumptions underlying the use of phenological indices in the assessment of species vulnerability to climate change also warrant more detailed empirical testing. Many phenological indices in frequent use are calculated as the mean timing of an event across the focal population. These ‘population mean indices’ are certainly preferable to indices of the timing of first events (Miller-Rushing *et al.* 2008), which only capture responses of a very limited proportion of the focal population. However, indices of a population’s mean timing assume that climate change does not alter the distribution of events within a season. This is not always true; for instance, the mean timing of avian breeding is sensitive to climatic influences on the frequency of second broods (Visser *et al.* 2003; Husby, Kruuk & Visser 2009). There has, however, been insufficient exploration of how climate change alters the distribution of breeding attempts in single-brooded species, and the consequences of this for using phenological indices as indicators of species sensitivity to climate change. If climate change has equivalent impacts on the timing of breeding initiation and termination then phenological indices of the mean timing of reproduction are robust (Fig. 2.1a). Different months of the breeding season can, however, exhibit divergent climatic trends that may result in different impacts on initiation and termination (Houghton *et al.* 2001; Halupka, Dyrcz & Borowiec 2008). Consequently, an advance in the population mean lay date could be observed even if the onset of reproduction has not advanced, due to earlier termination of breeding attempts (Dawson 2005; Fig. 2.1b). In contrast, mean breeding date will not advance, even if onset of breeding has advanced, if the end of the breeding season is delayed by a similar amount (Fig. 2.1c); such lengthening of the breeding season could arise if longer growing seasons (Menzel & Fabian 1999) increase food availability both early and late in the season. Finally, a shift in predation regime could alter the proportion of pairs building repeat nests, thus driving a change in a population's mean lay date that is unrelated to climate change; for example, an increase in nest predation rates is likely to generate more replacement nests later in the season, thus delaying mean breeding dates (Fig. 2.1d).

Here, we extend previous work that has analysed the effects of climate change on the distribution of breeding attempts in multi-brooded species by focusing on a single-brooded species. We assess whether population average lay date is a reliable indicator of the distribution of breeding events, and hence of phenological shifts and sensitivity to climate change. We use high-resolution data from an intensive 17-year study of the long-tailed tit *Aegithalos caudatus* in central England, and extensive national scale data collected over a 43-year period. This single-brooded species provides an ideal case study as it exhibits one of the most rapid advances in mean annual lay date amongst British birds (Baillie *et al.* 2012). Moreover, in contrast to almost all other avian species subject to intensive phenological studies, the long-tailed tit does not use nest boxes, and thus experiences high rates of nest predation (c. 70%), resulting in re-nests accounting for approximately 40% of nesting attempts per year (Hatchwell *et al.* 1999a). This allows us to determine the nature of associations between the timing and intensity of predation regimes and phenological indices of the timing of reproduction. We also provide the first empirical assessment of whether locally-derived models of avian phenology can be scaled up to predict phenological trends at larger spatial scales and in different time periods. This is an essential step towards predicting phenological trends under future climate change scenarios.

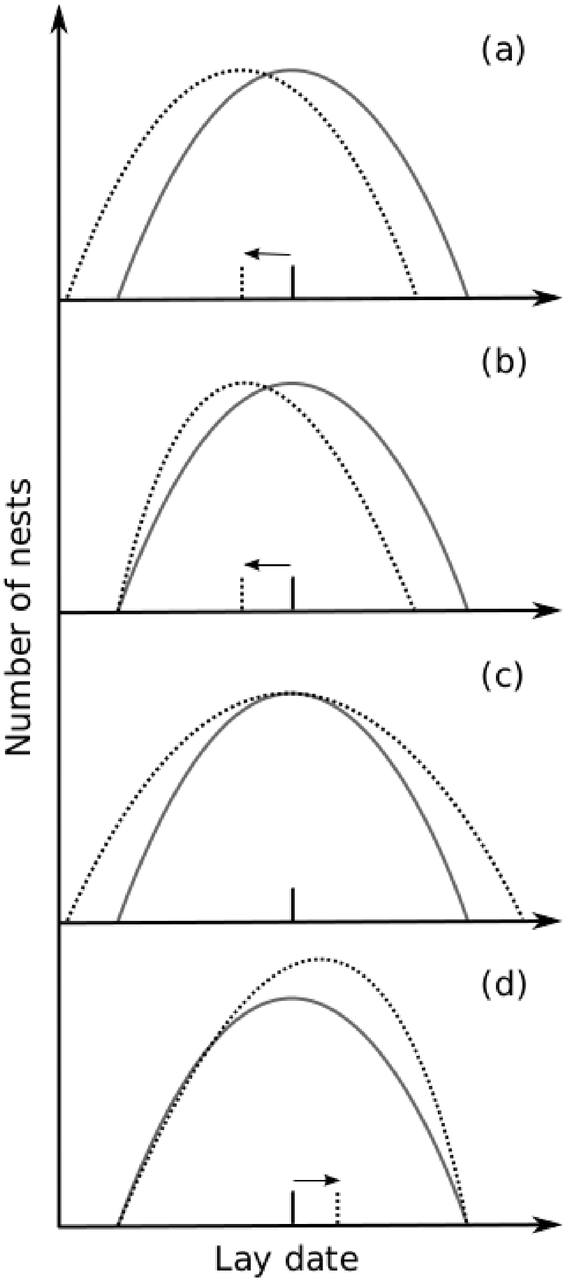

Figure 2.1 Hypothetical distributions of population lay dates prior to (solid line) and following (dotted line) climate change, showing resultant changes in mean lay date. Numerous responses are possible but this subset illustrates the problem with using population mean breeding date as a phenological indicator of species responses to climate change. Mean breeding date can advance when populations: (a) start and end breeding earlier or (b) start at the same time but end breeding earlier. Mean breeding date may also (c) exhibit no advance when breeding commences earlier if breeding continues for longer, and (d) exhibit changes that are unrelated to climate change, such as a later mean breeding date due to increased predation rates that increase the proportion of re-nests.

2.2 Methods

2.2.1 Study system

We studied a population of 25-72 pairs (mean 46 pairs) of long-tailed tits in the Rivelin Valley, Sheffield, UK (53°23'N 1°34'W) during the period 1995–2011. Long-tailed tits are single-brooded, but nest predation rates are high and pairs that fail frequently initiate a second or third re-nest attempt if there is sufficient time to raise a brood. Re-nests thus accounted for around 32% of nests per year over the current study (range = 0.26 – 0.40), and the proportion of re-nesting showed no temporal trend over the course of the study ($R^2_{1,13} = 0.05$, $P = 0.43$). The long-tailed tit is a facultative co-operative breeder and some failed breeders help other pairs rather than re-nesting themselves, particularly if they fail later in the season (MacColl & Hatchwell 2002; Hatchwell *et al.* 2004). At least 95% of adult birds in the study site are uniquely marked with colour-rings each breeding season and all pairs within the study site are monitored and their nests located by observation. A very small proportion (estimated to be <5%) of nesting attempts are not found each year, but through monitoring parental activity it is known that the vast majority of these are short-lived attempts that rapidly fail (Sharp *et al.* 2008). Nests are monitored approximately every two days. In the case of nest failure, the study site is searched intensively for re-nesting attempts. The date on which the first egg of each clutch is laid (hereafter referred to as first egg date) is recorded so that day 1 corresponds to 1 March, and is accurate to within one day for all accessible nests. Inaccessible nests comprise approximately 10% of the data, and their first egg date is estimated by observing the time at which parents stop lining nests, which typically occurs when laying starts, and/or by recording the date when females commence incubation (the last day of egg-laying) and assuming a clutch of 10 eggs (the modal clutch size in the study population; Hatchwell *et al.* 2004). Observations of nestling provisioning and fledging dates suggest that these lay dates for inaccessible nests are generally accurate to ± 2 days.

2.2.2 Datasets

Data were collected from the local Rivelin population of long-tailed tits during 1995–2011, including first egg dates for 824 nests (559 first nesting attempts and 265 re-nests) and failure dates for 590 nests (410 first attempts and 180 re-nests). Data from 2001 were omitted from all analyses because access to the field site was limited by an outbreak of foot and mouth disease, and data from 2003 were excluded in analyses regarding the timing of re-nesting and termination of breeding due to limited search effort for re-nests at the very end of the field season in that year. Weather data were obtained for the period 1968–2011 from the Weston Park Weather Station, located 5km from the centre of the Rivelin study site (53º38'N 1º49'W).

Monthly mean temperature and monthly total precipitation were calculated. These data were very strongly correlated with UK Climate Projections (UKCP) interpolated data (available until 2006, Jenkins, Perry & Prior 2008) for the 5km x 5km grid cell containing the study site (Pearson's correlations, henceforth r, with $n = 11$; May precipitation: $r = 0.84$; all other comparisons: $r > 0.96$). Food abundance data were also collected at four locations, from a total of 16 trees, within the Rivelin study site by collecting caterpillar frass samples throughout the spring for the period 2009–2012, as caterpillars are the primary food source of long-tailed tits provisioning nestlings. We thence calculated the annual date of peak caterpillar abundance, and assessed the association between peak date and spring weather variables to test the hypothesis that food abundance declines earlier in years with warmer spring temperatures (see Appendix 1 for full methods).

National data were obtained for the period 1968–2010 from the British Trust for Ornithology's (BTO) Nest Record Scheme (Crick, Baillie & Leech 2003). These nest records include an unknown proportion of first nesting attempts and re-nests, from various locations throughout the UK (mainly England) excluding the Rivelin Valley area. The mean annual lay date was calculated across all records within each year (mean annual sample size = 50; range = 18 – 123). For weather data, we used Central England Temperature from the HadCET database (Parker, Legg & Folland 1992), as used in previous analyses of climatic influences on lay dates using nest record card data (Crick *et al.* 1997; Crick & Sparks 1999).

2.2.3 Constructing phenological indices

Initiation date, re-nesting date, average lay date

The distribution of first egg dates within each year deviated from a normal distribution so we used median first egg dates as a phenological indicator, although there was a strong correlation between mean and median first egg dates (all attempts: $r_{14} = 0.944$, $P < 0.001$; first attempts: $r_{14} = 0.996$, $P < 0.001$; re-nests: $r_{13} = 0.921$, $P < 0.001$). Within each year, initiation date was the median of first egg dates from first attempts; re-nesting date was the median of first egg dates from re-nesting attempts; average lay date was the median of first egg dates from all attempts, thus corresponding to the standard phenological index used in most studies.

Termination date index

The time when pairs cease to initiate re-nests following nesting failure provides an index of the end of the breeding season. In each year we modelled the probability of a failed pair re-nesting rather than terminating breeding activity, as a function of failure date, using a series of generalised linear models with logit link function and binomial error structure. Data were excluded from nests in which: (a) pair bonds were disrupted by divorce or mortality; (b) failure date was before the median lay date of first attempts; and (c) the failed attempt was located close to the field site boundary and pairs were suspected to be re-nesting outside the study area. All of these annual models of termination date had high explanatory power (mean McFadden's $R^2 = 0.59$) and were statistically significant ($P < 0.05$) in all but one year in which $R^2 = 0.85$ (Appendix 2.1). Within each year, we used the predicted date at which 75% of breeding pairs did not re-nest as an index of annual termination date as this reflected the time when a large proportion of birds had stopped breeding and was robust to the inclusion of very late-terminating outliers, which only occur in some years. The 75% threshold termination date (henceforth 'termination index') was strongly correlated with the alternative termination thresholds of 50% ($r_{13} = 0.860$, $P < 0.001$) and 90% ($r_{13} = 0.957$, $P < 0.001$).

Breeding season length index

We calculated two indices of breeding season length. The first was the interval between the median initiation date and termination index for each year, which were not correlated with each other ($r_{13} = 0.16$, $P > 0.1$); the second was the interval between the 10th and 90th percentile of all known first egg dates within each year. These two indices were strongly correlated with each other ($r_{13} = 0.83$, $P < 0.001$) and we used the latter in subsequent analyses because it is more routinely used (e.g. Evans *et al.* 2005; Møller *et al.* 2010).

2.2.4 Predation indices

The timing and intensity of nest predation may influence the timing of re-nesting and termination, and consequently breeding season length (Fig. 2.1d). We therefore calculated two measures of predation timing to test for trends in predation patterns: (i) the annual time of predation, as the median date of all nest predation events; (ii) the annual time of predation of first nesting attempts, as the median date of predation events of first nesting attempts; these two indices of predation timing were highly correlated ($r_{14} = 0.96$, $P < 0.0001$) and we used the former index in subsequent analyses as it offered a more complete picture of predation timing. We also calculated two indices of predation intensity: (i) annual proportion of nests predated, which was the annual proportion of nests predated among nests known to have been predated or fledged; (ii) annual Mayfield predation estimate, which was the annual Mayfield estimate of predation risk throughout the nesting cycle; these two indices of predation intensity were highly correlated ($r_{14} = 0.98$, $P < 0.0001$) and we used the latter in subsequent analyses because it offers a more comprehensive measure of predation rates (Mayfield 1975). Annual Mayfield estimates were calculated via a three-part process: (i) we calculated daily nest survival rates at the egg-laying, incubation and chick-rearing stages using the Mayfield method (Mayfield 1975); (ii) we used these daily survival rates to calculate the probability of a nest surviving the entire duration of each stage by raising the daily rates to the power of the stage duration in days, assuming stage durations of nine days for egg-laying, 15 days for incubation, and 16 days for chick rearing (the typical durations of these stages in the focal population; Hatchwell *et al.* 2004); (iii) we calculated annual nest predation risk as the product of the three annual stage-specific survival probabilities, subtracted from one.

2.2.5 Assessing temporal trends

All statistical analyses were conducted in R (R Development Core Team 2010). We first assessed trends in local mean monthly spring temperature and precipitation, using year as a predictor (both linear and squared terms); trends were assessed over two time periods: 1995–2011, i.e. the duration of the focal study, and 1968–2010, i.e. the period over which long-tailed tit phenology was analysed at the national scale. We then investigated temporal trends in breeding events and predation, again using the linear and squared year terms as predictors and regressing them against each separate phenological index (initiation date, re-nesting date, average lay date, termination date index, and breeding season length index) and against each predation index (predation timing and predation intensity).

2.2.6 Mechanisms of phenological change: climate, predation, food, adaptation

At the study site, long-tailed tit pairs typically start nest-building in February/March and egg-laying in March/April; re-nesting attempts occur between March and May and pairs finish breeding by early June (MacColl & Hatchwell 2002). Therefore, to investigate the effects of climate on reproductive phenology we modelled: (a) initiation date in response to temperature and precipitation during February, March and April; (b) re-nesting date in response to temperature and precipitation during March, April and May, and the timing and intensity of predation; (c) termination index in response to temperature and precipitation during March, April and May, and the timing and intensity of predation; and (d) breeding season length in response to temperature and precipitation during February, March, April and May, and the timing and intensity of predation. We constructed multiple linear regression models with normal error structure (Shapiro-Wilk normality tests: $P > 0.3$ for all response variables). We used an information theoretic approach to model selection in which all possible models were constructed given the set of predictors; model fit was assessed using AICc and model averaging was conducted over the 95% confidence set of models (Burnham & Anderson 2002). Collinearity between climatic predictors was within the tolerance levels to which information theoretic methods are robust (variance inflation factor < 3.9 for all variables; Freckleton 2011; Appendix 2.2).

In order to test the hypothesis that the timing of breeding termination is influenced by the seasonal decline in caterpillar availability, we estimated the timing of peak caterpillar abundance in the Rivelin study site for the period 2009–2012, and determined the correlation between annual peak date and mean temperature during March and April. Full methods are described in Appendix 1.

Finally, we tested the hypothesis that local genetic adaptation may contribute to the observed changes in breeding phenology in the study population, because selection may act on the focal phenological traits (initiation and termination). Following the results of the climatic analysis, we modelled initiation date in response to March temperature and termination index in response to April temperature, comparing models in which year was included as an additive or interactive effect, in order to assess whether the observed temperature-phenology reaction norms have changed significantly over time. Such a temporal change in reaction norms would be compatible with the hypothesis that selection is driving evolutionary change in the form of phenological responses.

2.2.7 Predicting phenology at larger spatial and temporal scales

Comparisons between local (i.e. Rivelin Valley) and national (i.e. UK) phenological responses could only be conducted using population average lay date calculated across all attempts, as other phenological indices are unavailable at the national scale. We first compared climatic models of long-tailed tit average lay date at the national and local scales, using data for 1995–2010, i.e. the duration over which both local and national data were available. Second, we used the local climatic model of phenology to predict phenology at the national scale across a much larger time scale, i.e. 1968–2010, and regressed these predicted national annual lay dates against the national mean annual lay dates observed in the BTO dataset. If local climatic models of avian phenological responses can be scaled up to larger spatial and temporal scales we predict that the slope of this relationship will approximate unity. We assessed whether the performance of the model deteriorates further back in time, by calculating the square of the difference between predicted and observed values and regressing this against year (linear and quadratic terms; Piñeiro *et al.* 2008). We also assessed the performance of the locally-derived model over years entirely outside the temporal span of the locally-derived model (i.e. 1968–1994). In order to conduct a conservative test, March temperature was the only climatic variable used in these analyses as all other climatic variables had little influence on the average lay date of the Rivelin population (see Results).

2.3 Results

2.3.1 Extent of climatic change

Although spring mean monthly temperature and precipitation variables within the study region varied substantially between years, temporal trends within the study period (1995–2011, excluding 2001) were limited. The exception was April temperature which increased linearly (+0.12°C per year, $R^2_{1,14} = 0.22$, $P = 0.06$; Appendix 2.3). From 1968 to 2010 all spring mean monthly temperatures increased linearly; the increase was most marked in April (+0.05ºC per year, $R^2_{1,40} = 0.30$, $P < 0.001$; Appendix 2.3). Temporal trends in spring mean monthly precipitation between 1968 and 2010 were negligible (Appendix 2.3).

2.3.2 Temporal trends in phenological indices and predation

The range of annual median lay dates across all nesting attempts was 2 to 21 April (mean ± 1SE = 10 April ± 1.2 days), across first attempts it was 29 March to 20 April (mean = 8 April ± 1.4 days), and across re-nests it was 17 April to 3 May (mean = 25 April ± 1.4 days). The range of the annual termination index was 22 April to 10 May (mean = 30 April ± 1.5 days), and the breeding season length index, measured as the interval between the 10th and 90th percentile of all first egg lay dates, was 13 to 33 days (mean = 24 ± 1.3 days).

There was a linear trend towards advancing lay date over the period 1995–2011 for all three nesting categories (i.e. all attempts, first attempts, and re-nests) but this was significant only for re-nests, with the fitted model predicting an advance of 0.66 days per annum ($R^2_{1,13} = 0.44$, $P < 0.01$; Fig. 2.2a, Table 2.1). Termination date showed a significant linear advance from 1995 to 2011 of 0.97 days per annum ($R^2_{1,13} = 0.77$, $P < 0.0001$; Fig. 2.2b, Table 2.1). The breeding season length index exhibited a linear reduction of 0.51 days per annum ($R^2_{1,13} = 0.30$, $P < 0.05$; Fig. 2.2c, Table 2.1), equating to a 33% reduction in the average length of the reproductive laying window.

Predation showed no temporal trend, whether calculated over all predation events or just predation of first nesting attempts (Table 2.1). Similarly, neither index of predation intensity showed a temporal trend (Table 2.1), despite substantial variation between years (annual proportion of predations ranged from 0.52 to 0.85, mean ± 1SE = 0.72 ± 0.10; annual Mayfield estimates ranged from 0.47 to 0.80, mean ± 1SE = 0.67 ± 0.10; Appendix 2.4).

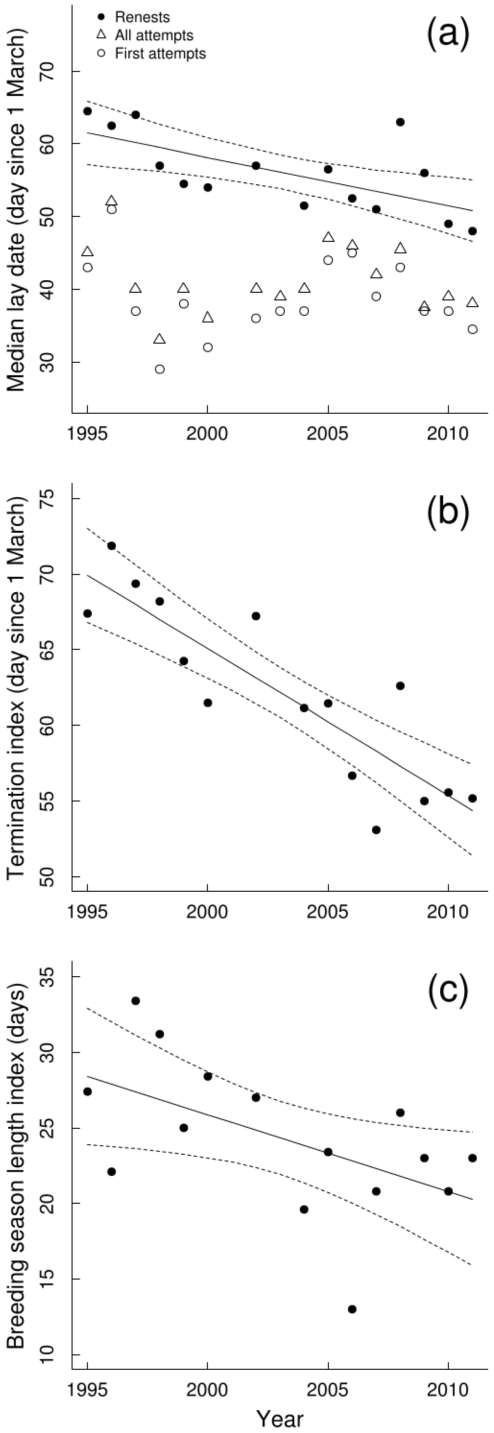

Figure 2.2 Temporal trends in long-tailed tit phenology in the Rivelin population (1995–2011), showing linear regressions (solid lines) ± 95% confidence intervals (dashed lines). (a) annual median lay dates of re-nests have advanced (est. ± 1SE = -0.66 ± 0.21, $R^2 = 0.44$), whilst annual median lay dates of all nesting attempts and first attempts show no significant change; (b) timing of termination has advanced (est. ± 1SE = -0.97 ± 0.15, $R^2 = 0.77$); (c) breeding season length has decreased (est. ± 1SE = -0.50 ± 0.22, $R^2 = 0.30$).

Table 2.1 Temporal trends in indices of long-tailed tit phenology and nest predation, in the Rivelin Valley, Sheffield (1995–2011). Shown are the results of general linear models, where * denotes variables showing evidence of a temporal trend, for five aspects of breeding phenology (initiation date i.e. median lay date of first attempts, re-nesting date, average lay date of all attempts, termination index, breeding season length index), two indices of predation timing (median predation date, median predation date of first attempts) and two indices of predation intensity (proportion of nests predated, Mayfield estimate of predation risk).

Index	Linear trend (days ± 1SE)	R^2	F_{df}	P	Linear model $\Delta\mathrm{AICc}_{\mathrm{null}}$
Initiation date	-0.10 ± 0.28	0.01	$0.14_{1,14}$	0.72	+3.02
Re-nesting date*	-0.66 ± 0.21	0.44	$10.07_{1,13}$	0.007	-5.42
Average lay date	-0.12 ± 0.24	0.02	$0.26_{1,14}$	0.62	+2.89
Termination index*	-0.97 ± 0.15	0.77	$42.50_{1,13}$	<0.0001	-18.59
Breeding season length index*	-0.51 ± 0.22	0.30	$5.47_{1,13}$	0.04	-2.09
Predation date	+0.03 ± 0.37	<0.01	$0.01_{1,14}$	0.93	+3.17
Predation date of 1st attempts	+0.07 ± 0.46	<0.01	$0.02_{1,14}$	0.88	+3.16
Proportion of nests predated	-0.007 ± 0.005	0.14	$2.28_{1,14}$	0.15	+0.77
Mayfield estimate of predation	+0.008 ± 0.005	0.15	$2.48_{1,14}$	0.14	+0.58

Linear and quadratic models were compared for each response variable by assessing the change in AICc with respect to the null model, where a negative $\Delta\mathrm{AICc}_{\mathrm{null}}$ indicates evidence of a temporal trend; linear models were always more parsimonious than quadratic ones, and linear trends are therefore displayed below with associated statistics. Note that data from 2001 were excluded from all models; data from 2003 were excluded from analyses of re-nesting, termination and breeding season lengh (see Methods).

2.3.3 Effects of climate, predation and food on avian phenology

Climate explained a consistently large proportion, between one third and two thirds, of the annual variation in long-tailed tit phenological indices. Warm March temperatures advanced the median lay date of all attempts (model averaged partial $R^2 = 0.54$, est. = -2.93, $n = 15$) and the median lay date of first attempts (model averaged partial $R^2 = 0.58$, est. = -3.44, $n = 15$; Fig. 2.3a). All other climatic variables had little influence on these phenological indices (Table 2.2). Median lay dates of re-nests advanced in years with warm Aprils (model averaged partial $R^2 = 0.35$, est. = -2.74, $n = 14$; Fig. 2.3b); there was also a marginal tendency for wet Aprils to advance the timing of re-nests (model averaged partial $R^2 = 0.06$, est. = -0.03, $n = 14$); all other climate variables, including March temperature, and the timing and intensity of predation had little influence on re-nesting dates (Table 2.2).

The index of termination date advanced in years with warm Aprils (model averaged partial $R^2 = 0.32$, est. = -2.79, $n = 14$; Fig. 2.3c); other climate variables, including March temperature, and the timing and intensity of predation had little influence (Table 2.2). Breeding seasons were longer in years with warm February (model averaged partial $R^2 = 0.24$, est. = +1.32, $n = 14$) and March temperatures (model averaged partial $R^2 = 0.10$, est. = +0.76, $n = 14$), and there was evidence that they were reduced in years with warm Aprils (model averaged partial $R^2 = 0.05$, est. = -0.6, $n = 14$; Table 2.2). All other climatic variables and the timing and intensity of predation had little influence on breeding season length (Table 2.2).

Caterpillar abundance peaked earlier in years with warmer April temperatures over the period 2009–2012 ($r = -0.72$); data were insufficient to estimate reliably the slope and statistical significance of this relationship ($n = 4$), but the observed relationship equates to a strong effect size (Cohen 1988). Peak caterpillar date showed no relationship with March temperature ($r = 0.05$, $n = 4$).

2.3.4 Microevolution versus phenotypic plasticity

There was a slight tendency for the relationship between March temperature and timing of initiation to become weaker over time, and for the relationship between April temperature and timing of termination to become stronger over time, but neither of these trends were significant (2-way ANOVA comparing additive '*temperature* + *year*' with interactive '*temperature* x *year*' models: Initiation: $F_1 = 0.172$, sum of squares = 2.00, $P = 0.69$; Termination: $F_1 = 0.002$, sum of squares = 0.017, $P = 0.97$).

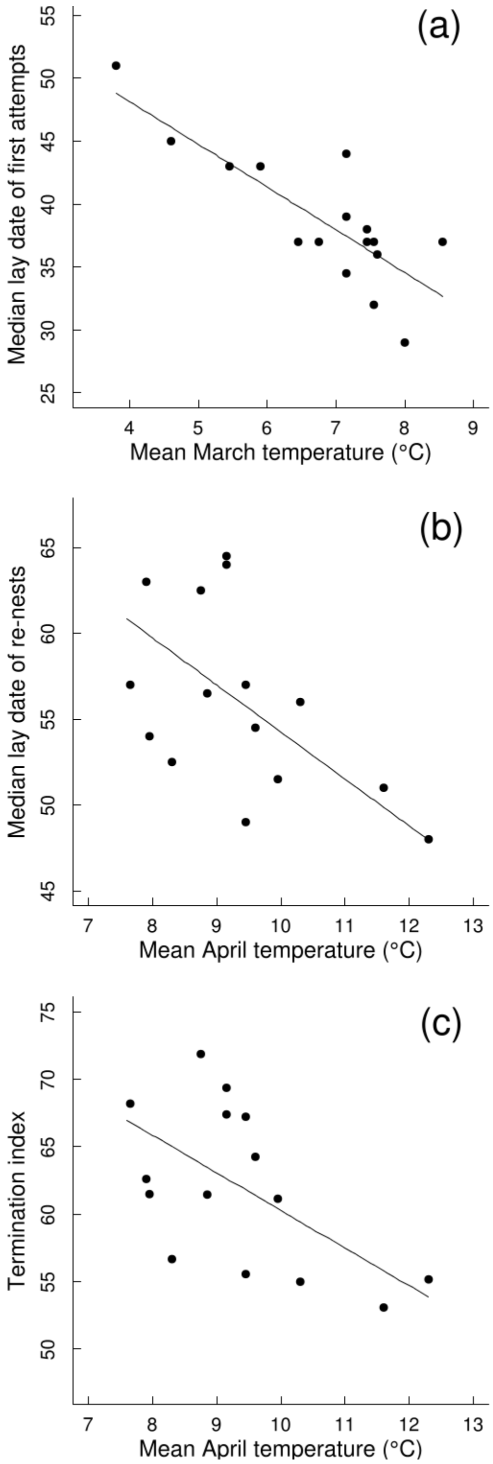

Figure 2.3 Associations between weather and long-tailed tit phenology in the Rivelin population (1995–2011), showing relationships in model-averaged estimates holding other variables at mean values. (a) median lay date of first attempts advances with warmer March temperature (est. ± 1SE = -3.40 ± 0.74, partial R^2 = 0.58); (b) median lay date of re-nests advances with warmer April temperature (est. ± 1SE = -2.74 ± 1.18, partial R^2 = 0.35); (c) termination date advances with warmer Aprils (est. ± 1SE = -2.79 ± 1.21, partial R^2 = 0.32). Date is days from 1 March.

Table 2.2 Model averaging results from multiple regressions of breeding phenology (median lay date of all attempts/first attempts/re-nest attempts, termination index, and breeding season length index) in response to monthly spring temperature (temp, ºC) and precipitation (prec, mm) in the Rivelin population of long-tailed tits, 1995–2011. Predation (pred) intensity and timing were also included as predictors in the latter three models. Variables not included are indicated by n/a. Variables not retained in the model average are indicated by 0.

Model	Feb temp	Mar temp	Apr temp	May temp	Feb prec	Mar prec	Apr prec	May prec	Pred intensity	Pred timing	**Mod ave R^2**
All attempts											
Estimate	-0.03	-2.93	-0.01	-0.16	<0.01	-0.01	<0.01	<0.01	n/a	n/a	
±1SE	0.22	0.72	0.25	0.54	0.01	0.02	0.01	0.01	n/a	n/a	
Partial R^2	<0.01	0.54	<0.01	<0.01	0.01	0.01	<0.01	<0.01	n/a	n/a	**0.65**
1st attempts											
Estimate	-0.14	-3.4	-0.01	n/a	<0.01	-0.01	-0.01	n/a	n/a	n/a	
±1SE	0.39	0.74	0.26	n/a	0.01	0.02	0.01	n/a	n/a	n/a	
Partial R^2	0.01	0.58	<0.01	n/a	<0.01	<0.01	0.01	n/a	n/a	n/a	**0.69**
Re-nest attempts											
Estimate	n/a	0	-2.74	0	n/a	0	-0.03	0	+3.34	0	
±1SE	n/a	0	1.18	0	n/a	0	0.04	0	8.79	0	
Partial R^2	n/a	0	0.32	0	n/a	0	0.06	0	0.02	0	**0.35**
Termination											
Estimate	n/a	0	-2.79	0	n/a	-0.02	0	0	0	0	
±1SE	n/a	0	1.21	0	n/a	0.05	0	0	0	0	
Partial R^2	n/a	0	0.32	0	n/a	0.02	0	0	0	0	**0.33**
Breeding season length											
Estimate	+1.32	+0.76	-0.60	-0.13	<0.01	-0.01	<0.01	-0.02	+0.02	-0.04	
±1SE	1.1	1.21	0.95	0.59	0.01	0.02	0.01	0.04	1.63	0.12	
Partial R^2	0.24	0.10	0.05	0.01	<0.01	0.01	<0.01	0.04	<0.01	0.02	**0.50**

2.3.5 Predicting phenology at larger spatial and temporal scales

The form of bivariate relationships between long-tailed tit phenology and March temperature during 1995–2010 at the local scale (est. = -2.94; 95% confidence intervals -4.29 to -1.58) was similar to that at the national scale (est. = -3.62; 95% CIs -4.94 to -2.31). Moreover, predictions of national mean lay date during 1968–2010, derived from the climatic (March temperature) model of the local Rivelin population's phenological response during 1995–2011, were strongly correlated with the observed values of the national population's mean lay date ($r_{40} = 0.68$, $P < 0.001$), and the slope of the relationship between predicted and observed values was very close to unity (est. = 1.17; 95% CIs 0.76 to 1.57; Fig. 2.4). Predictive capacity was still high when using the local phenology model to predict national phenology in years entirely outside the range of years during which local data were collected, i.e. 1968–1994 ($r_{25} = 0.63$, $P < 0.001$), and the slope between predicted and observed values in this period was lower, but again not significantly different from unity (est. = 0.76; 95% CIs 0.37 to 1.14; Fig. 2.4). Predictive capacity did not deteriorate over time (linear model of the squared difference between predicted and observed values, regressed against year: $F_{1,40} = 1.48$, $R^2 = 0.04$, $P = 0.23$; quadratic model: $F_{2,39} = 0.88$, $R^2 = 0.04$, $P = 0.42$), although the extent of advance in mean lay dates tended to be under-predicted from the March temperature model in recent years (1995–2011; Fig. 2.4). The range of March temperatures used when constructing the local model (1995–2011: 3.80 to 8.6°C) was similar to the range of March temperatures experienced by the national population over both time periods (1968–2010: 3.3 to 8.4 °C; 1968–1994: 3.3 to 8.3 °C). The residuals of the relationship between observed and predicted national mean annual lay dates were not associated with temperature (1968–2010: $r_{40} < 0.01$, $P > 0.05$; 1968–1994: $r_{25} < 0.01$, $P > 0.05$).

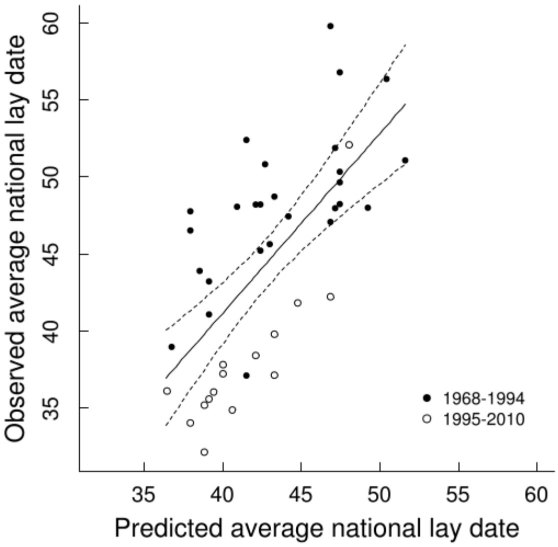

Figure 2.4 Predictions of national average long-tailed tit lay date derived from the local climatic model (i.e. average lay date in response to March temperature in the Rivelin population), compared to observed national average lay dates, 1968–2010. Filled circles represent the period excluding the period of study at the local scale (1968–1994); open circles represent the period for which both local and national data were available (1995–2010). The solid line represents the correlation between observed and predicted dates ($r_{40} = 0.68$, $P < 0.001$); dashed lines indicate 95% confidence intervals. The slope of the relationship is close to unity (1.17 ± 0.20) and is similar when restricting prediction to years not present in the local model (i.e. 1968–1994; filled circles: $r_{25} = 0.63$, $P < 0.001$). Date is days from 1 March.

2.4 Discussion

This study shows that the standard phenological index of mean population lay date does not detect key phenological responses that could have important demographic impacts, such as the substantial reduction in breeding season length observed here. More positively, we show that local phenological models can be successfully applied at larger spatial and temporal scales. This ability to scale up from local phenological models has rarely been demonstrated previously (but see Hodgson *et al.* 2011), and we are not aware of any such avian studies. We thus offer novel insight into an approach through which detailed information from intensive local studies can be used to develop broader-scale predictive models of climate change impacts.

2.4.1 Scaling up from local to national, short-term to long-term

The local and national models of lay date as a function of March temperature are statistically indistinguishable, and the locally-derived phenology model performs reasonably well in predicting previous mean lay dates at the national scale. We thereby show that intensive local studies that capture a broad range of phenological responses can provide useful inference at much larger spatial scales. Such spatial extrapolation is likely to be crucial for developing broad-scale predictive capacity in the face of climate change, because the inherent patchiness of phenological data at national and regional scales mean that such broad-scale data offer limited ability to detect patterns such as the divergent trends in breeding initiation and termination. It is important to note that there are inevitably limits to such spatial extrapolations, particularly in species with broad geographical ranges, such as the long-tailed tit. Applying local models to areas experiencing markedly different annual weather regimes would clearly be inappropriate, and multiple local studies in areas of contrasting climates are thus required in order to develop predictions across the species' large geographic range. However, the present study shows that local studies can be used to develop accurate phenological predictions at much broader spatial scales within regions experiencing similar climatic regimes. Given the key role of phenology in determining species responses to climate change (Miller-Rushing *et al.* 2010), this is an essential first step towards the goal of developing mechanistic models of species responses to future climate change (Diez *et al.* 2012).

Furthermore, the local model's predictive capacity was upheld when applied to a much longer and non-overlapping time period than that used to construct the model, and predictive capacity did not decrease further back in time or at higher temperatures. This indicates that temporal extrapolation from relatively short-term studies (17 years in this case) is possible. Much caution is needed when make predictions outside the range of climatic conditions experienced during the reference study. This is not a major issue in our study, however, as the range of climatic conditions used in the local model encompasses most of the predicted range of future climatic conditions across the UK over the next 60 years under a high carbon emissions scenario (March: used in model 3.8–8.6°C, predicted 6–9°C; April: used in model 7.7–12.3°C, predicted 7–12°C; Jenkins, Perry & Prior 2008). Although the increasing discrepancy between historic and future climatic variables further into the future will make longer-term predictions tricky, our analysis strongly suggests that data from intensive local studies can be used to predict future phenological shifts over time scales of several decades.

2.4.2 Phenological indices and potential demographic impacts

The standard phenological index of mean population lay date did not detect key phenological responses that could have important demographic impacts. The local population's mean lay date and initiation date showed no temporal trend, but timing of re-nesting and breeding termination have advanced significantly. This has led to an eight-day contraction of the breeding season length index, which equates to a 33% loss of the average reproductive laying window. This change may have little effect if late broods are unproductive, but in long-tailed tits, fledglings from late broods are as likely to recruit into the breeding population as those from broods raised earlier in the season (Sharp *et al.* 2008), perhaps partly because later broods are more likely to gain benefits from helpers in this co-operatively breeding species (MacColl & Hatchwell 2004). In many non-cooperatively breeding species late broods have greater fitness in some years (e.g. guillemots *Uria aalge*: Harris, Halley & Wanless 1992; great tits *Parus major*: Monrós, Belda & Barba 2002), or are essential for maintaining positive population growth rates (Green 1988; Farnsworth & Simons 2001; Grzybowski & Pease 2005; Podolsky, Simons & Collazo 2007; Wright *et al.* 2009). A decline in breeding season length over recent years has been observed in several single-brooded species across Denmark, despite increases in the duration of breeding seasons in several multi-brooded species (Møller 2010). This suggests that single-brooded species may experience stronger environmental constraints on breeding season length than multi-brooded species, at least in populations at the lower end of their thermal optimum. However, given the recent observed decline in the incidence of double-brooding in Dutch great tits (Husby, Kruuk & Visser 2009), and the results of the present study, it seems likely that breeding season durations in both single and multi-brooded species may become climatically constrained in the future.

The observed discrepancy between rates of advance in initiation and termination in the local study probably also explains the observation that in recent years (1995–2011) national mean lay dates have advanced more than predicted from March temperature alone (Fig. 2.5). The observed national advance is likely to be due partly to an advance in termination date due to warmer Aprils, rather than solely to advancing initiation due to warmer March temperatures; indeed, between 1995 and 2010 April temperatures increased nationally, whereas March temperatures showed no significant change (HadCET; Parker, Legg & Folland 1992). Given that such an advance in timing of termination at the national scale could have drastic demographic consequences, we show that assessments of species sensitivity to climate change based on average population lay date are inadequate. In addition to the scaling-up approach described above, we suggest that assessments based on broad-scale phenological data should incorporate information on the variance in timing of breeding, as well as simply the average timing. Such practice is currently rare, but would be straightforward even with existing data from national nest monitoring schemes (as demonstrated in North American tree swallows *Tachycineta bicolor*; Winkler, Dunn & McCulloch 2002). Although national monitoring data is inevitably less comprehensive than the data presented here, we suggest that the use at the national scale of a metric such as our breeding season length index (10^{th}–90^{th} percentile of first egg dates) would add an important dimension to phenological monitoring that could enable earlier detection of future ecological problems arising from climate change.

2.4.3 Microevolution versus phenotypic plasticity

There was no change in the form of the reaction norms between temperature and phenology (initiation and termination) in the Rivelin population over the 17 years of our study. This suggests that the majority of observed phenological change was due to phenotypic plasticity rather than selection pressure resulting in genetic adaptation. Lay date is a heritable trait, with passerine heritability estimates typically in the range of 0.16 to 0.45 (Sheldon, Kruuk & Merilä 2003), and selection pressures can generate divergence in breeding time reaction norms across conspecific populations (Caro *et al.* 2009; Gienapp, Väisänen & Brommer 2010). Evidence for microevolutionary change in breeding data is, however, very rare (Gienapp *et al.* 2008); indeed, it is often lacking even in studies that demonstrate heritability of lay dates (Sheldon, Kruuk & Merilä 2003; Gienapp, Postma & Visser 2006). Local adaptation of breeding time in response to climate may, however, be more prevalent than currently believed (Gienapp *et al.* 2008). This could limit the predictive capacity of local phenological models at broader spatial scales, given that populations can experience different selection pressures (Visser *et al.* 2003; Caro *et al.* 2009; Gienapp, Väisänen & Brommer 2010). Further work is required to quantify the extent to which microevolutionary change contributes to phenological shifts, but we provide initial evidence that phenotypic plasticity is more important than genetic change in our focal long-tailed tit population.

2.4.4 Mechanisms of phenological change

The climatic model of local long-tailed tit phenology explains the majority (65%) of the temporal variation in the population's mean lay date, with March temperature being the most important driver. Earlier breeding in years with warm March temperatures is likely to be driven largely by the alleviation of energetic and resource constraints; this topic has received copious attention in the literature and we therefore do not discuss it further here (e.g. Crick & Sparks 1999; Carey 2009; Schaper *et al.* 2011; Vatka, Orell & Rytkonen 2011). We have also presented rare evidence that the termination of breeding is highly sensitive to temperature, with breeding ending earlier in years with warm April temperatures (Fig. 2.3c). One plausible mechanism for this is an influence of April temperature on food availability. Caterpillars are the dominant component of long-tailed tit chick diets (Cramp & Perrins, 1993; PRG & BJH pers. obs.) and the optimum nestling food source in terms of nutrition and energetic value (Visser, Holleman & Gienapp 2006; Garcia-Navaz & Sanz 2011). Given that temporally matching breeding with the peak in caterpillar abundance benefits productivity and survival in ecologically similar species (van Noordwijk, McCleery & Perrins 1995; Thomas *et al.* 2001), we hypothesised that the timing of the seasonal decline in caterpillar availability may be an important determinant of the timing of breeding termination. Our limited data suggests that caterpillar abundance at the study site peaked earlier in years with warmer April temperature, but showed no relationship with March temperature. April temperature thus seems to have a similar influence on the timing of peak caterpillar abundance at our study site to that reported in other UK woodlands, in which peak caterpillar biomass typically advances by approximately 8.5 days per 1°C increase in spring temperature (Smith *et al.* 2011). Applying this relationship to our study site, in which April temperatures have increased by 1.9°C over the course of this study, indicates that if long-tailed tits track caterpillar phenology there should be a 17-day advance in breeding termination. This predicted advance in termination date is remarkably close to the observed advance of 16 days. It thus seems likely that earlier peaks in caterpillar abundance in years with warm Aprils contribute to the earlier termination of long-tailed tit breeding in these years. Earlier seasonal decline in caterpillar availability in warm years is thought to contribute to a decline in double-brooding of great tits (Husby, Kruuk & Visser 2009), and earlier gonadal regression in warmer years caused earlier cessation of breeding in an aviary study of starlings *Sturnus vulgaris* (Dawson 2005). There is thus mounting evidence that climate change is driving an advance in the timing of breeding termination in numerous species, and further study into the mechanisms behind this should be a priority for research.

Climate explained half the variation in breeding season length in our study population, primarily due to increased duration in years with warm February and March temperatures and shortening in years with warm Aprils. The effect of February temperature was unexpected given that February temperature was not closely associated with the timing of first breeding attempts. This pattern could partly arise because February and March temperatures are positively correlated, but the tolerance levels were sufficiently low to justify including both variables in the analysis. We consider it likely that warmer conditions in the pre-breeding period may enhance parental body condition through reducing energetic expenditure for thermoregulation and food acquisition (e.g. Crick & Sparks 1999; Carey 2009; Schaper *et al.* 2011; Vatka, Orell & Rytkonen 2011), enabling prolonged investment in energetically-demanding reproductive behaviour.

Finally, we found no evidence for a trend in the timing or intensity of nest predation in this species, and breeding phenology was not associated with either predation parameter. In the present study predation patterns are not a primary driver of breeding phenology, but species in different ecosystems or locations could be more susceptible to changing predation patterns (Adamík & Král 2008) and predation effects should therefore be taken into account in phenological monitoring schemes.

2.4.5 Conclusion

We have shown that climatic models of phenological responses derived from intensive local studies can scale up to predict responses at much larger spatial and temporal scales. Current patterns of climate change are leading to earlier termination of breeding in this population (associated with earlier declines in food availability), despite little change in the timing of breeding initiation. The consequence is a substantial loss of reproductive opportunity, with potential consequences for population productivity. These trends were not detected by the routinely-used phenological indicator of population mean lay date, demonstrating that the choice of phenological metric can bias estimates of species sensitivity to climate change. Developing predictive phenological models using indices that capture a more complete spectrum of phenological shifts is therefore of fundamental importance to developing mechanistic models of species vulnerability to future climatic change.

Chapter 3. Adult survival

This chapter is published as:

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Summary

Predicting climate change impacts on population size requires detailed understanding of how climate influences key demographic rates, such as survival. This knowledge is frequently unavailable, even in well-studied taxa such as birds. In temperate regions, most research into climatic effects on annual survival in resident passerines has focussed on winter temperature. Few studies have investigated potential precipitation effects and most assume little impact of breeding season weather. We use a 19-year capture-mark-recapture study to provide a rare empirical analysis of how variation in temperature and precipitation throughout the entire year influences adult annual survival in a temperate passerine, the long-tailed tit *Aegithalos caudatus*. We use model averaging to predict longer-term historical survival rates, and future survival until the year 2100. Our model explains 73% of the interannual variation in survival rates. In contrast to current theory, we find a strong effect of precipitation and no effect of variation in winter weather on adult annual survival, which is correlated most strongly with breeding season (spring) weather. Warm springs and autumns increase annual survival, but wet springs reduce survival and alter the form of the relationship between spring temperature and annual survival. There is little evidence for density dependence across the observed variation in population size. Using our model to estimate historical survival rates indicates that recent spring warming has led to an upward trend in survival rates, which has probably contributed to the observed long-term increase in the UK long-tailed tit population. Future climate change is predicted to further increase survival, under a broad range of carbon emissions scenarios and probabilistic climate change outcomes, even if precipitation increases substantially. We demonstrate the importance of considering weather over the entire annual cycle, and of considering precipitation and temperature in combination, in order to develop robust predictive models of demographic responses to climate change.

3.1 Introduction

Climate change is expected to become a major driver of species extinctions in the coming decades, with numerous shifts in the abundance and distribution of animal and plant species already documented across the globe (Walther *et al.* 2002). Such shifts are driven largely by local changes in population size as a result of altered productivity and survival (Huntley *et al.* 2007; Leech & Crick 2007). The mechanisms underpinning such demographic changes are not well understood (Seavy, Dybala & Snyder 2008; Balbontín *et al.* 2009; van de Pol *et al.* 2010), despite increasing evidence that incorporating demographic mechanisms into predictive models of future climate change impacts greatly improves their performance (Buckley *et al.* 2010; Bykova *et al.* 2012). In order to improve predictive capacity it is essential to advance understanding of how variation in climate drives demographic processes, by using historical data to uncover detailed relationships between climate and demography. The resultant models can then be combined with future climate projections to predict demographic shifts (Grosbois *et al.* 2006; Seavy, Dybala & Snyder 2008).

Survival is a key demographic trait. In small-bodied birds in temperate regions, climatic influences on survival are one of the most important demographic processes contributing to annual variation in population size (Newton 1998; Sæther, Sutherland & Engen 2004; Leech & Crick 2007). Following the ideas of Lack (1954), survival is thought to be influenced primarily by weather during the non-breeding season ('tub hypothesis'). Breeding season weather is thought to influence population size via changes in productivity, offspring quality and subsequent recruitment ('tap hypothesis'; Sæther, Sutherland & Engen 2004). This tub-tap hypothesis is supported by observations that temperate populations of several small-bodied resident species fluctuate according to weather during November to April (Newton 1998; Sæther *et al.* 2000; Sæther, Sutherland & Engen 2004), and by correlations between survival rates and winter conditions in many species (Lahti *et al.* 1998; Peach, Siriwardena & Gregory 1999; Perdeck, Visser & van Balen 2000; Doherty & Grubb 2002; Nilsson *et al.* 2011). Such correlations are, however, often weak and the majority of interannual variation in survival is frequently unexplained (Lahti *et al.* 1998; Peach, Siriwardena & Gregory 1999; Perdeck, Visser & van Balen 2000; Doherty & Grubb 2002). Consequently, there is still considerable uncertainty regarding the relative importance of weather at different times of year, and the precise demographic consequences of these weather effects (Sæther, Sutherland & Engen 2004; Grosbois *et al.* 2006; Robinson, Baillie & Crick 2007; Santisteban *et al.* 2012).

Previous studies have suggested that low temperatures can be detrimental for birds by increasing thermoregulatory costs and reducing food abundance or availability, particularly during winter when thermoregulatory investment is highest and food is most scarce (Clobert *et al.* 1988; Perdeck, Visser & van Balen 2000; Sæther *et al.* 2000). Precipitation may also increase energy demand or reduce feeding opportunities (Altwegg *et al.* 2003), and interactions between temperature and precipitation may be important. Insectivorous birds may, for example, be unable to glean sufficient food from vegetation that is covered in ice following cold and wet conditions (Robinson, Baillie & Crick 2007). Despite this recognition of the potential role of precipitation in determining avian survival rates, empirical assessments have largely focussed on the role of temperature (e.g. Clobert *et al.* 1988; Perdeck, Visser & van Balen 2000; Santisteban *et al.* 2012). Summer heat stress may also become a more important determinant of survival under future climatic conditions, even in temperate regions (Jiguet *et al.* 2006; Grosbois *et al.* 2006; Santisteban *et al.* 2012), but are rarely considered in models of survival rates.

Here we provide an empirical assessment of how climatic variation influences annual adult survival in a temperate passerine, using a 19-year capture-mark-recapture study of a population of long-tailed tits *Aegithalos caudatus* in the Rivelin Valley, Sheffield. We use a novel approach to simultaneously assess the effects of both temperature and precipitation throughout the entire annual cycle. We also test for potential interactions between temperature and precipitation, and for summer heat stress effects. Furthermore, we use model-averaged parameter estimates to infer historical survival rates and predict future survival until the end of the century under a broad range of probabilistic climates and future emissions scenarios. We consider all three emissions scenarios defined by UK Climate Projections 2009 (UKCP 2009), termed 'low', 'medium' and 'high'. These emissions scenarios are based respectively on the B1, A1B and A1F1 greenhouse gas emissions scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios, which are projected from a wide range of potential future socio-economic scenarios (for full details see Nakicenovic & Swart 2000).

The long-tailed tit is an ideal species for this analysis, because its small body size makes it particularly sensitive to fluctuations in weather conditions (Newton 1998; Leech & Crick 2007). The UK population has been increasing since the early 1980s, and the suggestion that this increase is a result of improved overwinter survival following recent climate change is currently untested (Baillie *et al.* 2012). Long-tailed tits are woodland residents that do not use nest boxes, and are subject to very low levels of winter food supplementation within our study site.

3.2 Methods

3.2.1 Study system and capture-mark-recapture data

We studied annual survival in a population of long-tailed tits in the temperate climate of the Rivelin Valley, Sheffield (53°23'N 1°34'W; altitude at centre of site = 168m a.s.l., range = 150–270m). The study area is approximately 2.5km^2, about half of which comprises mixed deciduous woodland that offers suitable breeding habitat for long-tailed tits, whilst the remainder is open pasture and therefore not used by long-tailed tits. The present analysis was restricted to adult survival (i.e. survival from the age of 9 months onwards), due to problems with distinguishing between dispersal and mortality during the first 9 months of life, when the majority of dispersal occurs (Sharp *et al.* 2008). Adult breeding population size in the study site ranged from 34 to 130 birds (Appendic 3.1), equating to a mean population density of about 70 adults per km^2 of breeding habitat. We used a capture-mark-recapture (CMR) approach (following Lebreton *et al.* 1992), constructing individual encounter histories for 985 individuals of known sex caught in the breeding seasons of 1994–2012, giving 19 encounter occasions. These 985 individuals comprised birds originally caught as unringed adults (673 individuals) and birds ringed as nestlings and recaptured/resighted as adults at least once (312 individuals). For this latter group, only adult encounters were considered. An additional 14 birds were excluded from the analysis because their sex was unknown. The sex of all other individuals was identified by behavioural observations and confirmed via genetic analysis of blood samples. We defined the capture/resighting period as the breeding season (March–May). This is the period of intensive capture/resighting effort within the site, but the vast majority of captures/resightings occurred during March.

3.2.2 Defining a reference survival model

Encounter histories were analysed using methods that provide robust estimates of survival rates (henceforth ɸ) whilst accounting for potential biases due to variation in recapture probabilities (henceforth p), using a logit link function to constrain estimates of ɸ and p to between 0 and 1 (Lebreton *et al.* 1992). In lieu of developing an *a priori* candidate set of models, we used several stages to develop a reference model for subsequent modelling of climatic effects on survival. We first fitted a global structural model, with the individual covariates of sex and ringing age (adult or nestling), which could influence survival and recapture probabilities. ɸ was allowed to vary between years, whereas p was assumed to be constant between years because field recapture/resighting protocols were standard across years (Meade & Hatchwell 2010). The exception was for 2001, when p was fixed to 0.4 to reflect the ~50% reduction in capture/resighting effort following access restrictions to the study site (Appendix 3.1). This value of p (0.4) reflected the estimated recapture rate in a model that allowed p to differ in 2001 compared to all other years. Our global structural model was thus ϕ(~time*sex*ringingAge) p(~sex*ringingAge), where * represents the interaction term with main effects included. We tested the goodness of fit of this global model using parametric bootstrap methods, which showed slight under-dispersion ($\hat{c}$ = 0.853). We then selected a more parsimonious structural reference model by comparing the global model to each of the reduced models nested within the global model (following Lebreton *et al.* 1992; Grosbois *et al.* 2006) and selecting the model with the lowest Akaike's Information Criterion corrected for small sample size (AICc, Burnham & Anderson 2002). The most parsimonious reduced model was ϕ(~time)p(sex), which we therefore defined as the reference model (Appendix 3.2). Hence p was modelled separately for males and females in all subsequent climatic models. The probability of recapture was high, at 0.92 ± 0.02 for males and 0.83 ± 0.03 for females (estimate ± 1SE). All analyses were run in R (R Development Core Team 2010), using package RMark (Laake & Rextad 2008) for CMR analyses as a wrapper to program MARK (White & Burnham 1999).

3.2.3 Climatic survival models

Daily weather data were obtained from Weston Park Weather Station (Museums Sheffield 2012), located approximately 5km east of the study site (53º38'N 1º49'W) and at a similar elevation (131m) to the study site (mean 168m). To validate our use of off-site weather data, we compared the weather station temperatures with mean monthly air temperature recorded at twenty points distributed throughout the study site during three years of the study (2010–2012). These data were recorded at 4-hour intervals using miniature data loggers mounted in a white solar radiation shield (DS1921G-F5 thermochron i-buttons). Temperatures at the study site and weather station were very strongly associated (linear regression: $R^2 = 0.997$, $P < 0.0001$, est. ± 1SE = 0.912 ± 0.009). No equivalent comparison of on- and off-site data was possible for precipitation, but personal observations (PRG, KLE, BJH) suggest that any variation in rainfall patterns on- and off-site is likely to be minor given the negligible difference in elevations of the study site and weather station. We are therefore confident that the off-site weather station captures on-site monthly and annual climatic variation accurately.

To investigate how annual survival is influenced by interannual variation in weather at certain times of year, we defined four seasons relevant to the biology of long-tailed tits: (1) March-April-May (spring: breeding season), (2) June-July-August (summer: immediately post-breeding, moulting), (3) September-October-November (autumn), (4) December-January-February (winter). We initially considered climatic indices that described the extent of periods of harsh weather (‘extreme indices’), as well as average weather patterns (‘average indices’).

The extreme indices initially considered were: the total number of days with (i) minimum temperature <0ºC (spring, autumn, winter) or maximum temperature > 25ºC (summer), (ii) total precipitation ≥ 10mm, (iii) minimum temperature < 0ºC and total precipitation > 1mm. Initial average indices considered were: (i) mean seasonal temperature (ºC), (ii) total seasonal precipitation (mm). However, extreme indices were highly correlated ($r > 0.8$) with their corresponding average indices (Appendix 3.3). We therefore considered only average indices in survival analyses, namely mean temperature and total precipitation during each of the four seasons (Appendix 3.4). These variables were not significantly correlated (pairwise comparisons: $r < 0.46$, $P > 0.05$), with the exception of precipitation in spring and autumn ($r = 0.56$, $P = 0.014$). This collinearity was well within the threshold to which information theoretic approaches are robust (variance inflation factor < 2.8 for all variables, Appendix 3.3; Freckleton 2011). All climatic indices (including past and future weather variables) were standardized by subtracting the mean and dividing by the standard deviation of the spring 1994 to winter 2011 time series, as recommended for CMR analyses (White & Burnham 1999).

To determine broad patterns between weather variables and survival, we first used a univariate approach to compare linear and quadratic models for all eight of these weather variables (x), thus constructing models of type $\phi(\sim x)p(\text{sex})$ and $\phi(\sim x+x^2)p(\text{sex})$. Given that we suspected within-season interactions between temperature (t) and precipitation (p) may be important, we then compared single-season models with interactive (t*p) versus additive (t+p) effects within each season. We ran these models both with and without quadratic terms for the main effects. Neither univariate nor single-season models showed evidence of a relationship between survival and weather during summer or winter, with AICc scores similar to or exceeding that of the null model, but they did show evidence of weather effects during spring and autumn, with potential within-season interactions and quadratic main effects (AICc < 10 compared to the best climatic model, Tables 3.1 & 3.2; Burnham & Anderson 2002). We therefore included in our full climatic model the linear and quadratic effects of temperature and precipitation during spring and autumn, and their linear within-season interactions. Due to limited degrees of freedom, we did not consider interactions of climatic parameters between different seasons as such interactions were assumed to be of low potential importance.

3.2.4 Model selection and model averaging

Our full climatic model comprised 10 climatic parameters. We compared all models that comprised three or more of these climatic parameters. From this candidate set, we identified the climatic survival model with the lowest AICc, and calculated the ΔAICc compared to this model for all other climatic models, henceforth termed '$\Delta\text{AICc}_{\text{climatic}}$'. All models with $\Delta\text{AICc}_{\text{climatic}} < 2$

were considered as having approximately equal support (Burnham & Anderson 2002). We termed these the 'ΔAICc < 2 top subset' of models. For all models, we calculated the proportion of temporal variation explained by weather variables, which is commonly used as a measure of effect size in CMR analyses. We used the formula $R^2\_Dev = dev(n)\text{-}dev(c) \ / \ dev(n)\text{-}dev(t)$, where dev($n/c/t$) represent the deviance of the null, covariate, and time-dependent models respectively (Grosbois *et al.* 2008). For simplicity, R^2_Dev is henceforth referred to as R^2.

We averaged the estimates of all 11 models in the ΔAICc < 2 top subset of models (following Grosbois *et al.* 2006; Martins *et al.* 2011). We calculated the partial R^2 of each climatic parameter in each of these 11 models, using the formula partial $R^2(x_i) = \text{var}_{ex}(c) - \text{var}_{ex}(c_{xi})$, where $\text{var}_{ex}(c)$ and $\text{var}_{ex}(c_{xi})$ represent the proportion of temporal variation explained by weather variables in models with and without climatic parameter x_i, respectively (Burnham & Anderson 2002). We then calculated model-averaged partial R^2 and parameter estimates by first multiplying the re-scaled Akaike weight of a model with the partial R^2 and parameter estimate of each climatic parameter in that model, and then summing these model-specific estimates across all 11 models in the set (Burnham & Anderson 2002).

3.2.5 Density dependence

We calculated an index of population density, which was the total number of adults plus fledglings at the end of the breeding season (season 1). We were unable to estimate population sizes separately for the other seasons, but these are highly likely to reflect population size at the end of the breeding season. Adult plus fledgling population size ranged from 73 to 336 (mean ± 1SD = 181 ± 61). This 'popSize' index showed little or no relationship with survival in univariate comparison, with the model ϕ(~popSize)p(sex) having the same AICc as the null model ϕ(~1)p(sex). To test for density dependence of weather effects, we re-ran the top climatic model with population density as a main effect and as an interactive effect with each individual weather variable, and compared their results with those of the corresponding models lacking density dependent effects.

3.2.6 Prediction of past and future survival

We investigated whether the recent increase in the UK population of long-tailed tits (Baillie *et al.* 2012) may be linked to recent weather patterns, by using the Rivelin model-averaged parameter estimates to predict past survival in the Rivelin population during 1966–2011 (corresponding to the period of national population monitoring by the British Trust for Ornithology; Baillie *et al.* 2012). Historical climate data were obtained from Weston Park Weather Station and were thus directly comparable to the data used to construct the survival models. To test for a general trend in estimated historical survival, we ran a linear and a quadratic regression through the annual survival probabilities for the period 1966–2011.

We investigated how climate change may influence long-tailed tit survival in the future by estimating survival under a range of future climatic scenarios, for each of three non-overlapping time periods encompassing the remainder of this century (2010–2039, 2040–69, 2070–99). Data on historical (1994–2011) and projected future (2010–2100) absolute climatic variables were extracted from UKCP 2009 for the 25 x 25km grid square including the Rivelin Valley close to its centre, and used to calculate a percentage change factor for each of the four climate variables appearing in the survival model average (i.e. mean temperature and total precipitation in spring and autumn). We then applied these projected percentage change estimates to the observed weather station data used in this study (i.e. mean seasonal values for the period 1994–2011 at the Weston Park Weather Station), to estimate future weather conditions for this study site.

Future weather variables were projected for each of the three emissions scenarios defined by UKCP 2009 (low, medium and high). These scenarios are based respectively on the B1, A1B and A1F1 greenhouse gas emissions scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (Nakicenovic & Swart 2000), and encompass a wide range of future potential emissions levels (UKCP 2009). A key feature of these data is that they provide probabilistic projections, i.e. they take uncertainty into account by calculating the likelihood of the estimated level of change. As recommended by UKCP, we used the 50% cumulative distribution function (CDF) level as the ‘likely’ estimate of moderate change, the 10% CDF as the low-end estimate of change (which is ‘highly likely’ to be lower than the observed change), and the 90% CDF as the high-end estimate (which is ‘highly likely’ to be higher than the observed change, UKCP 2009).

We then used the model-averaged parameter estimates from the Rivelin survival model to predict future survival for each of the three future time periods. For each period and under each emissions scenario, we produced three future survival scenarios that reflected our results (see below) that warmer temperatures increased survival and high precipitation decreased survival: ‘moderate’, based on the moderate (50% CDF) estimates for both temperature and precipitation; ‘best case’, based on the high-end (90% CDF) estimate for temperature and the low-end (10% CDF) estimate for precipitation; ‘worst case’, based on the low-end estimate for temperature and the high-end estimate for precipitation.

3.3 Results

3.3.1 Climatic effects on survival

Univariate and multivariate comparisons showed the most important periods to be spring and autumn, with low temperatures and high precipitation reducing annual survival (Fig. 3.1, Table 3.1). In contrast, interannual variations in summer and winter weather showed no relationship with annual survival (Table 3.1, Appendix 3.5). Quadratic models were generally slightly more parsimonious than linear models (Table 3.1), and there was some evidence of a temperature-precipitation interaction in spring and in autumn (Table 3.2). The full climatic model therefore comprised the linear and quadratic terms of temperature (t) and precipitation (p) in spring (season 1) and autumn (season 3), and the within-season linear interactions (:) of temperature and precipitation, thus $\phi(\sim t1+p1+t3+p3+t1^2+p1^2+t3^2+p3^2+t1{:}p1+t3{:}p3)p(sex)$.

Eleven models were retained in the ΔAICc < 2 top subset, all of which included the linear effects of spring temperature and precipitation and their interaction (Appendix 3.6). Weather explained a very large proportion (73%) of the interannual variation in survival rates (model averaged $R^2 = 0.73$; Fig. 3.2), showing a decrease in survival with increasing spring precipitation (partial $R^2 = 0.16$, est. = -0.21) and with decreasing spring and autumn temperature (partial $R^2 = 0.18$ and 0.17 respectively, est. = +0.25 for both; Table 3.3). Importantly, the strong interaction between temperature and precipitation in spring indicated that the negative effects of low temperatures were greatly exacerbated by high precipitation (Fig. 3.3). In contrast, the strong univariate relationship between annual survival and autumn precipitation was no longer apparent in multivariate models (partial $R^2 = 0.01$, est. = -0.05; Table 3.3). Density dependence was only weakly apparent; high population density seemed to slightly reduce annual survival (Table 3.4), but parameter estimates of the best model changed little regardless of whether population size was included as a main effect (Fig. 3.4) and there was little evidence of an interaction between population size and weather (Table 3.4).

3.3.2 Prediction of past and future survival

Predictions of historical annual survival rates in the Rivelin long-tailed tit population indicated substantial between-year variation over the period 1966–2011, but a general rising trend (linear regression: est ± 1SE = +0.006 ± 0.002, $F_{1,44} = 15.34$, $R^2 = 0.26$, $P < 0.001$; Fig. 3.5a). By contrast, there was no apparent trend in annual survival over the 1994–2012 period of the local study ($F_{1,16} = 0.35$, $R^2 = 0.02$, $P = 0.56$).

Future projections of climatic change for the 25 x 25km grid square including the Rivelin study site showed that mean spring and autumn temperature is expected to increase over the remainder of the century under all three emissions scenarios, even according to low-end estimates (Appendix 3.7). Total seasonal precipitation in spring and autumn is also expected to increase slightly under all emissions scenarios, according to the mid-likelihood estimates, but there is greater uncertainty around these estimates, and precipitation may actually decrease according to low-end estimates (Appendix 3.7). Despite this uncertainty, the overriding positive effects of increasing spring and autumn temperatures mean that future annual survival is expected to increase even under the worst-case scenario of a small temperature increase in spring/autumn and large precipitation increase in spring (Fig. 3.5).

Figure 3.1 Relationships between adult long-tailed tit survival estimates (●) from the reference model ɸ(~time)p(sex) and four weather variables, for the Rivelin population in the years 1994–2012. Solid lines indicate survival estimated from model-averaged parameter estimates for each weather variable, calculated over the range in weather experienced during the study. Only weather variables showing a univariate relationship with survival are displayed here: (a) mean spring temperature, model-averaged partial R^2 = 0.19, (b) total spring precipitation, model-averaged partial R^2 = 0.16, (c) mean autumn temperature, model-averaged partial R^2 = 0.16, (d) total autumn precipitation, model-averaged partial R^2 = 0.01. For relationships between survival and summer/winter weather, see Appendix 3.5.

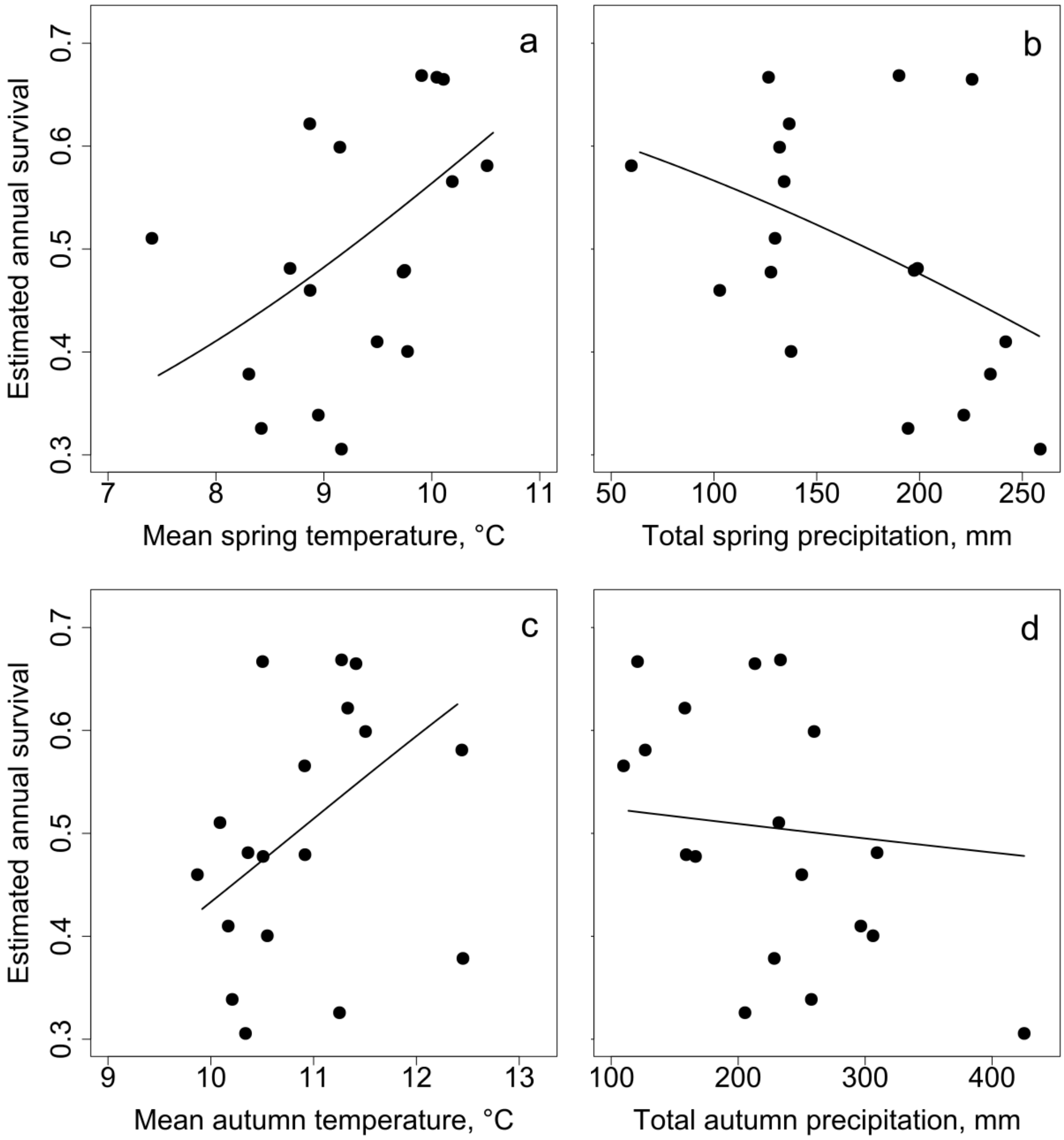


Table 3.1 Univariate climatic models of adult long-tailed tit survival in the Rivelin population, 1994–2012. Survival ϕ is modelled as a linear ($\sim x$) response to year (the reference model, 20 parameters, first row) and as a linear ($\sim x$) and quadratic ($\sim x+x^2$) response to each weather variable, where t indicates mean seasonal temperature, p total seasonal precipitation and the numerals 1-4 seasons as defined in the text (1 = spring, 2 = summer, 3 = autumn, 4 = winter). The null model (last row) contains no explanatory terms, only an intercept. In all models, recapture is modelled separately for males and females and is fixed to 0.4 in 2001. ΔAICc is the change in AICc relative to the temporal reference model; R^2 is proportion of temporal variation explained (deviance of temporal model = 451.21; deviance of null model = 523.68).

x	Linear			Quadratic			
	ΔAICc	R^2	Est. ± 1SE	ΔAICc	R^2	Est. ± 1SE (linear)	Est. ± 1SE (quadratic)
Year	0	1.00	--	--	--	--	--
t1	22.9	0.24	+0.24 ± 0.06	16.0	0.36	+0.31 ± 0.06	+0.15 ± 0.05
t2	39.0	0.01	+0.05 ± 0.06	40.9	0.02	+0.06 ± 0.06	-0.01 ± 0.05
t3	35.3	0.06	+0.12 ± 0.05	30.0	0.17	+0.23 ± 0.07	-0.14 ± 0.05
t4	38.5	0.02	-0.07 ± 0.06	38.8	0.04	-0.04 ± 0.06	+0.07 ± 0.05
p1	22.5	0.24	-0.23 ± 0.06	20.3	0.30	-0.26 ± 0.06	-0.12 ± 0.06
p2	40.0	0.00	+0.00 ± 0.06	30.2	0.16	-0.13 ± 0.07	+0.17 ± 0.05
p3	15.1	0.34	-0.30 ± 0.06	16.6	0.35	-0.29 ± 0.06	-0.03 ± 0.05
p4	39.8	<0.01	-0.02 ± 0.06	40.3	0.02	-0.01 ± 0.06	-0.06 ± 0.05
Null	37.9	0.00	--	--	--	--	--

Table 3.2 Single-season climatic models of adult long-tailed tit survival in the Rivelin population, 1994–2012. Survival was modelled in response to temperature and precipitation within each of four seasons; these main effects were fitted as both linear and quadratic terms in all models; within-season combined temperature/precipitation effects were fitted as both additive (t+p) and interactive (t*p) linear effects. For each model, $\Delta AICc_{time}$ indicates ΔAICc compared to the temporal reference model ϕ(time)p(sex); R^2 indicates proportion of temporal variation explained (deviance of temporal model = 451.2; deviance of null model = 523.7). 'Linear' and 'Quadratic' indicate models in which main effects were fitted as linear and quadratic terms respectively; interaction effects were fitted only as linear terms. The temporal reference model (20 parameters, first row) and null model (1 parameter, last row) are shown for reference purposes.

Season	Additive linear		Additive quadratic		Interactive linear		Interactive quadratic	
	$\Delta AICc_{time}$	R^2	$\Delta AICc_{time}$	R^2	$\Delta AICc_{time}$	R^2	$\Delta AICc_{time}$	R^2
Reference	*0.0*	*1.00*	--	--	--	--	--	--
1 Spring	14.6	0.38	7.0	0.54	8.0	0.50	6.1	0.58
2 Summer	40.9	0.02	29.5	0.23	42.5	0.02	26.5	0.30
3 Autumn	16.8	0.35	14.9	0.43	17.4	0.37	16.7	0.43
4 Winter	40.4	0.02	41.0	0.07	41.7	0.03	42.0	0.08
Null	*37.9*	*0.00*	--	--	--	--	--	--

Figure 3.2 Adult long-tailed tit survival estimates obtained from the reference model ϕ(~time)p(sex) compared to the final climatic model average, for the Rivelin population in the years 1994–2012. The final climatic model average included the linear and quadratic effects of temperature and precipitation during spring and autumn, and their within-season linear interactions. Closed cirles (●) with grey error bars represent survival estimates from the reference model with 95% CIs; solid line with dashed grey lines represents survival estimates from the climatic model average with 95% CIs.

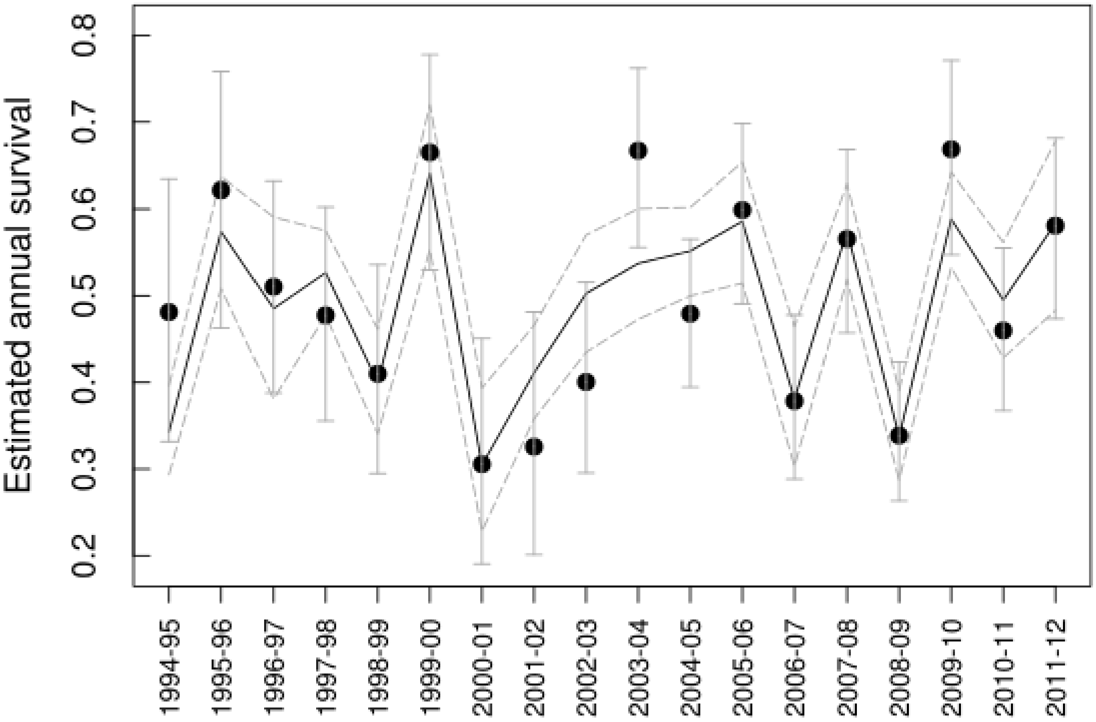


Table 3.3 The effects of weather on the survival of adult long-tailed tits in the Rivelin population, 1994–2012. Shown are the partial R^2 and parameter estimates from the climatic model average (constructed from the $\Delta\text{AICc}_{\text{climatic}}<2$ top subset of 11 models; Appendix 3.4) and from the best climatic model (Appendix 3.4). The overall model R^2 for the model average and best model were 0.729 and 0.733 respectively.

Parameter	Model average		Best model		
	Partial R^2	Est.	Partial R^2	Est.	95% CIs
Intercept	--	+0.02	--	+0.02	-0.09 to +0.13
Spring temp	0.19	+0.25	0.14	+0.22	+0.08 to +0.35
Autumn temp	0.16	+0.25	0.15	+0.24	+0.09 to +0.38
Spring prec	0.16	-0.21	0.11	-0.19	-0.32 to -0.06
Autumn prec	0.01	-0.05	0.03	-0.12	-0.29 to +0.04
Spring temp^2	0.01	+0.01	--	--	--
Autumn temp^2	0.00	0.00	--	--	--
Spring prec^2	<0.01	-0.01	--	--	--
Autumn prec^2	<0.01	<0.001	--	--	--
Spring temp x prec	0.22	+0.32	0.28	+0.34	+0.19 to +0.49
Autumn temp x prec	0.01	+0.03	--	--	--

Figure 3.3 The interaction between temperature and precipitation during spring, showing the model-averaged relationship between adult long-tailed tit survival and precipitation for three levels of temperature: warm, mid and cold correspond respectively to the warmest (10.5ºC), mean (9.3ºC), and coldest (7.4ºC) mean spring temperatures observed in the Rivelin site in the years 1994–2012.

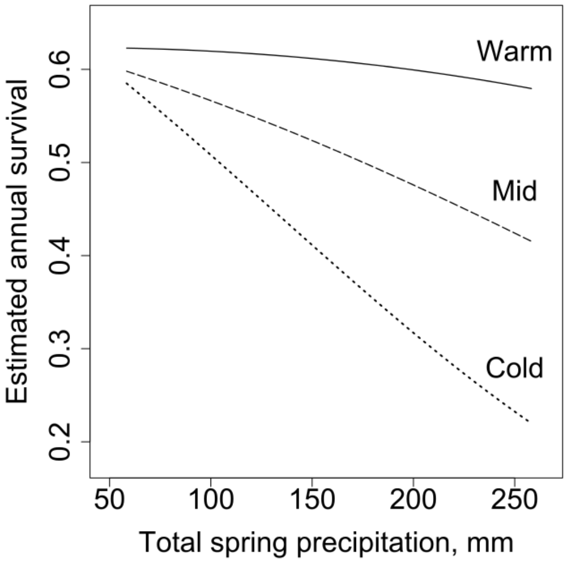


Figure 3.4 Adult long-tailed tit survival estimates obtained from the final climatic model average (solid grey line), compared to estimates from the best model both with (dashed line) and without (dotted line) population size as a main effect, for the Rivelin population in the years 1994–2012.

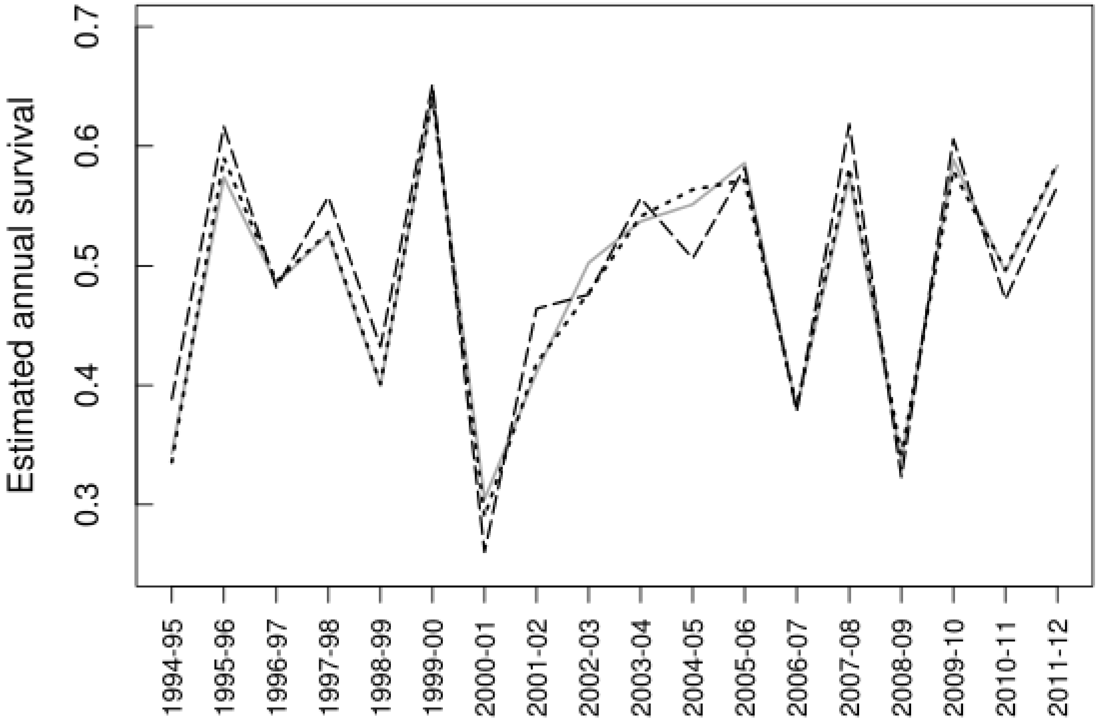
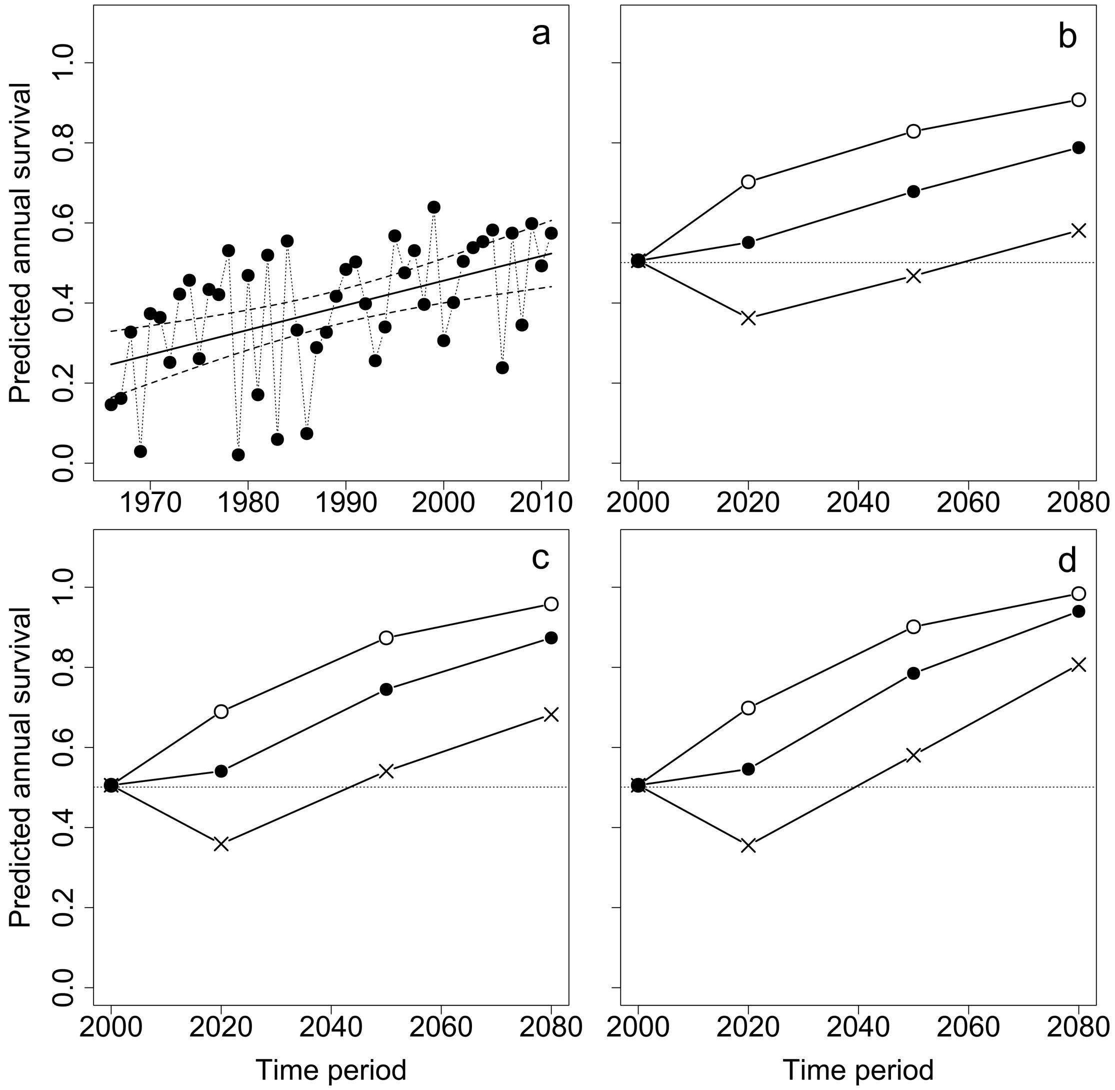


Table 3.4 Density-dependence of adult long-tailed tit survival in the Rivelin population, 1994-2012. Population size at the end of the spring breeding season was included as a covariate in the best climatic model of survival ϕ(~t1+p1+t3+p3+t1:p1)p(~sex), either a linear main effect, or as an interactive effect with a single weather variable; all interaction models also included the linear main effect. For each model, $\Delta AICc_{climatic}$ indicates ΔAICc compared to the best climatic model lacking density dependence; R^2 indicates proportion of temporal variation explained (deviance of temporal model = 451.21; deviance of null model = 523.68); slope(main) and slope(interaction) indicate the parameter estimates for the main effect of population size, and for its interaction with the relevant weather variable, respectively.

Type of density dependent effect included	$\Delta AICc_{climatic}$	R^2	Est. ± 1SE (main effect)	Est. ± 1SE (interaction)
Interaction with spring temp	-0.43	0.795	-0.134 ± 0.066	+0.006 ± 0.086
Interaction with autumn temp	-0.69	0.799	-0.127 ± 0.063	+0.054 ± 0.105
Interaction with spring prec	-0.62	0.798	-0.114 ± 0.075	+0.053 ± 0.121
Interaction with autumn prec	-0.53	0.796	-0.139 ± 0.066	+0.020 ± 0.061
Main effect only	-2.45	0.795	-0.133 ± 0.063	--
No density dependence	0.00	0.733	--	--

Figure 3.5 Estimates of (a) past and (b-d) future adult long-tailed tit survival in the Rivelin population, based on model-averaged parameter estimates. Past survival: (a) Historical survival was predicted for the period 1966–2011, using historic climate data; the solid line indicates the linear increase in survival through time, where est. ± 1SE = +0.006 ± 0.002, $R^2 = 0.26$, $P < 0.001$; dashed lines indicate 95% CIs. Future survival: (b) low, (c) medium, and (d) high emissions scenarios of future climate were used to predict future survival for three non-overlapping time periods (2010–2039; 2040–69; 2070–99); predictions were made for three potential climate change scenarios, where ○ indicates 'best case' climate projections (great temperature change, little precipitation change); ● indicates 'mid scenario' projections (moderate temperature change, moderate precipitation change); × indicates 'worst case' projections (little temperature change, great precipitation change); the recent historical (1994–2012) average survival in the Rivelin population is shown for reference purposes (dotted line).



3.4 Discussion

3.4.1 Climatic effects on survival

Adult long-tailed tit survival in our study population was strongly linked to interannual variability in weather, with the model average explaining 73% of the variation in annual survival. Weather during the spring breeding season exerted the strongest effects, with cool and wet conditions reducing annual survival, particularly when such conditions occurred simultaneously. Cold autumn temperatures also reduced survival on average. There was no evidence of an effect of interannual variability in winter weather on survival. This contrasts with previous suggestions that interannual variation in passerine survival is primarily determined by winter weather (e.g. Lack 1954; Cawthorne & Marchant 1980; Peach, Siriwardena & Gregory 1999; Sæther, Sutherland & Engen 2004). There was no evidence for adverse effects of high temperatures on survival rates, even though daily maximum temperatures exceeded 30 °C in six of the 19 years of study, and regularly exceeded 25 °C; this is of interest as summer heat stress events have been associated with population declines in some temperate passerines (Jiguet *et al.* 2006).

The strong reduction in adult survival observed in the Rivelin population following cold or wet breeding seasons does not support the tub-tap hypothesis (Sæther, Sutherland & Engen 2004), which states that interannual variation in breeding season weather influences demography by altering fecundity rather than survival. Breeding season weather has long been considered relatively unimportant in determining survival rates of small-bodied temperate passerines (e.g. Lack 1954; Sæther, Sutherland & Engen 2004; Moreno & Møller 2011), despite few rigorous tests of this suggestion (but see Grosbois *et al.* 2006; Glenn, Anthony & Forsman 2010). We show the value of a multivariate approach to assessments of weather effects on survival, which has revealed previously unrecognised climatic and seasonal drivers of annual survival.

The observed relationship between annual survival and spring conditions is unlikely to be a direct effect of weather on mortality at that time of year because adult long-tailed tits disappear from the study site very rarely during the breeding season (Russell 1999). Instead, the relationship between survival and spring conditions probably reflects an increased energetic investment under adverse conditions, which reduces parental body condition and increases subsequent mortality. Previous studies in various passerine species have shown that adverse weather conditions can increase reproductive investment through higher thermoregulatory and foraging costs (Newton 1998, and references therein; Bradbury *et al.* 2003); long-tailed tits also invest more in nest-building during adverse weather (McGowan *et al.* 2004). In short-lived r-selected species like the long-tailed tit, parents are expected to trade off reduced personal survival against increased productivity, given that they may not have another opportunity to reproduce before they die (Williams 1966; Pianka 1970; Ghalambor & Martin 2001). Increased parental effort, as measured by higher provisioning rates during chick-rearing, is associated with reduced survival of adult long-tailed tits to the subsequent breeding season (Meade *et al.* 2010). Furthermore, the decision of failed breeders to become helpers or not is partly dependent on their quality or condition, with higher quality individuals being more likely to help (Meade & Hatchwell 2010). Effects of variation in reproductive investment on subsequent survival have been widely reported in other short-lived species (e.g. Askenmo 1979; Nur 1984; Reid 1987), as well as in some long-lived species (e.g. Deschamps *et al.* 2009). However, few studies have shown an effect of variation in climate on this productivity vs. survival trade-off (Thomas *et al.* 2001; Václav & Sánchez 2008; Moreno & Møller 2011), and the underlying mechanisms remain poorly understood (Harshman & Zera 2007; Deschamps *et al.* 2009).

The lack of an effect of variation in winter temperatures on adult survival is somewhat surprising given the small body size and high thermoregulatory burden of the long-tailed tit. The observed strong negative effect of cold autumn temperatures suggests that individuals in poorer condition are susceptible to mortality as soon as weather becomes cooler, in autumn. Mean autumn temperature in the study site showed a similar range to that in spring (spring range = 7.4–10.5ºC, mean = 9.3ºC, autumn range = 9.9–12.5ºC, mean = 10.9ºC; Appendix 3.4), with sub-zero temperatures occurring in autumn in most years (15 of the 19 years of study; unpubl. data). As such, autumn may act as a filter by which individuals in poorer condition are removed from the population before winter arrives. This finding is not incompatible with previous observations of population crashes after harsh winters in small-bodied species in other geographical regions, where autumns may be relatively clement and winters relatively harsh (e.g. woodland species in Illinois; Graber & Graber 1979). However, the present study suggests that such findings cannot be generalised across temperate regions with contrasting climatic regimes, under which climate may exert critical effects during different time periods. Similarly, the present study does not contradict the observed negative effects of exceptionally harsh winters on avian survival (e.g. Cawthorne & Marchant 1980), given that no exceptionally harsh winters occurred during our study period (winter temperature range = 2.4–6.5ºC, mean = 4.7ºC; Appendix 3.4). However our study does suggest that winter weather is not the primary driver of population change in years with more usual weather conditions. Our results therefore bring into question the reliability of some previous assessments of avian survival that consider only winter temperature, as weather variables at other times of year may be key. Given that different months are likely to exhibit divergent climatic trends over the coming decades (Houghton *et al.* 2001), it is crucial to identify the critical temporal periods of climatic influence on survival rates.

The precise nature of temperature and precipitation effects cannot be identified with certainty from the present study because measures of average monthly conditions (mean temperature and total precipitation) were highly correlated with measures of extreme conditions (number of cold or wet days), and we were therefore unable to distinguish between the effects of average vs. extreme conditions. This suggests that average monthly weather conditions offer a valuable and readily available basis for the prediction of future responses to climate change.

3.4.2 Density dependence

Density dependence in the Rivelin population appeared to be low, regardless of whether climatic effects were taken into account. This contrasts with some previous studies in ecologically similar species such as the great tit *Parus major* (Clobert *et al.* 1988), perhaps indicating that the Rivelin population is well below the carrying capacity of the site. With an area of approximately 1.25km^2 of breeding habitat, the Rivelin site has an average adult population density of about 70 adults per km^2 during spring (range = 35 to 114 adults per km^2), which is low compared to equivalent densities of ecologically similar species such as the blue tit *Cyanistes caeruleus* (400 adults per km^2 in spring) and great tit (240 adults per km^2 in spring, Gibb 1954). Moreover, unlike cavity-nesting blue and great tits, long-tailed tits do not seem to be limited by nest site availability in the Rivelin site because they nest in a wide variety of locations (Hatchwell *et al.* 1999a) and do not defend breeding territories. For instance, pairs may raise chicks in nests located as little as 10m apart and many previous nesting locations are vacant each year despite being used again in subsequent years (PRG & BJH pers. obs.). The present study does not exclude the possibility that density dependence may be important in other long-tailed tit populations, where population densities may exceed the range assessed here (58–269 birds per km^2 of breeding habitat, at the end of the breeding season). However, we currently find no evidence for strong density dependent effects on annual survival. This suggests that any beneficial impacts of climate change on population size are, at least initially, unlikely to be counteracted by density-related declines in survival rates.

3.4.3 Prediction of past and future survival

The range of climates assessed over the course of this study was similar to the range in expected future climates in the study site (Appendix 3.6 & 3.7) and therefore enables prediction of the direction of future changes in average annual survival under various projected climatic scenarios. In so doing our objective is to predict the future general trend, rather than making precise predictions for specific years that take stochastic variation in the general climatic trends into account. We encompass the full range of probabilistic estimates and emissions scenarios

(Fig. 3.5b-d). This has rarely been attempted previously (but see Martins *et al.* 2011; Jenouvrier *et al.* 2012) and, to our knowledge, offers the first such example in a temperate passerine. The extent and direction of future climatic change is far from certain, yet our projections indicate that survival will increase by the end of the century under all emissions scenarios, even if the most extreme probabilistic climatic projections occur. This is because the expected increases in spring and autumn temperatures (UKCP 2009) are expected to override the negative effects of any increase in precipitation. It is important to note that these projections do not incorporate potential alterations in interspecific relationships under future global change scenarios. Previously, it has been suggested that warmer winters may benefit some species under future climates (Catchpole *et al.* 1999; Peach, Siriwardena & Gregory 1999; Nilsson *et al.* 2011), and recent increases in the UK population size of some passerines have been attributed to recent winter warming (Baillie *et al.* 2012). However, many such studies assess the effects of winter weather in isolation, and our study thus brings to light the possibility that winter effects are overridden by weather effects at other times of year. Furthermore, previous studies fail to assess the interaction between temperature and precipitation, thus drastically limiting their capacity to inform future survival projections. This is particularly important as we find that the magnitude of precipitation alters the form of the relationship between temperature and annual survival, and that there is substantial potential for precipitation to increase in the future (UKCP 2009).

The UK long-tailed tit population has gradually increased over the past four decades, more than doubling between 1966 and 2010 (Baillie *et al.* 2012). Spring and autumn temperatures have been increasing nationally over this same time period (Parker, Legg & Folland 1992), suggesting that climate change-induced increases in survival rates may have contributed to this population increase. A more complete test of this hypothesis requires population modelling that takes both survival and productivity into account. It is notable, however, that back-casting of survival probabilities in the Rivelin over this historical time period suggests that survival rates have increased over the period of national population increase (Fig. 3.5a). Moreover, past years with very low predicted survival in the Rivelin population (1979, 1981, 1983, 1986, Fig. 3.5a) coincide with a period of low UK population size (1979–1987, Baillie *et al.* 2012); such low survival may be an underestimate, but probably reflects the general trend in survival rates. Although we did not model juvenile survival rates (due to difficulty in distinguishing between dispersal and mortality in the first year of life; Sharp *et al.* 2008), juvenile mortality appears to be highest in the period shortly after fledging in this species (C. Napper, pers. comm.) and many other passerines (Naef-Daenzer, Widmer & Nuber 2001; Yackel Adams, Skagen & Savidge 2006). It therefore seems likely that juvenile and adult survival rates follow a similar pattern in long-tailed tits, as shown in willow tits *Parus montanus* (Lahti *et al.* 1998) and red-backed shrikes *Lanius collurio* (Schaub, Jakober & Stauber 2011). The apparent covariation of adult survival and population size over the past four decades is therefore highly suggestive that climate-driven changes in survival, due to warmer springs and autumns, could have contributed to the recent increases in long-tailed tit population size, although other factors are also likely to have contributed.

3.4.4 Conclusion

We have provided evidence that contradicts two common perceptions regarding climatic impacts on the annual survival of temperate passerines. First, in contrast to the tub-tap hypothesis, we have shown that interannual variation in weather during the breeding season has the strongest influence on annual survival rates in this population, whilst variation in winter temperature had no discernible effect over the range of temperatures encountered during the 19 years of this study. Second, whilst precipitation is often ignored in models of survival rates in temperate passerines, we found a strong effect of breeding season precipitation on adult survival, which furthermore influenced the relationship between survival and temperature. Our local climatic model explained 73% of the variation in annual survival rates. Historical inference from this model suggests that long-tailed tit survival rates have increased significantly over recent decades in response to climatic warming during spring and autumn. This upward trend in survival rates is predicted to continue over the coming century under even the most extreme climatic projections, although such trends could be influenced by future novel alterations in ecological interactions that were not incorporated into our projections. Recent increases in survival seem likely to have contributed to the recent population growth of this species across the UK, suggesting that future changes in survival may influence population size in a range of species. Crucially, this study highlights the importance of a multivariate approach to assessments of climatic effects on survival, an approach that has been rare to date. Future research into the effects of climate on avian survival must assess responses to both temperature and precipitation, and their interaction, over the entire annual cycle, in order to improve predictive models of demographic responses to climate change.

Chapter 4. Productivity

Summary

Weather has long been recognised as a factor influencing passerine productivity, yet the precise nature of weather effects are variable between species, and it is unclear if such effects are a key mechanism of population control in the majority of passerines. This is particularly true of species with high nest predation rates, and those in which productivity is strongly density dependent. Such knowledge is of fundamental interest in understanding the mechanisms controlling and regulating passerine populations, and is important for predicting the future impacts of climate change on ecological systems. We use a 19-year study of long-tailed tits *Aegithalos caudatus* in central England to explore these issues. We assess the effects of temperature and precipitation during nest-specific periods on key aspects of individual productivity, and the effects of predation and monthly weather on population productivity. We investigate the impacts of year-round weather on recruitment rates, and test for density dependence at key stages of the reproductive cycle. We find minor effects of weather on fledgling production, which is driven largely by nest predation in this population, as well as being reduced by short breeding seasons. Predation rates are not determined by monthly weather during the spring or winter, but may be influenced by daily conditions. Recruitment rates at the population level are strongly influenced by temperature during March and May, but these effects are opposing, with a warm March being detrimental and a warm May being beneficial for recruitment. Future climate change is unlikely to bring about substantial increases in productivity in this population, due to the strong density dependence of recruitment. Indeed, continued warming of March temperatures and further reductions in breeding season length could lead to a decline in population-level productivity. Ultimately, the consequences of future climate change will depend on relative rates of warming between different months.

4.1 Introduction

Productivity is a key demographic trait that is likely to be affected by climate change. In temperate passerines, spring temperature and precipitation may influence the production of eggs and fledglings via direct mechanisms (e.g. physical damage to nests during heavy precipitation; Skagen & Adams 2012) and indirect effects on food availability and predation rates (e.g. Lack 1954; Rotenberry & Wiens 1991; Morrison & Bolger 2002; Collister & Wilson 2007; Adamík & Král 2008; Sofaer *et al.* 2013). However, it is unclear whether such effects are a key mechanism controlling population size in most passerines (Reed, Jenouvrier & Visser 2013). This is of particular interest in species experiencing high nest predation rates, because any effects of weather on individual productivity may be swamped by the effects of predation at the population level (Wilson & Arcese 2006). Furthermore, density dependence may be a key mechanism regulating productivity in many species (Newton 1998). To develop understanding of climate change impacts on animal populations, and accurate predictions of future demographic responses, it is therefore important to identify the effects of weather and predation on annual rates of productivity, and the possible density dependence thereof.

In passerine birds breeding in temperate regions, temperature and precipitation can influence productivity at various stages of the reproductive cycle. During the pre-laying and laying periods, warmer weather can promote larger egg size in some species (Stevenson & Bryant 2000; Lessels, Dingemanse & Both 2002; Johnson & Golden 2006) and increased clutch size in others (Rotenberry & Wiens 1991; Haywood 1993; Hendricks 2003). During incubation, ambient temperatures may influence the proportion of time spent on the nest (Conway & Martin 2000), and warmer incubation temperatures may improve hatching success (Martin 1987) or fledging success (Reid, Monaghan & Ruxton 2000). During the nestling period, warmer and drier conditions can increase chick mass and survival (Ardia, Pérez & Clotfelter 2010; Schroeder *et al.* 2012), and post-fledging survival may be increased by warmer weather in the weeks immediately following fledging (Sankamethawee, Gale & Hardesty 2009; Gruebler & Naef-Daenzer 2010). Recruitment rates can also be influenced by weather during the remainder of the year (Robinson, Baillie & Crick 2007; Dybala *et al.* 2013). However, despite such documented weather effects, many studies find no effects of weather on various aspects of passerine productivity (e.g. Rotenberry & Wiens 1991; Winkler *et al.* 2002; Bradbury *et al.* 2003; Chase, Nur & Geupel 2005; Johnson & Golden 2006), whilst others suggest that apparent weather effects may rather be date effects, arising due to correlations between temperature and date within a season (Westneat, Stewart & Hatch 2009). It is therefore debatable to what extent general trends of climatic effects on productivity exist, and further case studies are needed.

To develop realistic projections of future demographic responses to climate change, it is important to consider weather effects alongside other factors influencing population productivity, particularly predation and density dependence. Weather during the breeding season and the preceding winter may affect predation rates by altering predator abundance, and breeding season weather can influence predator behaviour (Aars & Ims 2002; Chase, Nur & Geupel 2005; Merritt, Lima & Bozinovic 2005; Adamík & Král 2008). However predation rates can also fluctuate independently of weather (Wilson & Arcese 2006), for instance through between-year changes in habitat structure (Martin & Joron 2003) or through altered abundance in response to non-climatic factors (Schmidt, Rush & Ostfeld 2008). Meanwhile, density dependence can operate at every stage of the breeding cycle, dampening productivity through increased competition for resources and increased rates of predation on nests and fledglings (Krebs 1971; Dunn 1977; Newton 1998). For instance, some species demonstrate density-dependent reductions in clutch size (Perrins 1965; Both 2000; Ahola *et al.* 2009), fledging success (Ahola *et al.* 2009), and recruitment probability (Norman & Peach 2013). However other studies find productivity to be density-independent (e.g. Chase, Nur & Geupel 2005), and the precise form and strength of density dependence is likely to be highly variable between species and populations (Newton 1998). In some studies, the apparent absence of density-dependence may arise because short-term studies generally encompass a limited range of population densities relative to the interannual density variation present in that species.

Alongside the complex interplay of weather, predation and density dependence outlined above, assessing the factors determining passerine productivity is further complicated by scale effects. Whilst some processes may operate at the individual level, for instance warmer nestling periods improving chick condition, others may operate at the population level, for instance higher nest predation rates reducing the proportion of nests fledging successfully. This necessitates an approach that combines analysis of weather effects at both the individual level, with a view to identifying mechanisms, and the population level, to elucidate whether individual effects result in significant alterations in annual productivity (Reed, Jenouvrier & Visser 2013).

Here, we assess the impacts of weather on individual and population-level productivity and predation rates in a single-brooded passerine, the long-tailed tit *Aegithalos caudatus.* We use a 19-year study of an individually colour-marked population inhabiting the temperate climate of the Rivelin Valley, Sheffield, UK. The long-tailed tit is an excellent species for this analysis, because it suffers very high rates of nest predation by corvids and small mammals as it does not use nest boxes (>70% of nests are predated annually; Gullett *et al.* 2013), allowing us to investigate the effects of winter and breeding season weather on predation rates and subsequent productivity. Furthermore, the considerable interannual variation in population density (37–104 adults per km^2 of breeding habitat during the years 1995–2012) enables us to explore density dependence issues. The current study builds on recent research showing that harsh (cold and wet) breeding season weather reduces the annual survival probabilities of adult long-tailed tits, which was suggested to be a result of adult breeders trading reduced personal survival against increased reproductive success (Gullett *et al.* 2014). Such a trade-off could buffer populations from reduced productivity in harsh-weather years, an idea that we seek to address here. This study also offers a rare opportunity to measure juvenile recruitment over a period of almost two decades, enabling us to assess the effects of both breeding-season and year-round weather on juvenile recruitment.

At the individual level, we assess the impacts of weather during nest-specific periods on productivity during each stage of the breeding cycle (egg-laying, incubation, nestling period, fledging, recruitment). At the population level, we assess the impacts of monthly temperature and precipitation during the breeding season and the preceding winter on annual nest predation rate, and on five measures of annual productivity: clutch size, brood size of fledged nests, number of fledglings per breeding female, number of male recruits per breeding female (thus taking brood losses during the nesting cycle into account), and proportion of fledged males recruited (thus excluding losses during the nesting cycle). We also investigate the effects of weather throughout the entire year on the proportion of fledged males recruited. We test for density dependence at both the individual and the population level.

4.2 Methods

4.2.1 Study system

We studied individual and population-level productivity during 1995–2013 in a population of long-tailed tits in the temperate climate of the Rivelin Valley, Sheffield (53°23'N 1°34'W; altitude at centre of site = 168m a.s.l., range = 150–270m). The study area is approximately 2.5km^2, about half of which comprises mixed deciduous woodland/scrub that offers suitable breeding habitat for long-tailed tits, whilst the remainder is open pasture and therefore not used by long-tailed tits. Adult breeding population size in the study site ranged from 46 to 130 birds, equating to a mean population density of about 70 adults per km^2 of breeding habitat. Long-tailed tits are single-brooded, but pairs that fail frequently initiate a second or third re-nest attempt if there is sufficient time to raise a brood, with re-nests accounting for around 32% of nests per year (Gullett *et al.* 2013). The long-tailed tit is a facultative co-operative breeder and some failed breeders help other pairs with provisioning nestlings rather than re-nesting themselves, particularly if they fail later in the season (Hatchwell *et al.* 2004). At least 95% of adults in the study site are uniquely marked with colour rings each breeding season and all pairs within the study site are monitored and their nests located by observation. The date on which the first egg of each clutch is laid (hereafter termed lay date) is recorded so that day 1 corresponds to 1 January, accurate to ± 1 day for all accessible nests and ± 2 days for inaccessible nests (c. 10% of all nests). Brood size of accessible nests is measured on day 11 (± 1 day) of the nestling period, when the nestling mass (± 0.1g) and tarsus (± 0.1mm) are measured and a blood sample collected by brachial venipuncture, under Home Office licence. Blood samples are used to genetically determine the sex of fledglings (Griffiths *et al.* 1998). Males are the philopatric sex in long-tailed tits, with many females dispersing beyond the boundary of our study site (Sharp *et al.* 2008, 2011), and our analyses of recruitment therefore consider males only.

4.2.2 Datasets

Productivity and predation data were collected from the Rivelin population of long-tailed tits during 1995–2013. Data from 2001 were omitted from all analyses because access to the field site was limited by an outbreak of foot and mouth disease; recruitment of birds from the 2000 cohort could not be estimated for the same reason. Sample sizes for each analysis are given in Tables 4.1 & 4.2. Daily weather data were obtained from Weston Park Weather Station (Museums Sheffield 2013), located approximately 5km east of the study site (53º38'N 1º49'W) and at a similar elevation (131m) to the study site (mean 168m). Temperatures recorded on-site are very strongly correlated with weather station temperatures (Gullett *et al.* 2014), but we used the latter because on-site data were not available for all years.

4.2.3 Statistical approach

All analyses were conducted in R (R Core Development Team 2013). Our general approach was to model productivity as a function of weather variables and non-climatic variables likely to influence productivity (Tables 4.1 & 4.2). For population-level productivity and predation analyses, we used linear models, as response variables were annual means. For individual-level analyses we used linear mixed models in package lme4 (Bates *et al.* 2014), with year specified as a random effect in all models, including null models. We did not control for female identity as the majority of females had only one record in the dataset (on average in each analysis 73% of all data points came from unique females, and no single female contributed more than 1.5% of the data to each analysis). Error structures were modelled as binomial with logit link function for analyses of hatching, fledging and recruitment probabilities, with the response specified as a 2-column variable of the form 'number of successes vs. number of failures', to account for unequal sample sizes between years. Error structures for all other responses were modelled as normal. Mixed models with normal error structure were fitted using restricted maximum likelihood for parameter estimation, whilst fitting of binomial models and model comparison used maximum likelihood (Bartoń 2013). For all non-binary predictor variables, we compared the quadratic and linear equivalents of their relationship with each response, and included both linear and quadratic terms in subsequent analyses if the AICc of the quadratic model was ≥2 AICc points lower than that of the corresponding linear model. The only exception was in analyses of individual hatching/fledging probability in response to egg/nestling temperature, where evidence for a quadratic relationship was driven by a very small number of points with high leverage, and these effects were therefore modelled as linear. Where a predictor was modelled as quadratic in the full model, the quadratic term was only allowed to occur in a model in combination with the linear term.

For each response, we constructed a predictor set comprising all relevant weather variables plus specific non-climatic parameters as detailed in Tables 4.1 & 4.2. We used an information theoretic approach to model comparison over this predictor set, using package MuMIn (Bartoń 2013), and assessed model fit using Akaike Information Criterion corrected for small sample size (AICc). For each analysis, we derived model averaged parameter estimates and associated unconditional standard errors over all models differing by two AICc points or less. However, in analyses of individual-level productivity, variables retained in the model average but not appearing in the most parsimonious ('best') model had very low support (95% confidence intervals overlapping zero in all cases) and best models are therefore reported in the main text for the sake of clarity. For each response, we calculated the difference in AICc of the best model compared to the null model, and considered that the tested variables had no significant influence over the response if the null model was more parsimonious. As a measure of explanatory power of best models, we calculated either R^2 (for general linear models) or D^2 (for generalized linear models), where D^2 = (null deviance – model deviance) / null deviance; we calculated corresponding partial R^2 and D^2 values of each variable appearing in the best models. For population-level analyses, model-averaged R/D^2 were calculated by averaging partial R^2 and D^2 values of all models in the model average set, weighted by the Akaike weight of each component model.

4.2.4 Individual-level productivity analyses

We defined six individual-level productivity outcomes, and assessed the impact of weather during the period preceding the response event. Thus, we assessed (i) clutch size in response to weather during the pre-laying and laying periods; (ii) hatching probability in response to weather during the egg period; (iii) fledging probability in response to weather during the nestling period; (iv) number of fledglings and (v) nestling mass in response to weather during the nestling period up until the day on which brood size and mass were recorded (the first 11 days of the nestling period ± 1 day); (vi) recruitment probability in response to weather during the post-fledging period. We used 14 days as the relevant period for pre-laying and post-fledging weather effects based on biological knowledge. We also checked for the presence of stronger effects occurring during alternative periods with durations of 4, 8, 12, 16 and 32 days pre-laying/post-fledging; use of these alternative periods generated very similar results and we are thus confident that our use of a 14-day period is appropriate (Appendix 4.1).

Weather data were extracted for each focal period of each individual nesting attempt. In all analyses, temperature was the daily mean (ºC) during the focal period, as this represents conditions experienced every day, that could influence thermoregulation, food availability and predator activity. In analyses of clutch size, precipitation was the daily mean (mm, log-transformed to approximate normality after adding a constant of one), as we hypothesised that average weather conditions were likely to influence female condition and subsequent reproductive investment. For all other responses, we considered that precipitation effects were more likely to result from extreme precipitation events, rather than average precipitation values, because extreme precipitation events appear to cause partial and complete clutch/brood loss in rare cases and can hinder parental foraging (BJH & PRG pers. obs.). We therefore calculated an index of extreme precipitation events, which was the presence/absence of days on which precipitation exceeded the amount falling on the wettest 10% of days during the focal period across all years, equating to >6.4, 5.9, 6.0 mm per day during the egg, nestling and post-fledging periods, respectively. The exception was for analyses of recruitment, because the majority of post-fledging periods encountered precipitation exceeding the 10% threshold on at least one day, resulting in insufficient power to test for an effect; we therefore used a threshold of the wettest 5% of days for analyses of recruitment, to generate an adequate sample size between both response groups (see Appendix 4.2 for comparison of alternative indices). We controlled for non-climatic variables as detailed in Table 4.1.

4.2.5 Population-level productivity analyses

We defined five response variables describing population-level productivity. These were: (i) annual mean clutch size of complete clutches; (ii) annual mean brood size of fledged nests on day 11 of the nestling period, as a proxy for the number of fledglings per successful nest, because in broods that survive to fledging the vast majority of nestlings alive on day 11 fledge successfully (Hatchwell *et al.* 2004); (iii) annual mean number of fledglings per breeding female; (iv) annual mean number of male recruits per breeding female (log-transformed to approximate normality); (v) recruitment probability of fledged males.

We assessed the effects of mean monthly temperature and total monthly precipitation during each month of the breeding season, March–May, on the first four of these productivity outcomes; we did not use measures of extreme precipitation/cold events, as these are highly correlated with indices of average weather patterns (Gullett *et al.* 2013). Clutch size and brood size were also assessed in response to monthly temperature and precipitation during each month of the winter preceding breeding, December–February. Finally, recruitment probability was assessed in response to weather during each month of the year from egg-laying to recruiting, i.e. March–February. Due to the large number of potential predictors, we first ran four single-season models, in which the predictors were mean temperature and total precipitation during each month of spring (March–May), summer (June–August), autumn (September–November) or winter (December–February). We conducted model-averaging over each single-season model and all variables appearing in each model average (i.e. in models differing by two AICc points or less) were then entered into a year-round model. The year-round model therefore comprised temperature during March, May, September, January and February, and precipitation during August (Table 4.2).

We controlled for non-climatic variables as detailed in Table 4.2. Due to the large number of potential predictors compared to our number of data points, we first modelled each response variable as a function of non-climatic parameters only (Table 4.2). We compared the AICc of all models comprising every possible combination of one or more of these non-climatic parameters and identified the parameters retained in models within two AICc points of the most parsimonious as the variables to control for in all subsequent analyses of the focal response (see Table 4.2 for all non-climatic variables initially considered and ultimately controlled for).

4.2.6 Predation analyses

Finally, we investigated predation rates in response to weather in the current breeding season and the preceding winter, which could affect predator behaviour and/or abundance. We calculated a measure of daily predation risk of nests known to have been predated or fledged, following the Mayfield method (Mayfield 1975). Thus, daily predation risk was the number of nests predated over the course of the breeding season, divided by the number of active nest days during the entire breeding season (Mayfield 1975). We first assessed the effects of average weather conditions, which were mean temperature and total precipitation during the winter (December–February) and each month of the breeding season, March–May. In a second set of analyses, we assessed the effects of extreme winter conditions, which may impact predator abundance, and extreme precipitation events during the breeding season, which may impact predator behaviour more than average conditions. Extreme weather variables were therefore mean temperature and total precipitation during the coldest and the wettest month between December and February, and the number of very wet days occurring in each month of the breeding season, where 'very wet days' were those when precipitation exceeded 5.9 mm, which was the amount falling on the wettest 10% of days when chicks were in the nest over the course of the study; monthly mean temperature during each month of the breeding season was also included. To control for potential effects of variation in nest density on predation rate (Dunn 1977), we included breeder population size in year *n* as a predictor in all predictor sets.

Table 4.1 Variables included in individual-level productivity analyses, and their corresponding sample sizes. Quadratic effects of continuous predictors were considered in every case and were included if they outperformed their linear equivalent by ≥ 2 AICc points. Models were mixed effects models with year specified as a random effect and all other predictors as fixed effects; error structure was modelled as normal for analyses of clutch size, brood size and nestling mass, and binomial (with logit link) for hatching, fledging and recruitment probabilities.

Response *Total sample size*	**Climatic predictors**	**Non-climatic predictors**
Clutch size *n = 465 clutches*	Pre-laying temperature Pre-laying precipitation Laying temperature Laying precipitation	Relative lay date Relative lay date^2
Hatching probability *n = 926 clutches*	Egg temperature Egg wet days	Relative lay date Annual nest predation rate
Fledging probability *n = 358 broods*	Nestling temperature Nestling wet days	Relative lay date Annual nest predation rate
Fledged brood size *n = 223 broods*	Nestling$_{11}$ temperature Nestling$_{11}$ wet days	Relative lay date Number of helpers at nest Clutch size
Nestling mass *n = 266 broods*	Nestling$_{11}$ temperature Nestling$_{11}$ wet days	Relative lay date Number of helpers at nest Brood size Nestling tarsus
Recruitment probability *n = 723 fledglings from 192 broods*	Nestling temperature Nestling wet days Post-fledging temperature Post-fledging wet days	Relative lay date Ad + juv population size Nestling condition

Climatic predictors: pre-laying period = 14 days preceding first egg; laying period = day before first egg until day before last egg laid; egg period = day first egg laid until day before eggs hatched; nestling period = period for which chicks present in nest; nestling$_{11}$ period = portion of nestling period up to day of measuring at that nest, usually day 11 of nestling period; post-fledging period = 14 days following fledging; temp = mean daily temperature (ºC); prec = mean daily precipitation (mm); wet days = presence/absence of days of heavy rainfall. Non-climatic predictors: relative lay date = day on which first egg laid relative to date of first egg from all clutches within that season; annual nest predation rate = daily percentage risk of nest being predated; number of helpers at nest = number of non-parent helper birds present during nestling period; clutch size = absolute clutch size, or median clutch size in that year if absolute clutch size unknown; brood size = number of fledglings alive in nest on day of measuring; nestling tarsus = mean tarsus length (mm) in that brood on day of weighing; ad + juv population size = number of adults plus fledglings at end of breeding season; nestling condition = brood mean nestling mass (g) divided by brood mean nestling tarsus length (mm). Number of helpers was not included as a predictor in analyses of clutch size or hatching probability, because non-parent birds help only during the nestling phase in the vast majority of cases; neither was helping included in analyses of recruitment, as helpers influence recruitment probability through their effect on nestling condition (Hatchwell *et al.* 2004), which we thus control for instead.

Table 4.2 Variables included in population-level productivity analyses, and their corresponding sample sizes. Quadratic effects of predictors were considered in every case but none outperformed their linear equivalent by two AICc points or more, and all relationships were thus modelled as linear. Models of recruitment probability were generalised linear models with binomial error structure and logit link function; all others were general linear models with normal error structure. Non-climatic predictors *'considered, not included'* were those considered in the initial stage of non-climatic model comparison but which showed no evidence of influencing the focal productivity response and were therefore not controlled for in subsequent analyses.

Response *Sample size*	**Climatic predictors**	**Non-climatic predictors** *Considered, not included*
Mean clutch size *n = 18*	Mar/Apr/May temp + prec *or* Dec/Jan/Feb temp + prec	Adult population size Proportion 1st attempts *Breeding season length*
Mean brood size *n = 18*	Mar/Apr/May temp + prec *or* Dec/Jan/Feb temp + prec	Proportion 1st attempts Mean clutch size *Adult population size* *Breeding season length* *Nest predation rate* *Helpers per fledged nest*
Mean number fledglings per breeding female *n = 18*	Mar/Apr/May temp + prec	Adult population size Nest predation rate Breeding season length *Proportion 1st attempts*
Mean number male recruits per breeding female (log-transformed) *n = 16*	Mar/Apr/May temp + prec	Ad + juv population size Nest predation rate *Helpers per fledged nest* *Proportion 1st attempts* *Breeding season length*
Recruitment probability of male fledglings *n = 16*	Mar/May/Sept/Jan/Feb temp + Aug prec	Ad + juv population size Helpers per ♂ fledgling *Proportion 1st attempts*

Climatic predictors: temp = mean daily temperature (ºC); prec = mean daily precipitation (mm). Non-climatic predictors: adult population size = number of breeding adults; breeding season length = 80th percentile of first egg dates; proportion 1st attempts = proportion of nests in the focal analysis that were first attempts (i.e. the proportion amongst nests in which a full clutch was laid in analyses of clutch size, and proportion amongst nests which fledged in all other analyses; nest predation rate = daily percentage risk of nest being predated; helpers per fledged nest or per ♂ fledgling = mean number of helpers per fledged nest or per male fledgling in the population, with helpers at failed nests excluded; ad + juv population size = number of adults plus fledglings at end of breeding season.

4.3 Results

Over 19 years, there was great interannual variation in both monthly weather and annual productivity in the Rivelin population of long-tailed tits (Table 4.3). Population size was also highly variable, with the number of breeding adults ranging from 46 to 130 between years (Table 4.3). Predation was the major cause of nest failure, accounting for the loss of 72% of all nests over the course of the study (n = 1265).

4.3.1 Weather effects on individual-level productivity

There were no effects of weather on clutch size, brood size of fledged nests, or nestling mass, but hatching, fledging and recruitment probabilities did show some association with weather (Table 4.4). Specifically, hatching probability increased when the incubation period was warmer (partial D^2 = 0.02; Fig. 4.1a) and fledging probability increased when the nestling period was warmer (partial D^2 = 0.04; Fig. 4.1b) or when there were some very wet days during the nestling period (partial D^2 = 0.07; Fig. 4.1c). Recruitment was very slightly higher when there were no very wet days during the post-fledging period (partial D^2 = 0.01; Fig. 4.1d).

4.3.2 Weather effects on population-level productivity

There were no effects of spring weather on mean annual clutch size or mean number of fledglings per breeding attempt (Table 4.5), nor any effects of winter weather on clutch or brood size (Appendix 4.3). There was some suggestion that fledged broods were larger in years with higher precipitation during March (partial R^2 = 0.09) or May (partial R^2 = 0.04; Table 4.4). Spring weather strongly influenced both measures of recruitment (Table 4.5). Specifically, warm March temperatures reduced the number of recruits per breeding female (partial R^2 = 0.34; Fig. 4.2a) and the probability of fledglings recruiting (partial D^2 = 0.23), and warmer May temperatures increased the number of recruits per breeding female (partial R^2 = 0.46; Fig 4.2b) and the probability of fledglings recruiting (partial D^2 = 0.36). In contrast, recruitment was influenced very little by monthly weather during the remainder of the year (Table 4.5).

4.3.3 Predation effects and associations with weather

The probability of a nest being depredated was variable between years, with daily nest predation risk ranging from 1.93% to 4.90% (Table 4.3). At the population-level, annual nest predation risk was the main determinant of the number of fledglings per breeding female, with increased productivity when predation rate was lower (partial $R^2 = 0.45$; Fig. 4.3, Table 4.5). Variation in predation risk across years was not substantially related to either winter or breeding season weather, with the null model having a lower AICc than all predictor models (Appendix 4.4).

4.3.4 Density dependence and effects of other non-climatic variables

There was evidence for density dependence of recruitment at both levels of analysis. At the individual level, low-population years had slightly higher recruitment (partial $D^2 = 0.02$; Fig. 4.4a; Table 4.4), and at the population level, years of low population size were strongly associated with more recruits per breeding female (partial $R^2 = 0.29$; Table 4.5) and a higher proportion of fledglings recruiting (partial $D^2 = 0.67$; Fig. 4.4b, Table 4.5). There was also some evidence for density-dependence of clutch size at the population level (partial $D^2 = 0.09$; Table 4.5).

Other non-climatic variables showed limited explanatory capacity. At the individual level, relative timing of breeding within a season had some effects, with earlier nests having slightly higher hatching (partial $D^2 = 0.01$) and fledging probabilities (partial $D^2 = 0.02$), increased nestling mass (partial $D^2 = 0.01$), and higher recruitment probabilities (partial $D^2 = 0.04$; Table 4.4). Also, nestlings from broods with more helpers tended to be heavier (partial $D^2 = 0.02$) and nestlings from broods in higher condition on day 11 of the nestling period were more likely to recruit at the individual level (partial $D^2 = 0.01$; Table 4.4). At the population level, clutch size showed a strong positive association with the proportion of clutches that were first attempts (partial $R^2 = 0.29$; Table 4.5). Similarly, brood size of fledged nests was unsurprisingly strongly positively correlated with mean clutch size (partial $R^2 = 0.26$) and less strongly so with the proportion of fledged nests that were first attempts (partial $R^2 = 0.05$; Table 4.5). Finally, the number of fledglings per breeding female tended to be higher in years with longer breeding seasons (partial $R^2 = 0.05$; Table 4.5).

Table 4.3 Summary of interannual variation in population-level productivity outcomes, monthly weather and non-climatic predictor variables used in population-level productivity analyses, in the Rivelin population of long-tailed tits. Shown are the mean, standard deviation (SD) and range of each variable during the period 1995–2013 (excluding 2001).

Variable	Mean	SD	Range
Population-level responses			
Clutch size	9.62	0.29	9.3 - 10.3
Number of fledglings per breeding ♀	2.62	0.95	1.1 - 4.3
Brood size of fledged nests	7.78	0.64	6.8 - 9.1
Number of ♂ recruits per breeding ♀	0.26	0.20	0.03 - 0.77
Proportion of ♂ fledglings recruited	0.22	0.10	0.06 - 0.40
Predation rate (daily % risk)	3.33	0.90	1.93 - 4.90
Climatic predictors			
December temperature (ºC)	4.5	1.5	0.4 - 6.5
January temperature (ºC)	4.5	1.3	1.8 - 7.0
February temperature (ºC)	5.0	1.6	2.3 - 8.2
March temperature (ºC)	6.6	1.7	2.2 - 9.2
April temperature (ºC)	9.1	1.3	7.3 - 12.3
May temperature (ºC)	12.0	0.9	9.2 - 13.3
December precipitation (mm)	83.9	36.2	18.8 - 136.0
January precipitation (mm)	73.6	42.8	8.5 - 157.7
February precipitation (mm)	65.7	36.8	9.3 - 173.9
March precipitation (mm)	48.6	24.4	10.2 - 98.8
April precipitation (mm)	64.2	49.1	5.8 - 180.6
May precipitation (mm)	56.1	26.7	17.5 - 129.8
Non-climatic predictors			
Adult population size	91.9	24.3	46 - 130
Adult plus fledgling population size	216.8	62.6	136 - 353
Breeding season length (days)	23.8	4.6	13.0 - 33.4
Proportion of 1st attempts	0.68	0.12	0.43 - 0.88
Mean number of helpers per successful ♀	1.39	0.64	0.85 - 3.00

Table 4.4 The effects of weather on individual-level productivity outcomes in the Rivelin population, 1995–2013. Productivity outcomes were (a) clutch size of full clutches, (b) brood size of fledged nests, (c) hatching probability, (d) fledging probability, (e) nestling mass and (f) recruitment probability of fledged males, modelled in response to weather during nest-specific periods of the breeding season. Non-climatic parameters were controlled for as detailed in Table 4.1. Best models are displayed, showing the model D^2, and the parameter estimate (est), standard error (SE) and partial D^2 of each variable retained in the best model.

Variable	Est.	SE	Partial D^2
(a) Clutch size: $D^2 = 0.10$			
Intercept	*+9.769*	*0.119*	--
Relative lay date	+0.025	0.013	0.10
Relative lay date^2	-0.002	<0.001	
(b) Brood size: $D^2 = 0.05$			
Intercept	*-1.967*	*1.279*	--
Clutch size	+1.003	0.129	0.05
Number of helpers	+0.195	0.113	<0.01
(c) Hatching probability: $D^2 = 0.04$			
Intercept	*-0.714*	*0.565*	--
Relative lay date	-0.052	0.009	0.03
Predation rate	-0.411	0.109	0.01
Egg temperature	+0.263	0.051	0.02
(d) Fledging probability: $D^2 = 0.12$			
Intercept	*-4.261*	*0.975*	--
Relative lay date	-0.041	0.014	0.02
Nestling temperature	+0.368	0.088	0.04
Nestling wet days	+1.721	0.291	0.07
(e) Nestling mass: $D^2 = 0.50$			
Intercept	*-1.150*	*0.512*	--
Relative lay date	+0.004	0.002	0.01
Number of helpers	+0.056	0.002	0.02
Tarsus length	+0.467	0.028	0.48
Brood size	-0.010	0.006	0.01
(f) Recruitment: $D^2 = 0.07$			
Intercept	*-2.973*	*2.087*	--
Relative lay date	-0.046	0.012	0.04
Population size	-0.003	0.002	0.02
Nestling condition	+7.831	5.036	0.01
Post-fledging wet days	-0.517	0.198	0.01

Table 4.5 The effects of weather on population-level productivity outcomes in the Rivelin population, 1995–2013. Productivity outcomes were (a) mean clutch size, (b) mean brood size of fledged nests, (c) number of fledglings per breeding female, (d) number of recruits per breeding female, and (e) recruitment probability of fledged males, modelled in response to mean temperature (temp) and total precipitation (prec) during each month of (a-d) the breeding season, March–May or (e) the year from hatching to recruiting, March–February. Non-climatic parameters were controlled for as detailed in Table 4.2. Model averages are displayed, showing the model average D/R^2 and number of models in each model average set, and the parameter estimate (est), standard error (SE) and partial D/R^2 of each variable retained.

Variable	Est.	SE	Partial D/R^2
(a) Clutch size: $R^2 = 0.35$, 2 models			
Intercept	*+8.560*	*0.546*	--
Proportion 1st nests	+1.624	0.623	0.29
Population size	-0.004	0.002	0.09
(b) Brood size: $R^2 = 0.47$, 6 models			
Intercept	*-4.101*	*4.109*	--
Clutch size	+1.136	0.430	0.26
Proportion 1st nests	+1.903	0.978	0.05
March prec	+0.009	0.005	0.09
May prec	+0.008	0.004	0.04
(c) Fledglings per ♀: $R^2 = 0.48$, 3 models			
Intercept	*+4.424*	*1.179*	--
Predation rate	-0.732	0.212	0.45
Season length	+0.072	0.038	0.05
Population size	-0.010	0.007	0.01
(d) Recruits per ♀: $R^2 = 0.70$, 2 models			
Intercept	*-5.791*	*2.011*	--
Population size	-0.009	0.003	0.29
Predation rate	-0.317	0.171	0.03
March temp	-0.430	0.133	0.34
May temp	+0.774	0.194	0.46
(e) Recruitment probability: $D^2 = 0.81$, 2 models			
Intercept	*-5.501*	*2.036*	--
Population size	-0.009	0.002	0.67
March temp	-0.277	0.094	0.23
May temp	+0.544	0.149	0.36
Sept temp	+0.217	0.109	0.04

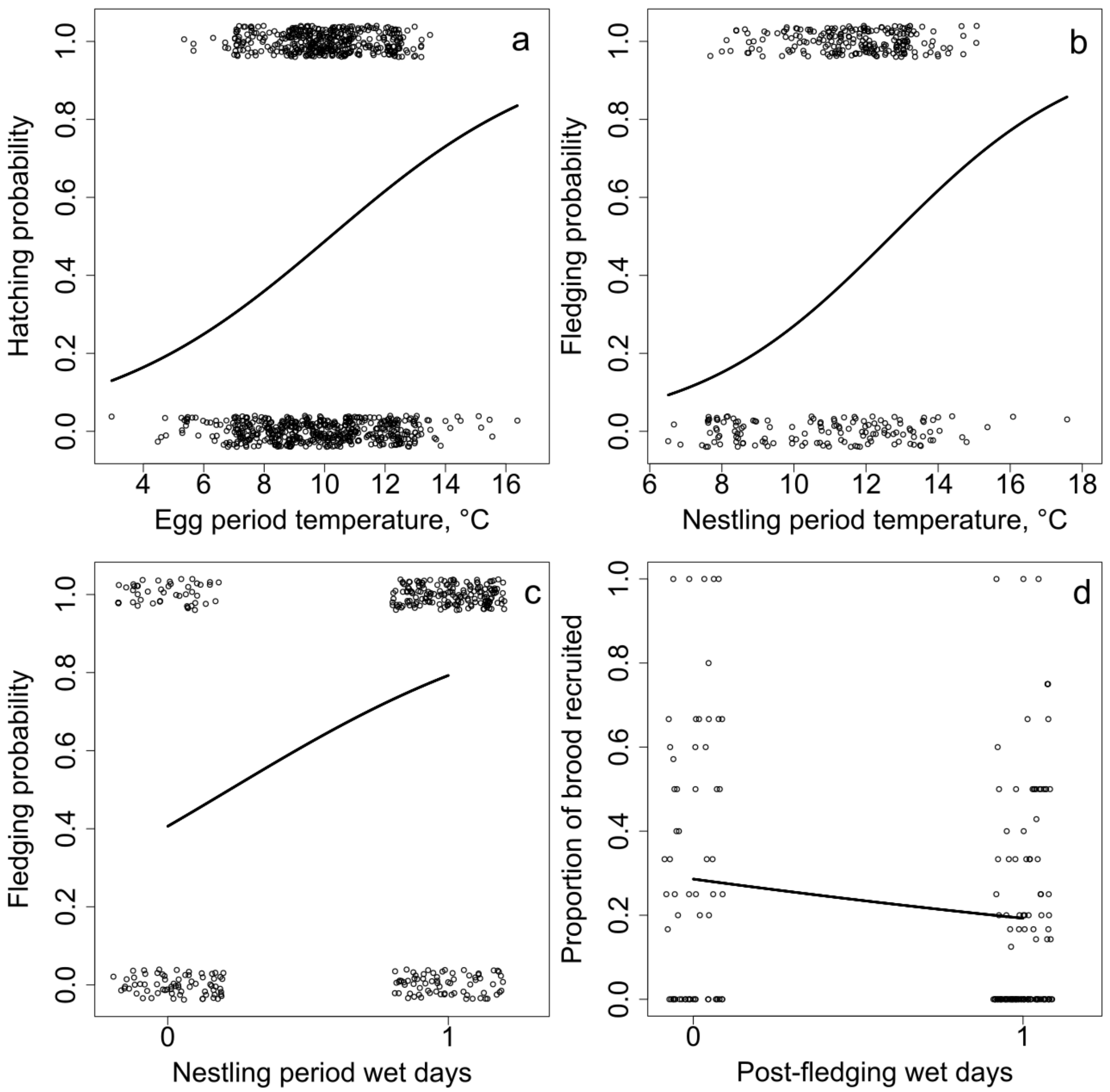


Figure 4.1 Individual productivity outcomes in response to weather during nest-specific and seasonal periods, in the Rivelin population of long-tailed tits during 1995–2013. Shown are (a) hatching probability in response to temperature during the egg period; (b) fledging probability in response to temperature during the nestling period; (c) fledging probability in response to the presence/absence of exceptionally wet days during the nestling period; (d) proportion of brood recruited in response to the presence/absence of exceptionally wet days during the post-fledging period. In all plots, data points are jittered vertically; in plots (c-d) points are also jittered horizontally to enable visualisation of binary effects. Plotted lines show the relationships in the most parsimonious models, controlling for non-focal predictors at their median value (see Table 4.4 for parameter estimates and non-focal predictors).

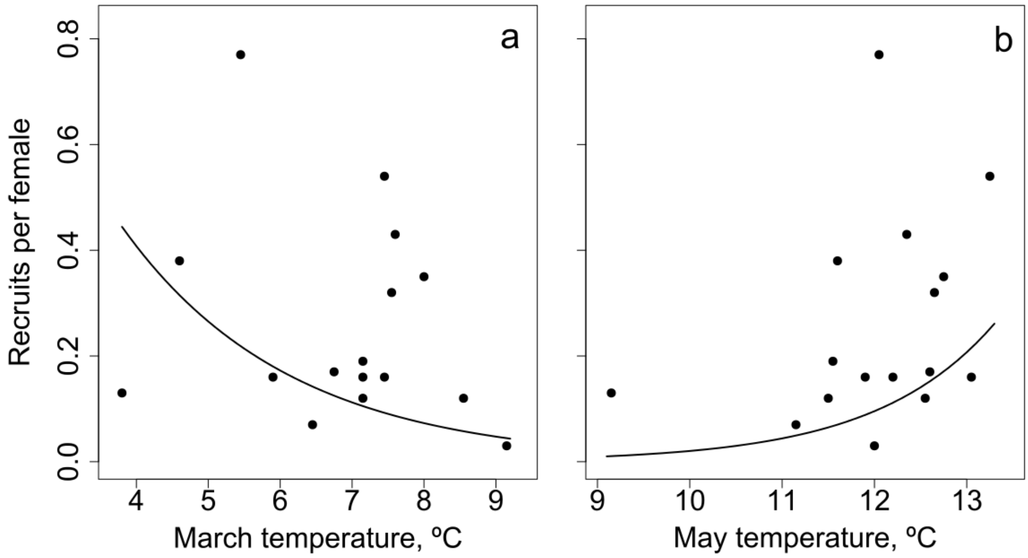


Figure 4.2 The number of recruits per breeding female in response to mean temperature during (a) March and (b) May, in the Rivelin population of long-tailed tits during 1995–2013. The plotted lines show model-averaged parameter estimates with non-focal predictors held at their median value, where est. ± 1SE = (a) -0.430 ± 0.133, partial R^2 = 0.34; (b) +0.774 ± 0.194, partial R^2 = 0.46.

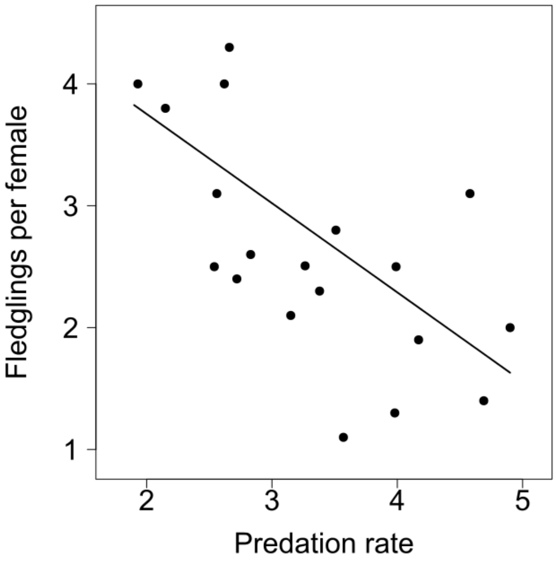


Figure 4.3 The number of fledglings per breeding female in response to annual predation rate, in the Rivelin population of long-tailed tits during 1995–2013, where predation rate was the daily percentage risk of a nest being predated. The plotted line shows the model-averaged parameter estimate with non-focal predictors held at their median value, where est. ± 1SE = -0.732 ± 0.212, partial $R^2 = 0.45$.

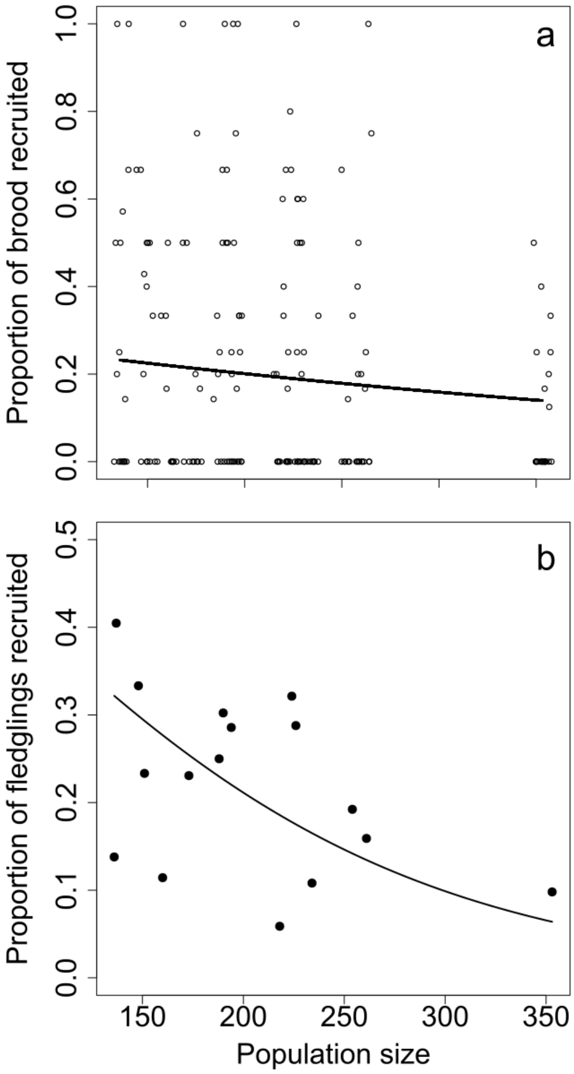


Figure 4.4 The density dependence of male recruitment at (a) the individual and (b) the population level, in the Rivelin population of long-tailed tits during 1995–2013. Population size was the number of breeding adults plus the number of fledged individuals in each year. The plotted lines are the relationships in the most parsimonious models, with non-focal predictors held at their median value, where est. ± 1SE = (a) -0.003 ± 0.002, partial $D^2 = 0.01$; (b) -0.009 ± 0.002, partial $R^2 = 0.64$; note that the relationship in the population level model average was almost identical: -0.009 ± 0.002, model-averaged partial $R^2 = 0.67$.

4.4 Discussion

Over the 19 years of this study, breeding long-tailed tits experienced massive variation in weather conditions, both in terms of monthly means and in terms of conditions during specific periods of a nest's existence. For instance, mean monthly March temperature ranged from 2.2ºC to 9.2ºC, and the mean temperature of the incubation period ranged from 2.6ºC to 14.2ºC. However, although individual productivity outcomes showed some associations with weather, the effects on population-level fledgling production were weak. Instead, fledgling production was controlled primarily through nest predation, which showed little association with monthly weather conditions. In contrast, we found significant effects of March and May temperature on population-level recruitment rates, which were also strongly regulated by density dependence.

4.4.1 Effects of weather and predation on fledgling production

At the individual level, warmer incubation and nestling periods were associated with increased hatching and fledging probabilities, respectively. However, the overall explanatory capacity of these relationships was low, and weather was not related to the number of fledglings produced per breeding female at the population level. This may indicate that parents minimise the potential negative impacts of harsh weather on productivity by redirecting energetic investment towards reproduction at the cost of their own survival, as suggested by the fact that adults have lower survival to the next year after cold and/or wet breeding seasons (Gullett *et al.* 2014). For instance, parents may spend more time brooding young chicks in cold weather (Wiebe & Elchuk 2003; BJH & PRG pers. obs.), and long-tailed tits increase their nest-building investment in cooler ambient conditions, by lining nests with a higher mass of feathers (McGowan *et al.* 2004). Given that long-tailed tit nests are extremely well insulated and waterproofed compared to those of many other passerine species (McGowan *et al.* 2004), long-tailed tit chicks are likely to be relatively buffered against the negative impacts of inclement weather compared to open-nesting species. Indeed, whilst some open-nesting species suffer high brood losses in wet weather (Skagen & Yackel Adams 2012), in long-tailed tits complete nest failure as a direct result of weather is very rare (<2% of nests over the course of this study; unpubl. data).

In line with the lack of strong weather effects on individual productivity, fledgling production at the population level was largely determined by annual nest predation rate. Nest predation is a major factor influencing brood production in a number of passerine species (e.g. Morrison & Bolger 2002; Schmidt *et al.* 2005; Adamík & Král 2008; Le Tortorec *et al.* 2013) and the long-tailed tit is no exception, with more than 70% of nests predated each year in this population. We found no substantial effects of monthly weather on annual predation rates, despite previous findings that both spring and winter weather influence the abundance of small mammals in temperate habitats (Aars & Ims 2002; Merritt, Lima & Bozinovic 2005; Adamík & Král 2008). However, long-tailed tit nests are predated not only by small mammals but also by corvids, which do not show population declines after harsh winters (Baillie *et al.* 2014). It therefore seems unsurprising that weather does not strongly influence overall predator abundance in this population.

Despite this lack of monthly weather effects on annual predation rates, the current study suggests that day-to-day variation in predation rates may be influenced by daily weather conditions. Importantly, the strongest effect of weather on individual productivity in this study was an increased fledging probability when some very wet days occurred during the nestling period; the most likely explanation for this is that heavy rainfall may reduce predator activity, as shown in some previous studies (Chase, Nur & Geupel 2005). Weather may also influence daily predation risk by altering parental behaviour. Specifically, wetter weather during the nestling period can reduce provisioning rates, both in long-tailed tits (BJH & PRG pers. obs.) and other species (Dawson, Lawrie & O'Brien 2005; Shen *et al.* 2012); this reduction in parental activity at the nest could reduce the risk of a predator locating a nest (Skutch 1949), as shown in some other passerines (Martin, Scott & Menge 2000; Eggers *et al.* 2005). Similarly, colder temperatures during the egg and nestling periods (which were associated with reduced hatching and fledging probabilities) may increase predation rates by increasing parental activity at the nest, as males may provision chicks and incubating females more frequently when thermoregulatory energy demands are higher (Eggers *et al.* 2005). A more thorough investigation of daily variation in nest predation risk in response to sporadic weather events is therefore needed, particularly as such processes could become increasingly important under future climates given that extreme precipitation events are expected to become more common (Stocker *et al.* 2013).

We also found that population-level fledgling production was reduced in years with shorter breeding seasons, which has implications for future productivity in this population given that climate change is expected to drive a reduction in breeding season length over the coming decades, due to warming of April temperatures (Gullett *et al.* 2013). However, in keeping with previous studies in this population (Hatchwell *et al.* 2004; Sharp *et al.* 2008), we found that helpers increased the mass of nestlings, which may offer a mechanism by which the negative impacts of reductions in breeding season length could be minimised in this species. Most temperate passerines are not co-operative and therefore do not share this possibility, which may place them at greater risk of reduced productivity in the future.

4.4.2 Effects of weather and predation on recruitment

Recruitment was influenced by weather, being reduced by the presence of very wet days during the post-fledging period at the individual level, and being higher in years with warmer May temperatures at the population level (with May being the period when most young are in the nest and fledge; mean fledge date ± 1SD = 23 May ± 10 days). Previous studies have suggested that weather during the post-fledging period influences survival amongst various passerines due to the limited thermoregulatory, foraging and predator-evasion abilities of recent fledglings (Yackel Adams, Skagen & Savidge 2006; Greño, Belda & Barba 2008; Gruebler & Naef-Daenzer 2010). Such effects seem likely to explain our finding that wet post-fledging weather was correlated with reduced recruitment probability at the individual level. However, we observed no effect of post-fledging temperature on individual recruitment probability, nor any effect of temperature during the nestling period on nestling mass. The positive association between May temperature and population-level recruitment thus seems unlikely to be purely an effect of temperature on fledgling condition and we suggest instead that this relationship is due to processes occurring at the population level. For instances, warm May temperatures could enhance the abundance of non-caterpillar food sources such as aphids (Bale *et al.* 2002). Alternatively, post-fledging predation rates could be reduced if fledgling production amongst other small-bodied passerines is higher in years with warm May temperatures, because species that predate long-tailed tits would have an increased source of prey in the form of other passerines. We were unable to include a direct measure of post-fledging predation pressure on recruitment in this study, and it is likely that such effects are substantial, as recent fledglings are highly vulnerable to predation (Yackel Adams, Skagen & Savidge 2006). Elucidating the impacts of weather on post-fledging predation rates, and identifying other mechanisms controlling post-fledging survival, should therefore be priorities for future research.

Recruitment rates at the population level were also higher in years with cold March temperatures. One possible explanation for this is that long-tailed tits build more insulated nests when conditions are cooler (McGowan *et al.* 2004); given that most first nesting attempts are built during March in the vast majority of years (Gullett *et al.* 2013), cold March weather may ultimately increase the temperature inside the nest via such an increase in parental investment. Warmer nests could improve nestling condition (Lack 1966; Ardia, Pérez & Clotfelter 2010) and subsequent recruitment (e.g. Magrath 1991; Both *et al.* 1999; Monrós, Belda & Barba 2002; Sharp *et al.* 2008). Another possibility is that colder March temperatures promote greater synchrony between the timing of peak food availability and demand, resulting in nestlings receiving a higher-quality diet. Evidence for this lies in the fact that in years with very mild March temperatures, breeding initiation (which is largely determined by March temperature in this population; Gullett *et al.* 2013) can occur too early with respect to the temporal peak in food abundance (which is largely determined by early-April temperature in this population), leading to a lower quality of the nestling diet (Gullett *et al.* in prep.). This suggestion requires further investigation when more years of data are available concerning the phenology of key food sources, nestling diet and subsequent recruitment.

In contrast to the strong effects of March and May temperature, we found that non-breeding season weather had little influence on recruitment rates. This contrasts with the classic view that winter weather is an important factor influencing first-year survival (Lack 1954; Sæther, Sutherland & Engen 2004). A recent analysis in the same population found that breeding season weather was the major determinant of annual adult survival (Gullett *et al.* 2014), and the current study suggests that this is true of first-year survival also. This is not altogether surprising, given that the majority of first-year mortality is thought to occur in the first few weeks after fledging in long-tailed tits (C. Napper, pers. comm.) and other passerine species (Perrins 1965; Naef-Daenzer, Widmer & Nuber 2001; Yackel Adams, Skagen & Savidge 2006; Sankamethawee, Gale & Hardesty 2009). Consequently, the current study adds further support to recent findings that the breeding season is the time of greatest climatic influence on the demography of this species (Gullett *et al.* 2013, 2014).

4.4.3 Density dependence

Recruitment rates were strongly density dependent in this population, suggesting that this is a key mechanism of population regulation in the long-tailed tit, particularly as adult survival is largely independent of population density in the Rivelin site (Gullett *et al.* 2014). A similar situation has has been shown in several other passerine species (Nilsson 1984; Arcese *et al.* 1992; Newton 1998; Norman & Peach 2013). It is important to note that in the current study, we could not distinguish between mortality and dispersal, and part of the density dependence observed could therefore be a result of increased dispersal of first-year individuals out of the study site in years when fledgling production is high. However, we believe to have minimised such an effect by assessing the recruitment of only male fledglings, which rarely disperse out of the Rivelin site (Sharp *et al.* 2008). We also found some evidence of reduced clutch size and number of fledglings in years with high population density, as found in some previous studies of great tits and blue tits (Perrins 1965; Dhondt, Kempenaers & Adriaesen 1992; Ahola *et al.* 2009). However, the error associated with these estimates was large, suggesting that any effects of population size on egg and fledgling production are likely to contribute very little to population regulation in this species, at least under the range of densities and habitat conditions present during this study.

4.4.4 Conclusion

We have shown that the effects of weather on fledgling production are minor in this population, perhaps partly due to the high parental investment in nest-building in this species. Instead, fledgling production is driven largely by nest predation rates, which are not determined by monthly weather during the spring or winter, suggesting that predation rates are unlikely to change consistently under future climates. Weather did influence recruitment rates, but the opposing effects of March and May temperature at the population level highlight the fact that the consequences of future climate change will depend on the relative rate of warming between different months. Furthermore, any benefits of future climate change are unlikely to bring about substantial increases in recruitment in this population, due to the strong density dependence observed in this study. Instead, it seems possible that recruitment may decline in the future following continued warming of March temperatures, and fledgling production may decline if warming during April continues to drive reductions in breeding season length. Further research that elucidates the mechanisms driving the observed weather effects will be crucial for developing reliable predictions of the effects of climate change on passerine productivity.

Chapter 5. Phenological mismatch

Summary

Phenology is an important determinant of biotic interactions, and interspecific variation in rates of climate-induced phenological change can disrupt such interactions. One key example is that of insectivorous passerine birds breeding in temperate woodlands, which are suggested to be advancing their timing of reproduction insufficiently to keep pace with the advancing phenology of their main breeding-season food source, caterpillars. However, the current and future extent of temporal mismatching is unclear, and the consequences for avian productivity remain elusive. We use a long-term population study of long-tailed tits *Aegithalos caudatus* in central England, combined with five years of caterpillar phenology data and three years of nestling dietary data from the same area. We determine the potential for climate change to alter the extent of mismatch and dietary caterpillar content of birds breeding in temperate woodlands, and assess the impacts of such mismatch on nestling mass and skeletal growth. This study is amongst the first to assess mismatch in a species that shows a recent regional increase in population size and an extreme extent of advance in average timing of breeding (16 days during 1968–2011 across the UK). We found that over the course of five years, the timing of peak caterpillar abundance was strongly related to temperature during early April, whereas the onset of breeding was determined largely by March temperature, indicating a high potential for future mismatching. Dietary caterpillar content of long-tailed tit nestlings was strongly influenced by the date relative to the caterpillar peak, suggesting that mismatch can act as a reliable proxy for dietary caterpillar content in insectivorous passerines breeding in temperate deciduous woodlands. Nestlings in broods fledging substantially before the caterpillar peak had reduced mass and skeletal growth, suggesting that changes in the degree of mismatch occurring under future climates could alter productivity in the future.

5.1 Introduction

Predicting the consequences of climate change is a major challenge for ecologists today. Widespread phenological shifts have been documented in numerous species across the globe (Walther *et al.* 2002), but the pattern and rate of phenological change differs between species, and interspecific interactions are consequently becoming disrupted, with potentially large impacts on population viability (Walther *et al.* 2002; Visser & Both 2005; van Asch & Visser 2007; Parmesan 2007). One such interaction that has received considerable attention is that of insectivorous passerine birds in temperate woodlands and their caterpillar prey species, which show a brief temporal peak in abundance in spring (e.g. Visser, Holleman & Gienapp 2006; Charmantier *et al.* 2008; Both *et al.* 2009). Given that the timing of breeding and the timing of the caterpillar peak are strongly influenced by temperature (e.g. Perrins 1991), climate change may create temporal mismatches between the timing of peak food demand and supply, and such mismatches have been suggested as a mechanism for population decline in some passerine birds (Both *et al.* 2006; Goodenough *et al.* 2009). However, it is unclear to what extent temporal mismatches are occurring, and what the consequences may be for avian productivity (Stevenson & Bryant 2000; Both 2010; Vatka, Orrell & Rytkönen 2011; Burger *et al.* 2012; Reed, Jenouvrier & Visser 2013). Such knowledge is crucial for understanding the mechanisms controlling productivity in birds, and for improving predictions of future population responses to climate change (Parmesan 2007).

Predicting the extent of future mismatch as a result of climate change requires knowledge of the thermal control of the timing of peak caterpillar abundance and passerine timing of breeding in the same location. Warmer temperatures are known to advance the timing of both peak caterpillar abundance (Visser, Holleman & Gienapp 2006; Smith *et al.* 2011) and the onset of breeding in passerines (Thomas *et al.* 2001; Charmantier *et al.* 2008; Both *et al.* 2009). Notably, caterpillar peak date and the onset of breeding have been shown to respond to temperature during different parts of the spring in great tits *Parus major* (Visser, Holleman & Gienapp 2006) and willow tits *Poecile montanus* (Vatka, Orrell & Rytkönen 2011). Given that climatic warming is occurring to different extents in different months (Stocker *et al.* 2013), mismatch is likely if caterpillars and birds respond to temperature during different periods. However, the periods during which temperature determines the phenology of avian reproduction and caterpillar abundance are poorly documented in most systems. Furthermore, the distribution of nesting dates within a population in a given year is not merely a function of breeding onset, but is also influenced by the timing of the end of the breeding season. If the decision to end breeding is linked to declining food availability, the timing of breeding termination would also be expected to show a relationship with caterpillar peak date and thus temperature. However, no study to our knowledge has assessed the seasonal pattern of correlations between temperature and the timing of both breeding initiation and termination, and the timing of the caterpillar peak. Developing such knowledge would greatly improve our ability to predict the likely effects of climate change on population size in insectivorous passerines.

Mismatch with the timing of peak caterpillar abundance has been linked to reduced nestling mass in great tits, blue tits *Cyanistes caeruleus* and pied flycatchers *Ficedula hypoleuca* (Thomas *et al.* 2001; Tremblay *et al.* 2003; Visser, Holleman & Gienapp 2006; Burger *et al.* 2012). Mismatch could therefore lead to productivity declines, because reduced nestling mass is correlated with lower rates of post-fledging survival and recruitment in numerous passerines (e.g. Perrins 1965; Tinbergen & Boerlijst 1990; Magrath 1991; Both, Visser & Verboven 1999; Naef-Daenzer, Widmer & Nuber 2001; Monros, Belda & Barba 2002). Such negative impacts of mismatch are assumed to be a result of reduced diet quality amongst mismatched nestlings. However, there is a dearth of studies that directly assess the effects of dietary caterpillar content on nestling mass, rather than using mismatch as a proxy (but see Wilkin, King & Sheldon 2009). Very few studies have assessed the extent to which nestling diet is determined by the timing of breeding with respect to the caterpillar peak, particularly in the earlier part of the season (but see García-Navas & Sanz 2011a; Burger *et al.* 2012 for such an analysis during late-season nesting attempts). Given that mismatch increases parental foraging costs in several passerine species (Adams *et al.* 1994; Tinbergen & Dietz 1994; Thomas *et al.* 2001; Tremblay *et al.* 2005), a reduction in diet quality may be mitigated by increased parental effort, as parents may increase reproductive investment at the cost of their own survival (Thomas *et al.* 2001). Furthermore, some authors suggest that matching their timing of breeding to the period of peak food abundance may be relatively unimportant for birds breeding in habitats where caterpillars are super-abundant (Tremblay *et al.* 2003).

In addition to influencing nestling mass, mismatch could influence nestling skeletal growth independently of mass gain. Amongst the very few passerine mismatch studies that assess mass and size independently, the effects of mismatch on nestling tarsal length are mixed, with one study finding a marginal increase in nestling mass but no change in tarsal length (Wilkin, King & Sheldon 2009), and another finding both mass and tarsus length to be reduced when hatching was experimentally delayed (Buse *et al.* 1999). Accelerated skeletal growth rates could increase productivity if larger fledglings have higher survival rates (Naef-Daenzer, Widmer & Nuber 2001), and/or are able to fledge earlier (Tjørve & Underhill 2009; Węgrzyn 2013). Research into the effects of dietary caterpillar content on both nestling mass and skeletal growth rates is therefore important for understanding the consequences of mismatch.

The aims of this study are threefold: (i) to gauge the potential for climate change to alter the extent of mismatch experienced by birds breeding in temperate woodlands, based on whether the timing of the caterpillar peak and the timing of breeding initiation and termination respond to temperature during the same periods in spring; (ii) to assess the extent to which the nestling diet is determined by date with respect to the peak in caterpillar abundance in the earlier part of the breeding season; (iii) to assess the effects of dietary caterpillar content and mismatch on nestling mass and size. We use a long-term study of a population of long-tailed tits *Aegithalos caudatus* in the Rivelin Valley, Sheffield, in combination with five years (2009–2013) of data on caterpillar abundance from the same area. Additionally, we use three years (2011–2013) of data on the composition of the nestling diet, collected by recording the provisioning behaviour of parents at nests. This study is among the first to assess mismatch in a species that shows a recent regional increase in population size (Baillie *et al.* 2014). Timing of breeding in this species is highly responsive to monthly temperature during spring (Gullett *et al.* 2013), and we therefore aim to assess whether such phenological flexibility is contributing to the recent success of the long-tailed tit by enabling it to maintain synchrony with the timing of peak caterpillar abundance.

5.2 Methods

5.2.1 Study system

We studied temporal patterns in spring caterpillar abundance and breeding mismatch in a population of long-tailed tits over the period 2009–2013, and timing of breeding over the period 1995–2013 (with 2001 excluded due to site access restrictions). We studied a population in the temperate climate of the Rivelin Valley, Sheffield (53°23'N 1°34'W; altitude at centre of site = 168m a.s.l., range = 150–270m). The Rivelin population has been monitored intensively since 1994, and routine field protocols are described in full elsewhere (Gullett *et al.* 2013, 2014). Adult breeding population size ranged from 71 to 130 birds during 2009–2013 and 48 to 136 birds during 1995–2013. Annual timing of breeding initiation was measured as the median first egg date of all first nesting attempts within the population each year. An index of annual timing of breeding termination was measured as the date when 75% of females had terminated breeding (with 2003 excluded due to reduced nest-searching effort at the end of the season; see Gullett *et al.* 2013 for full explanation of this index). The long-tailed tit is an early-season breeder, but timing of breeding is highly variable between years, commencing earlier (2.9 days $°C^{-1}$) when March is warmer and terminating earlier (2.7 days $°C^{-1}$) when April is warmer (Gullett *et al.* 2013; average timing of breeding during 1995–2013: initiation = 8 April, range = 28 March to 20 April; termination = 2 May, range = 22 April to 19 May). Long-tailed tits are primarily insectivorous, provisioning nestlings with a diet of caterpillars, flying insects, and spiders (Cramp & Simmons 1983). Long-tailed tits do not defend their foraging ranges from conspecifics.

5.2.2 Datasets

Caterpillar abundance

We measured the annual timing of the peak in caterpillar abundance in the Rivelin Valley over five years (2009–2013), using the frass-fall method of Tinbergen (1960). Caterpillar abundance was estimated for 16 trees within the study site, with two silver birch *Betula pendula* and two native oak *Quercus spp.* monitored at each of four locations representing the variation in elevation and aspect within the study area. Silver birch and oak are among the most abundant tree species present throughout the site and show very different leafing phenologies, with birch typically bursting in mid- to late April across the study site and oak about two weeks later, in early to mid-May (PRG & KLE unpubl. data). Both tree species are known to be key food species for the abundant larvae of winter moth *Operophtera brumata* and other lepidopteran species (including primarily green oak tortrix *Tortrix viridana*, scarce umber *Agriopis aurantiaria* and mottled umber *Erranis defoliaria*; F. Botterill pers. comm.), and are two of the main forage locations of long-tailed tits in the study site (P. Gullett unpubl. data). At each tree, we collected caterpillar frass falling from the canopy by placing a wooden frame (50 cm x 50 cm) covered in nylon mesh beneath the canopy centre. Collection was conducted approximately every four days (precise timing was constrained to dry and relatively windless periods), with approximately 10 sampling sessions per year. Full details of the sampling protocol are described in Appendix 1. Mean frass mass (hr^{-1}) was converted to caterpillar biomass, correcting for increased frass-fall rates under higher ambient temperatures. We used the equation derived by Tinbergen & Dietz (1994): caterpillar biomass = $(24.38 \times F) - (0.767 \times F \times T)$, where F = frass dry mass (mg) and T = ambient temperature (ºC). Ambient temperature was calculated as the mean of hourly temperature recordings for every hour during which frass was collected, measured at the Weston Park Weather Station (see *Weather data*, below).

For each of the sixteen sample trees, we estimated the annual peak caterpillar abundance as the Julian date of observed maximum caterpillar biomass at that tree. Peak timing did not differ between the two tree species (paired *t*-test of observed peak date at birch versus oak within each site and within each year: $t_{19} = -0.15$, $P = 0.88$; mean ± 1SD peak date across all years: birch = 23 May ± 13 days, oak = 23 May ± 11 days). Similarly, caterpillar peak dates did not differ significantly or consistently between locations (Friedman rank sum test of location-specific anomaly from earliest date: Friedman $\chi^2_3 = 4.3$, $P = 0.23$). We therefore calculated the caterpillar peak date by combining biomass across all sixteen sampling trees in subsequent analyses, as we are confident that this accurately reflects the timing of caterpillar peak abundance experienced by long-tailed tits nesting in the Rivelin Valley. Thus, in each year caterpillar peak date in the Rivelin study site was estimated as the Julian date of maximum observed caterpillar biomass averaged across all sixteen sampling trees, or as the midpoint between two dates if two samples differed by <10% biomass. Caterpillar peak date was also estimated from annual quadratic regression models of caterpillar biomass in response to date. Observed and modelled annual caterpillar peak dates were very similar (paired *t*-test: $t_4 = -0.18$, $P = 0.87$; difference between observed and modelled date: range = 0–4 days, mean ± 1SD = 1.6 ± 1.5) and we therefore used observed caterpillar peak in all subsequent analyses. Additionally, an index of annual caterpillar abundance was estimated as the per-tree average caterpillar biomass present on the observed peak date within each year. This was used to test for a temporal trend in caterpillar abundance within the study site, using a general linear model of caterpillar abundance in response to year.

Mismatch

Mismatch was calculated for each nest that reached day 12 of the nestling period during 2009–2013 (18% of all nests initiated during that period). Mismatch was the difference in days from the caterpillar peak date to day 12 of the nestling period, where a negative value indicates that nestlings were early with respect to the peak in caterpillar abundance and a positive value indicates that nestlings were late with respect to the peak. We used day 12 as this is likely to represent the timing of peak food requirements of breeding long-tailed tits, when provisioning rates reach an asymptote (MacColl & Hatchwell 2003).

Dietary caterpillar content

For each hatched nest during 2011–2013, we recorded parental provisioning behaviour over the course of the nestling period. Nests were watched every two days for a minimum of one hour, commencing when nestlings were two days old and continuing until the day of fledging (mean ± 1SD = 16.7 ± 1.3 days). The identity of each feed was recorded as 'caterpillar' (22% of identified feeds), 'no caterpillar' (44%), or 'predominantly caterpillar' (i.e. feeds containing both caterpillars and insects/spiders, but predominantly caterpillars in the vast majority of cases; 34%). A provisioning watch continued for a minimum of 60 minutes and until at least 8 feeds had been successfully identified, or was excluded if this was not achieved, in order to maintain the reliability of dietary estimates (in fact, 99% of watches had at least 10 identified feeds).

For each nest surviving to day 12 of the nestling period, we calculated an index of the 'dietary caterpillar content' of nestlings, which was the overall proportion of feeds containing caterpillars across all provisioning watches in that nest up to day 12. We used day 12 as the cut-off, because we were interested in the effects of diet on nestling size and so wished to estimate diet up to the time at which nestlings are measured, typically on day 11 (provisioning watches were not performed on day 11 and we believe that provisioning on day 12 is very similar to that occurring on day 11, thus improving the accuracy of our estimates of nestling diet up to the time of measuring). There was no evidence that diet influenced the probability of a brood surviving to day 12, with all 11 nest failures before day 12 during the three years being caused by predation rather than nestling starvation. We included only those nests for which at least one provisioning watch was performed successfully during each of three stages of the nestling period (chick age 1-4, 5-8 and 9-12 days), thus accounting for the potential variation in diet over the course of each nestling period. This resulted in estimation of dietary caterpillar content at a total of 40 nests (16 nests in 2011, 13 nests in 2012, 11 nests in 2013), based on a total of 194 provisioning watches with an average of 16 ± 6 identified feeds per watch and an average duration of 67 ± 11 minutes (mean ± 1SD).

Nestling morphometrics and nest-specific variables

Brood size, nestling mass (to 0.1g) and nestling tarsus length (to 0.1mm) were measured on day 11 (± 1 day) of the nestling period by a single recorder (B.J. Hatchwell), for all accessible nests surviving to that age. The number of helpers present at each nest during the nestling period was recorded for all nests. Average provisioning rate at a nest was calculated as the total number of feeds per hour per provisioning watch, averaged over all watches performed between days two and 12 of the nestling period, for broods watched in each of the time periods specified previously (at least one watch at chick age 1-4, 5-8 and 9-12 days). Relative lay date at a nest was calculated as the day on which the first egg was laid in the Rivelin population in that year, subtracted from the first egg date of the focal nest.

Weather data

Daily and hourly weather data were obtained from Weston Park Weather Station (Museums Sheffield 2013), located approximately 5km east of the study site (53º38'N 1º49'W) and at a similar elevation (131m) to the study site (mean 168m). Weather station temperatures are very strongly correlated with temperatures on-site (R^2 = 0.997; Gullett *et al.* 2014). Average temperatures were calculated for overlapping fortnightly and weekly periods starting on each consecutive day over the course of late winter and spring (February–May).

5.2.3 Analyses

Statistical approach

All analyses were conducted in R (R Core Development Team 2013). Mixed effects models were run in package lme4 (Bates *et al.* 2014) and model comparison via AICc values was conducted in package MuMIn (Bartoń 2013). In all analyses we compared the linear and quadratic equivalents of each predictor using AICc, and included the quadratic in subsequent analyses if it outperformed the linear equivalent by ≥2 AICc points. Explanatory power of models was assessed via R^2 for linear models, and D^2 (proportion of deviance explained) for generalized linear models. Explanatory power of individual variables was assessed by calculating partial R^2 or partial D^2, following Zimmermann *et al.* (2007), using the formula: partial R^2 or D^2 of variable i = (R^2 or D^2 of full model) – (R^2 or D^2 of model lacking variable i). Where given, correlation coefficients are Pearson product-moment correlations, henceforth r.

Effects of temperature on caterpillar and avian phenology

To assess if caterpillar and avian phenology responded to temperature over different time windows we quantified the associations between fortnightly and weekly temperatures and timing of breeding (1995–2013) and timing of the caterpillar peak (2009–2013). We considered all temperature periods from 1 February until the date of the latest occurrence of the focal response during the years of study; this meant that sample sizes were not equal across later dates, but as we were comparing correlation coefficients and not significance values we merely caution that confidence is inevitably lower for correlations during the latest periods. We thus assessed timing of breeding initiation in relation to temperature from 1 February until 20 April, timing of termination in relation to temperature from 1 February until 19 May, and caterpillar peak timing in relation to temperature from 1 February until 9 June. For each time window (fortnightly and weekly, with windows starting on every consecutive day of the specified period) we calculated the Pearson's correlation coefficient between the average temperature during the time window and the timing of the focal response. We calculated the period of maximum thermal influence as the period during which correlation coefficients were within 90% of their highest (i.e. most negative) absolute value for each phenological response. Finally, we repeated the analyses with data on timing of breeding initiation/termination from the years 2009–2013 only, to enable direct comparison of thermal effects on the timing of breeding and on the caterpillar peak over the same time period. Results were very similar whether using the shorter or longer-term datasets for avian phenology, and whether assessing weekly or fortnightly mean temperatures; results henceforth therefore refer to fortnightly analyses over the 1995–2013 time period, with analyses using weekly time periods and shorter-term datasets reported in Appendix 5.1.

Effects of mismatch on the nestling diet

We assessed the relationship between the degree of mismatch experienced by a nest and the average dietary caterpillar content at that nest, during 2011–2013. We used a generalized linear model with binomial error structure and logit link function, controlling for year as a categorical factor. To account for the different numbers of feeds between different nests, 'dietary caterpillar content' was specified as a two-column response variable of 'number of feeds containing caterpillars' versus 'number of feeds not containing caterpillars'. In a second analysis, we assessed the effect of mismatch on the caterpillar content of all individual provisioning watches; this showed a very similar pattern to the nest-level analysis, and is therefore reported in Appendix 5.2.

Effects of mismatch and diet on nestling mass and tarsus length

We assessed the effect of mismatch on nestling size during 2009–2013, for 69 nests (12, 17, 13, 15, 12 nests in years 2009–13 respectively). We modelled brood mean nestling mass in response to mismatch, controlling for tarsus length due to its high correlation with nestling mass ($R^2 = 0.63$, $P < 0.0001$; Appendix 5.3). We used a general linear model with normal error structure, controlling for year, brood size and the number of helpers present at the nest, which may influence nestling mass (Hatchwell *et al.* 2004). We could not control for relative lay date, as this was too strongly correlated with mismatch ($r_{67} = 0.65$, $P < 0.0001$). We did not control for the identity of breeding pairs as only two pairs (3% of 67 pairs recorded) were present more than once in the dataset (twice in both cases). In a second analysis, we assessed the effect of mismatch on brood mean tarsus length, again controlling for year, brood size and number of helpers. All relationships were modelled as linear after checking for non-linearity as described previously (see *Statistical approach* above).

We then assessed the effect of dietary caterpillar content on nestling size, using three years of data from 33 nests (12, 11, 10 nests in the years 2011–13). We modelled brood mean nestling mass in response to dietary caterpillar content during days two to 12 of the nestling period. We used a general linear model with normal error structure, again controlling for tarsus length, year and brood size, as well as provisioning rate and relative lay date. Again, we did not control for the identity of breeding pairs as only one pair was present more than once (twice) in the dataset, and all relationships were modelled as linear. Finally, we repeated this analysis with the response variable of tarsus length, controlling for year, brood size, provisioning rate and relative lay date.

5.3 Results

5.3.1 Effects of temperature on caterpillar and avian phenology

There was a clear seasonal peak in caterpillar abundance in the Rivelin Valley in all years during 2009–2013 (Fig. 5.1). The timing of the caterpillar peak varied substantially between years, from 7 May in the earliest year (2011) to 9 June in the latest year (2013), yet peak date was identical in the remaining three years (28 May). The index of caterpillar abundance increased significantly over the course of the study ($R^2 = 0.98$, $P < 0.001$; annual range of peak caterpillar biomass: 16–165mg/hr). The timing of breeding initiation was strongly associated with the temperature during the entire month of March (period of strongest correlation = 3 March – 3 April; Fig. 5.2), whereas the timing of breeding termination was linked to temperature during a slightly later period, from 16 March to 10 April (Fig. 5.2). The caterpillar peak date was most strongly linked to temperature from 25 March to 16 April, which was after the onset of breeding in most years, although there were also brief periods of strong correlation with the temperature during the first two weeks of February and the middle two weeks of May (Fig. 5.2).

5.3.2 Effects of mismatch on the nestling diet

Dietary caterpillar content at a nest was strongly linked to the degree of mismatch experienced by that nest, with a lower proportion of caterpillars provided to nestlings fledging substantially before the peak compared to those fledging around the time of the peak (Fig. 5.3; partial $D^2 = 0.38$, $P < 0.0001$, $n = 40$ nests). Nestlings that were being reared after the caterpillar peak date, with a mismatch of up to +10 days, did not experience a reduction in provisioning with caterpillars (inflection point of curve = 10.4 days of mismatch; Fig. 5.3). This equates to no reduction in caterpillar provision to birds fledging up to six days after the caterpillar peak (because average fledging age is 16 days and a mismatch of +10 days means that the caterpillar peak was 10 days after the date when nestlings were 12 days old, and therefore six days after fledging). Fledging later than this did, however, result in reduced dietary caterpillar content in the single very late nest that we observed (Fig. 5.3).

5.3.3 Effects of mismatch and diet on nestling mass and growth

There was considerable variation in mean nestling mass between broods, ranging from 5.49 to 8.44g (mean ± 1SD = 7.26 ± 0.50). Similarly, there was considerable variation in mean nestling tarsus length between broods, ranging from 15.39 to 19.60mm (mean ± 1SD = 18.09 ± 0.80). Brood mean nestling mass was associated with the degree of mismatch experienced by a nest, with nestlings fledging close to or soon after the peak being heavier than those fledging substantially before the peak (partial $R^2 = 0.03$, $P = 0.06$; Fig. 5.4a). However nestling mass was not significantly related to the proportion of caterpillars in the diet, after controlling for tarsus length (partial $R^2 = 0.01$, $P = 0.42$; Fig. 5.4a, Table 5.1). Brood mean tarsus length showed a stronger pattern, with nestlings fledging close to or soon after the peak having longer tarsi than those fledging substantially before the peak (partial $R^2 = 0.07$, $P = 0.02$; Fig. 5.4c) and nestlings with a higher proportion of caterpillars in the diet having longer tarsi (partial $R^2 = 0.10$, $P = 0.05$; Fig. 5.4d, Table 5.2).

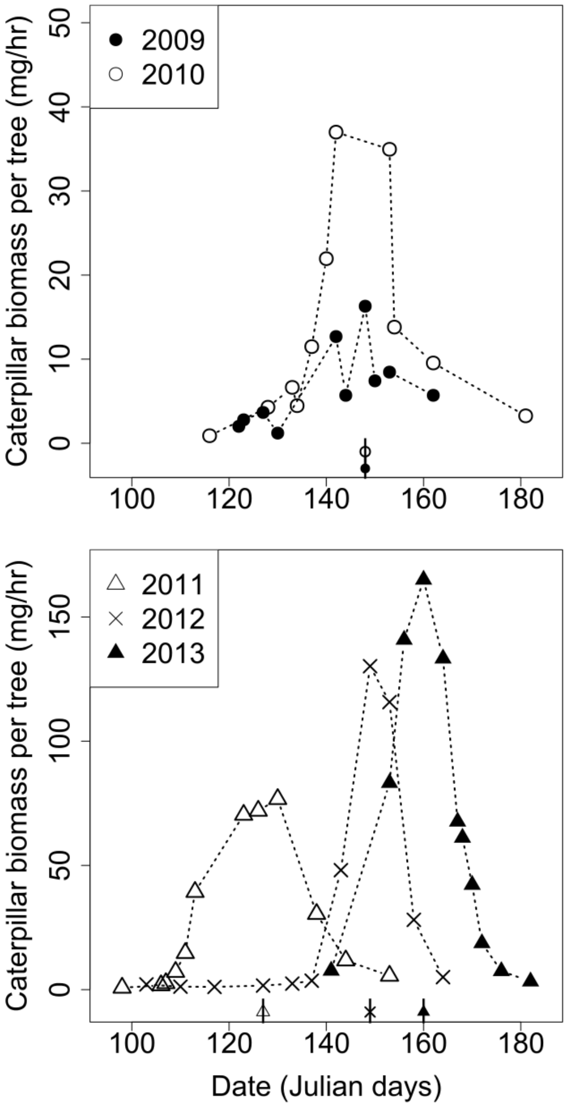


Figure 5.1 Caterpillar peak date in the Rivelin study site in each year during (a) 2009-2010 and (b) 2011-2013, showing the average caterpillar biomass (mg/hour) per sample tree for each sampling occasion. Estimated caterpillar peak date (as used in subsequent analyses) is shown on the *x* axis for each year. Note that peak abundance over the five years increased by an order of magnitude; the *y* axis therefore differs between the two panels to enable visualisation of the very low peak abundance in 2009.

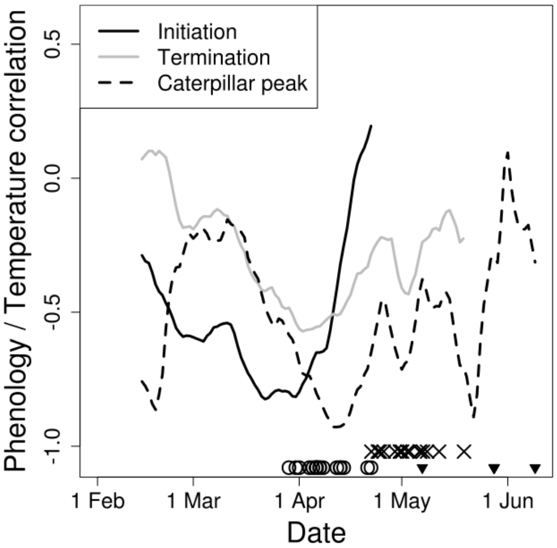


Figure 5.2 The correlation between temperature (ºC) during overlapping fortnightly periods and three phenological responses: long-tailed tit breeding initiation (solid black line), long-tailed tit breeding termination (solid grey line), and caterpillar peak date (dashed line). Data are from the Rivelin Valley during 1995–2013 (initiation and termination date) or 2009–2013 (caterpillar peak date). Mean daily temperature was calculated for fortnightly periods starting at 1-day intervals from 1 February, ending with the fortnight preceding the latest date of the focal phenological response over the course of the study. Date on the *y* axis indicates the temperature during the fortnight preceding the date shown (e.g. 1 April indicates the period from 17 March to 1 April inclusive). For each response, the period during which correlation coefficients were within 90% of their highest absolute value were as follows: breeding initiation: 3 March – 3 April; breeding termination: 16 March – 10 April; caterpillar peak: 25 March – 16 April. The annual timing of each response is shown just above the *x* axis, where breeding initiation = ○, breeding termination = ×, and caterpillar peak date = ▼. Note that in three years, caterpillar peak date occurred on the same date (28 May).

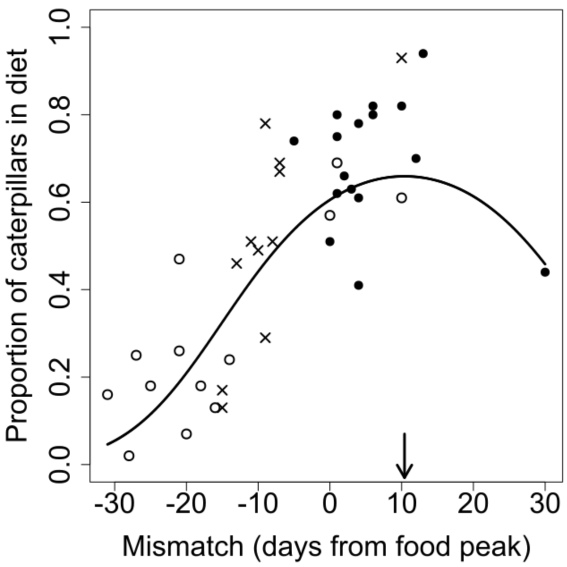


Figure 5.3 The relationship between mismatch and the dietary caterpillar content of a brood, where a negative mismatch value indicates that breeding was early with respect to the caterpillar peak. Data are from the Rivelin population of long-tailed tits over three years: 2011 (●), 2012 (○) and 2013 (×). The plotted line is the relationship in a generalized linear model with binomial error structure and logit link function, controlling for year, where model $D^2 = 0.65$ and the effect of mismatch was highly significant: est. ± 1 SE (linear term) = +0.178 ± 0.014, (quadratic term) = -0.002 ± 0.0002, partial $D^2 = 0.38$, $P < 0.0001$, $n = 40$ nests. The inflection point of the curve (↓) indicates the degree of late-mismatch beyond which dietary caterpillar content is expected to decline. Note that the quadratic nature of the mismatch effect is largely driven by a single nest as the vast majority of long-tailed tits bred early with respect to the caterpillar peak.

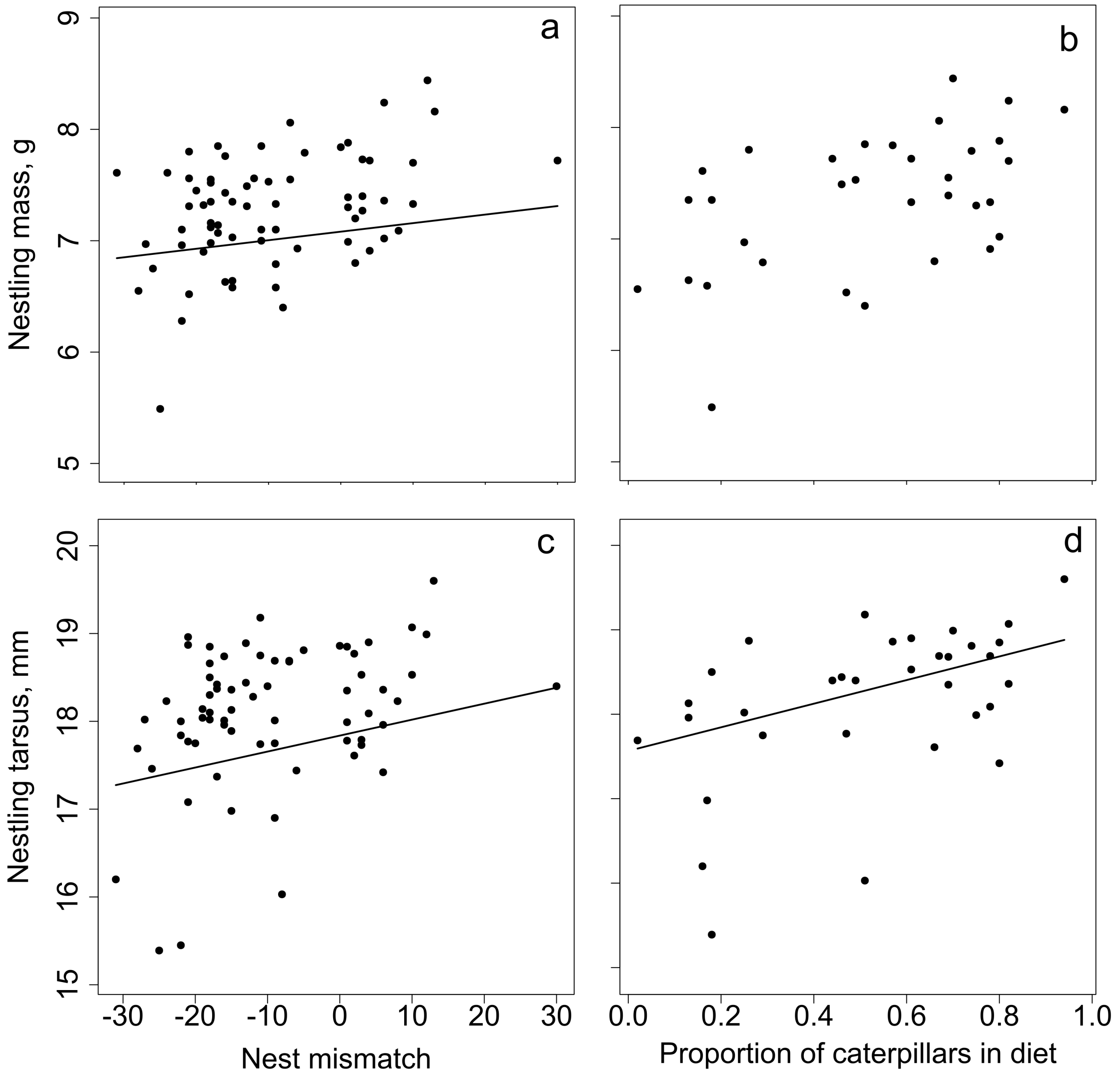


Figure 5.4 Brood-mean nestling (a,b) mass and (c,d) tarsus in response to (a,c) mismatch during the years 2009-2013, and (b,d) dietary caterpillar richness during the years 2011-2013, in the Rivelin population of long-tailed tits. Plotted lines are relationships in general linear models where there was evidence of a significant effect ($P \leq 0.05$), where (a) est. ± 1SE = +0.008 ± 0.004, partial $R^2 = 0.03$, controlling for tarsus length, brood size, number of helpers and year; (c) est. ± 1SE = +0.018 ± 0.008, partial $R^2 = 0.07$, controlling for brood size, number of helpers and year; (d) est. ± 1SE = +1.398 ± 0.688, partial $R^2 = 0.10$, controlling for brood size, provisioning rate, relative lay date and year; non-focal parameters are held at their median value. For further details, see Tables 5.1 & 5.2.

Table 5.1 The effect of (a) mismatch and (b) dietary caterpillar content on brood-mean nestling mass, in the Rivelin population of long-tailed tits. Data were available for (a) five years (2009–2013) from 69 nests, and (b) three years (2011–2013) from 33 nests. In each analysis, several nest-specific predictors were also controlled for; quadratic terms were not included as the linear model had a lower AICc in every case. Displayed are the parameter estimate ± 1SE, *t*, *P* value and partial R^2 of each predictor included.

Predictor	Estimate ± 1SE	*t*	*P*	Partial R^2
(a) Mismatch: model $R^2 = 0.54$				
Mismatch	+0.008 ± 0.004	1.935	0.057	0.03
Tarsus length	+0.433 ± 0.061	7.055	<0.001	0.36
Brood size	-0.017 ± 0.012	1.429	0.158	0.02
Number of helpers	+0.014 ± 0.038	0.364	0.717	<0.01
Year	-0.021 ± 0.032	0.655	0.508	<0.01
(b) Dietary caterpillar content: model $R^2 = 0.64$				
Caterpillar content	+0.315 ± 0.388	0.809	0.426	0.01
Tarsus length	+0.498 ± 0.101	4.914	<0.001	0.34
Brood size	-0.001 ± 0.022	0.299	0.767	<0.01
Provisioning rate	-0.014 ± 0.027	0.533	0.598	<0.01
Relative lay date	-0.001 ± 0.008	0.079	0.938	<0.01
Year	+0.002 ± 0.121	0.018	0.986	<0.01

Table 5.2 The effect of (a) mismatch and (b) dietary caterpillar content on brood-mean nestling tarsus length, in the Rivelin population of long-tailed tits. Data were available for (a) five years (2009–2013) from 69 nests, and (b) three years (2011–2013) from 33 nests. In each analysis, several nest-specific predictors were also controlled for; quadratic terms were not included as the linear model had a lower AICc in every case. Displayed are the parameter estimate ± 1SE, *t*, *P* value and partial R^2 of each predictor included in each model.

Predictor	Estimate ± 1SE	*t*	*P*	Partial R^2
(a) Mismatch: model $R^2 = 0.23$				
Mismatch	+0.018 ± 0.008	2.349	0.022	0.07
Brood size	+0.061 ± 0.023	2.611	0.011	0.08
Number of helpers	-0.061 ± 0.077	0.800	0.424	<0.01
Year	-0.052 ± 0.065	0.805	0.424	<0.01
(b) Dietary caterpillar content: model $R^2 = 0.37$				
Caterpillar content	+1.398 ± 0.688	2.033	0.052	0.10
Brood size	+0.077 ±0.039	1.975	0.059	0.09
Provisioning rate	+0.040 ± 0.051	0.785	0.439	0.01
Relative lay date	+0.015 ± 0.014	1.045	0.306	0.03
Year	-0.021 ± 0.231	0.091	0.928	<0.01

5.4 Discussion

Over the five years of this study, there was a sharp seasonal peak in caterpillar abundance in the Rivelin Valley each spring, but the timing of this peak was highly variable between years, ranging from 7 May in the earliest year to 9 June in the latest. The timing of the caterpillar peak was strongly related to temperature during early April, whereas the onset of breeding was determined largely by March temperature, indicating that there is high potential for variation in spring temperatures to influence the degree of mismatching in this population. Dietary caterpillar content of long-tailed tit nestlings was largely determined by the date relative to the date of the caterpillar peak, suggesting that mismatch can act as a reliable proxy for dietary caterpillar content in this population. Nestlings from broods fledging close to or soon after the peak were heavier and had longer tarsi than those fledging substantially before the peak, suggesting a possible benefit of phenological synchrony with the peak in caterpillar abundance.

5.4.1 Effects of temperature on caterpillar and avian phenology

Temperature influenced the timing of breeding initiation and the caterpillar peak during different periods of spring, with initiation occurring earlier when March was warmer but caterpillar abundance being most strongly related to temperature during late March and early April, by which time egg-laying of long-tailed tits had already commenced in the majority of years. This suggests that breeding initiation in this species responds to temperature directly (as shown previously in great tits; Stevenson & Bryant 2000), rather than responding to temperature-related alterations in the timing of the caterpillar peak. Given that different months are expected to show different patterns of warming over the coming decades (Stocker *et al.* 2013), it seems highly likely that the degree of mismatching between the timing of peak food supply and demand in this species will change in the future. A similar situation is likely to occur in other species, with differential thermal influence on caterpillar and passerine phenology having been demonstrated in both species in which it has been investigated, namely great tits (Visser, Holleman & Gienapp 2006) and willow tits (Vatka, Orrell & Rytkönen 2011).

It is important to note that in some habitats, caterpillar abundance shows a less distinct temporal peak (e.g. coniferous woodlands; Blondel *et al.* 1993; Veen *et al.* 2010), and in such habitats, reproductive success may be relatively unaffected by seasonal changes in caterpillar abundance (Veen *et al.* 2010). However it is interesting that in this study, we found no evidence for differences in the timing of caterpillar phenology in two broadleaved tree species, silver birch and oak, that exhibit very different bud-burst phenologies. Furthermore, altered selection pressures under future climates may lead to genetic adaptation in phenological responses to temperature in some populations, reducing the potential for negative consequences of phenological mismatch (van Asch *et al.* 2007; Reed, Jenouvrier & Visser 2013). Such adaptation does not seem to have occurred in the Rivelin population of long-tailed tits over the past two decades (Gullett *et al.* 2013), but it remains possible that this will change in the future. It is also possible that differing extents of phenological change at lower trophic levels could lead to shifts in the overall abundance of caterpillars present in the system, if lepidopteran egg-hatch becomes mismatched with the timing of budburst (van Asch *et al.* 2007).

Compared to initiation, the timing of breeding termination showed a more similar pattern of temperature-correlation to that shown by caterpillar peak timing, suggesting that the behavioural switch from breeding to non-breeding is linked to the seasonal decline in caterpillar availability. Such a response seems likely to have evolved in order to avoid late-season breeding attempts with insufficient food availability, yet no study to our knowledge has explicitly demonstrated such a link. Indeed, during the five years for which caterpillar data were collected in this population, out of a total of 51 fledged broods, only one fledged more than 10 days after the peak. This further suggests that caterpillar availability plays a role in the control of breeding termination in this species. Interestingly, temperature-phenology correlations were less strong for breeding termination than for initiation, indicating that factors other than current ambient temperature influence the timing of termination. In particular, birds may use caterpillar abundance and/or size *per se* as a cue to terminate breeding, which would reduce the influence of current ambient temperature on the timing of breeding termination because the timing of the caterpillar peak is determined not only by the influence of temperature on caterpillar developmental rates, but also by the timing of lepidopteran egg-hatch (van Ash & Visser 2007). Indeed, the fact that lepidopteran eggs hatch earlier when late-winter conditions are warmer (van Ash & Visser 2007) could explain the strong correlation between late-February temperature and the timing of the caterpillar peak observed in this study. It is also important to note that in this cooperatively-breeding species, the option to help raise the chicks of a close relative following personal breeding failure offers an alternative way to increase individual fitness (Hatchwell *et al.* 2004), which may contribute to the relatively early timing of breeding termination exhibited by this species.

5.4.2 Effects of mismatch on the nestling diet

The composition of the nestling diet was strongly influenced by the date relative to the date of the caterpillar peak, with nests fledging before the caterpillar peak receiving a lower proportion of caterpillars in their diet compared to those fledging within a week of the peak. Given that dietary information is time-consuming to collect and frequently unavailable in long-term studies, the degree of temporal mismatch between peak food supply and demand has commonly been used as a proxy for dietary caterpillar content (Both 2010), despite little evidence that diet is strongly determined by mismatch (Burger *et al.* 2012). Mismatch has been shown to be a reliable proxy for dietary caterpillar content in oak habitats in the latter part of the season, i.e. after the caterpillar peak (García-Navas & Sanz 2011a; Burger *et al.* 2012) and the current study supports this in a mixed deciduous woodland during the earlier part of the season, i.e. before the caterpillar peak. However, it is important to note that the correlation between mismatch and dietary caterpillar content was far from perfect. This indicates that factors other than mismatch also contribute to diet, suggesting that whilst mismatch can act as a reliable proxy for dietary caterpillar content at the population level, individual nests may experience a considerably different diet than predicted from mismatch alone. For instance, the spatial distribution of caterpillars can influence their delivery rate to chicks (Naef-Daenzer & Keller 1999), and it may be that parental condition influences their ability to increase foraging effort during times of low caterpillar availability (García-Navas & Sanz 2011b). Furthermore, in some habitats dietary caterpillar content may be limited by overall abundance of caterpillars in the habitat (Tremblay *et al.* 2003). This was not the case in the current study, however, with average dietary caterpillar content in the lower-abundance year being almost twice that occurring in the year when caterpillar abundance was two-fold higher (average proportion of caterpillars in diet was 69% in 2011 compared to 33% in 2012). Nonetheless, we join with Burger *et al.* (2012) in cautioning that in other habitats with a less distinct seasonal peak and different absolute abundance of caterpillars, mismatch may be a relatively uninformative indicator of nestling diet.

5.4.3 Effects of caterpillars on nestling mass and tarsus length

Timing of breeding with respect to the caterpillar peak was associated with nestling mass and tarsal length in this population, with nestlings that fledged around the time of the caterpillar peak being heavier and having longer tarsi at 11 days old than those fledging substantially before the peak. Consistent with this mismatch effect, tarsal length, but not mass, was positively related to the proportion of caterpillars in the diet. In this population, fledglings that were heavier as nestlings are more likely to recruit into the breeding population the following year (Hatchwell *et al.* 2004; Sharp *et al.* 2008), and population productivity may therefore be increased in years in which the thermal environment promotes synchrony in the timing of breeding and the timing of the caterpillar peak. Meanwhile, increased tarsal growth could increase productivity by enabling chicks to fledge at a younger age, as shown in the blackcap *Sylvia atricapilla* (Węgrzyn 2013), and/or by enabling chicks to fledge at a larger size thus increasing their chances of survival during the first few weeks of life (Tjørve & Underhill 2009). Whilst several previous studies have shown that mismatch is linked to reduced nestling mass in great tits, blue tits and pied flycatchers (Nager & van Noordwijk 1995; Thomas *et al.* 2001; Tremblay *et al.* 2003; Visser, Holleman & Gienapp 2006; Burger *et al.* 2012), few studies have considered the potential effects of mismatch on tarsus length, and those that have offer contrasting results. Specifically, one study of blue tits found no change in tarsus length despite a marginal increase in nestling mass (Wilkin, King & Sheldon 2009), whilst another study in blue tits and great tits found that both mass and tarsus length were reduced when hatching was delayed experimentally (Buse *et al.* 1999).

The fact that we did not observe a significant effect of dietary caterpillar content on nestling mass is somewhat surprising. This could indicate that dietary caterpillar content is not the sole factor driving the observed effect of mismatch on nestling mass; for instance, over the course of the season, changes in the nutritional compostition of caterpillars (e.g. antioxidant and vitamin content; Arnold *et al.* 2010) may lead to increased mass gain irrespective of the proportion of caterpillars in the diet. However we consider it possible that the lack of significance in this relationship could be due in part to the small sample size (n = 33 nests) and strong correlation of mass and tarsus length (Appendix 5.3). Further data are thus required before strong conclusions can be drawn regarding the effects of dietary caterpillar richness on nestling mass and growth in this population. It is also important to note that conditions during the post-fledging period can influence fledgling survival and recruitment. In this population, most mismatched individuals bred early with respect to the peak, and any reduction in nestling growth suffered by early-mismatched broods may therefore be offset by the abundant supply of caterpillars during their first few weeks of life, potentially reducing post-fledging mortality (Naef-Daenzer, Widmer & Nuber 2001). In contrast, late-mismatched nests may suffer the double whammy of reduced nestling growth and increased competition for food sources during the post-fledging period. A key focus for future research in this area should therefore be to investigate the effects of mismatch on post-fledging mortality and subsequent recruitment.

5.4.4 Consequences for population size

We found that long-tailed tits were highly plastic in their timing of breeding, and suggest that this plasticity may be contributing to recent increases in their population size nationally (Baillie *et al.* 2014) by enabling this species to keep pace with advancing caterpillar phenology. Evidence for this lies in the finding that the caterpillar peak date in Wytham Woods, 200 km south of our study site, advanced by approximately two weeks during the period 1961–2007 (Charmantier *et al.* 2008), and that over a similar time period, long-tailed tits across the UK have advanced their timing of breeding by a very similar amount: 16 days during 1968–2011 (Baillie *et al.* 2014). In contrast, previous authors have suggested that climate change is advancing the timing of the caterpillar peak more markedly than the timing of breeding in blue tits, great tits, coal tits *Parus ater* and pied flycatchers (Visser *et al.* 1998; Both & Visser 2005; Both *et al.* 2009; Reed, Jenouvrier & Visser 2013). Furthermore, whilst some of the advance in average lay date of long-tailed tits at the national scale may be due to advancing termination date (Gullett *et al.* 2013), the extent of advance is greater in this species than in any other insectivorous passerine across the UK (Baillie *et al.* 2014). This suggests that long-tailed tits may be maintaining synchrony with peak caterpillar abundance more successfully than some of their competitor species, thus increasing food availability for long-tailed tits during the breeding season. Such a reduction in food competition may benefit not only productivity, but also adult survival, through reduced parental effort in provisioning chicks and recent fledglings, as suggested by the increased energetic expenditure of temporally mismatched blue tit parents (Thomas *et al.* 2001) and the increased foraging effort of mismatched blue tits and great tits (Naef-Daenzer & Keller 1999).

5.4.5 Conclusion

We have shown that the timing of breeding initiation in long-tailed tits is not directly linked to the timing of the caterpillar peak, with the two phenologies responding to temperature during different periods. The degree of mismatch in this population is therefore likely to change with future climate change, given that the pattern and extent of future climate change is not expected to be uniform across months (Stocker *et al.* 2013). We have demonstrated that mismatch strongly affects the caterpillar content of the nestling diet, and influences nestling mass and tarsus growth, which could have consequences for productivity. It is important to emphasize that different populations are likely to show different patterns of mismatch over the coming decades, and more case studies of a wider range of species and habitats are needed. Crucially, future research should aim to advance our understanding of the thermal control of caterpillar peak timing in order to build a reliable predictive model of caterpillar peak date under future climates, which would greatly improve predictive models of future demographic impacts of climate change on temperate woodland passerines.

Chapter 6. General discussion

With climates changing at an unprecedented rate (Stocker *et al.* 2013) and species extinctions likely to ensue (Thomas *et al.* 2004), developing reliable predictive models of future species responses to climate change is an important task for ecologists today. There is increasing recognition of the need for such models to incorporate demographic mechanisms of population change (Robinson, Baillie & Crick 2007; Buckley *et al.* 2010; Pearce-Higgins & Gill 2010; Bykova *et al.* 2012; Fennell *et al.* 2013), yet such understanding is currently inadequate (Miller-Rushing *et al.* 2010; Sæther & Engen 2010; van de Pol *et al.* 2010), despite weather having long been recognised as a key driver of avian demography (Lack 1954; Perrins 1965; Newton 1998). In this thesis, I have addressed these issues using the long-tailed tit as a model species. I have assessed how the phenology, survival and productivity of the long-tailed tit respond to temperature and precipitation over the entire annual cycle and have examined historical trends in the demography of this population, as well as developing projections of how its demography may change under future climates. Through the course of this thesis, I have examined several key mechanisms that may explain recent increases in the UK long-tailed tit population (Baillie *et al.* 2014) and the local Rivelin population (Appendix 3.1), adding to the growing body of literature that seeks to inform the prediction of climate change impacts on passerine birds, and contributing to fundamental knowledge of the effects of weather on avian demography.

6.1 Evidence for past and future effects of climate change

This thesis has revealed that weather is an important driver of the phenology and demography of the long-tailed tit. Recent climate change has been of sufficient magnitude such that some of its effects on long-tailed tits are apparent over a relatively short time-scale. Specifically, over 17 years of study in the Rivelin population, I observed a significant advance in the timing of breeding termination and of re-nesting, and a shortening of breeding season length. Meanwhile other effects are likely to become increasingly evident over the coming decades. In particular, my results indicate that over a historical time period of 45 years, adult annual survival in the Rivelin population has probably increased significantly in response to recent climatic warming, and predictions under future climates suggest that survival is likely to continue increasing over the next century, under a broad range of future emissions and climate change scenarios. In contrast, juvenile recruitment is unlikely to increase in the future despite potentially positive effects of warming May temperatures, due to reduced recruitment from years with warm March temperatures, and the strong density dependence of recruitment in this population. Furthermore the relationships I observed between temperature and the timing of peak caterpillar abundance suggest that the peak has been getting earlier in recent decades and will continue to do so, which is likely to drive continued advance in the timing of breeding termination and further shortening of the breeding season. Thus, whilst fledgling production does not appear to respond strongly to climate *per se*, being driven largely by nest predation at present, phenological change could have long-term negative consequences for productivity.

6.2 Demographic drivers and mechanisms

In the following sections I will summarise the evidence presented in this thesis in support of – or contradiction to – various mechanisms via which climate has been hypothesised to contribute to increases in passerine population size. Specifically, I focus on the potential for climate change to lead to a lengthening of passerine breeding seasons, increased adult survival, increased productivity, and altered interspecific interactions. I discuss these results in the context of previous mechanistic studies of weather effects on the demography of passerine birds.

6.2.1 Longer breeding seasons?

In chapter two, I showed that divergent warming patterns between different periods of the spring have driven a reduction in breeding season length in the Rivelin population of long-tailed tits, equivalent to a loss of between one quarter and one third of the typical window during which laying is initiated. Specifically, warming of April temperatures over the past two decades has resulted in earlier termination of breeding, while the less marked change in March temperatures (which determine the timing of breeding initiation) means that breeding seasons are not starting significantly earlier. Consequently, it is likely that part of the 16-day advance in national UK lay dates since 1968 (Baillie *et al.* 2014) is due to an advance in breeding termination and hence fewer late nests, because climatic warming in March and April over this time period has diverged, with temperatures having warmed significantly in April but not March. It therefore seems highly unlikely that altered breeding season length is the mechanism driving the increase in population size at either the local or the national level.

Indeed, it seems likely that continued shortening of the breeding season could bring about a reduction in population-level productivity, because I found that shorter breeding seasons were associated with a reduction in the number of fledglings produced per breeding female (chapter four). Continued contraction of the breeding season could occur if April continues to warm at a faster rate than March, or if breeding initiation is constrained by factors other than ambient temperature, such as energetic limitations (Perrins 1970) or food availability (Nager, Rüeger & van Noordwijk 1997). Although we have not yet seen negative impacts of such an effect on population size, further reductions in breeding season length could bring about a tipping point in this respect. Amongst single-brooded species, contraction of the breeding season could be particularly detrimental for species experiencing high nest predation rates, such as the long-tailed tit, because re-nesting attempts following predation form an important component of population-level productivity. Although an advance in the timing of predation events could theoretically occur, which could alleviate the potential future problems of reduced breeding season length, I did not observe a trend towards earlier timing of predation events (chapter two). Moreover I would not expect to see such a trend developing in the future, due to the opportunistic nature of predation and the fact that population size and food demands of corvid and mustelid nest predators doubtless increase over the course of the long-tailed tit breeding season (see Corbet & Harris 1991; Robinson 2005). Previous authors have also shown a decline in breeding season length over recent years in some single-brooded species (Møller 2010) and a decline in the incidence of double-brooding in multi-brooded species (Husby, Kruuk & Visser 2009), whilst other species seem to show the opposite trend (Møller 2010). It therefore seems likely that alterations in breeding season length, as a consequence of divergent warming patterns between different parts of the year, could be a key mechanism driving future trends in population demography, but the direction of this effect is likely to differ between species.

6.2.2 Increasing adult survival?

In chapter three, I showed that adult annual survival in the Rivelin population is highly variable between years (annual survival rate varied from 30% to 63%), but that there has been no temporal trend in survival over the course of the past two decades. However, over the past 45 years, during which period the extent of climate change is much greater, I can infer that survival is likely to have increased, due mainly to warming in spring and autumn. Given the strong negative effect of breeding season precipitation that I observed, it is possible that the increased frequency of extreme precipitation events expected in the future (Stocker *et al.* 2013) could reduce survival on a sporadic basis. However, the general trend towards warming spring and autumn temperatures expected over the coming century (UKCP 2009) means that survival is expected to increase further, under a broad range of future emissions and probabilistic climate scenarios (chapter three). It is possible that as populations continue to grow, density dependence may act to dampen further increases in survival. However, during this study I observed negligible density dependence over a wide range of adult population densities (27 to 104 per km^2), and densities of up to 180 adults per km^2 are known to exist in a nearby long-tailed tit population (Melton Wood, located 27km north-east of the Rivelin site; Sharp *et al.* 2011), suggesting that, all else being equal, the Rivelin population is still some way below carrying capacity. Assuming that the Rivelin population is representative of other populations across the UK, it seems highly likely that increasing adult survival has contributed to the increase in the UK long-tailed tit population size observed over the past 45 years.

The mechanisms responsible for the positive effect of warm and dry weather during the breeding season and autumn are likely to be linked to both thermoregulatory benefits and food availability. Heavy rainfall hinders foraging (Dawson, Lawrie & O'Brien 2005; Shen *et al.* 2012) and cold weather increases the energetic requirements of both parents and chicks (Leech & Crick 2007), as well as increasing nest-building investment in long-tailed tits (McGowan *et al.* 2004). Adverse breeding conditions are therefore likely to increase energetic investment (Newton 1998; Bradbury *et al.* 2003), reducing parental body condition and subsequent survival. My finding that the effects of weather on productivity in the Rivelin population were low suggests that parents do indeed increase their investment to guard against reduced productivity in harsh-weather years (chapter four), and increased parental effort (as measured by higher provisioning rates during chick-rearing) has previously been linked to reduced survival of adult long-tailed tits to the subsequent breeding season (Meade *et al.* 2010). Several previous authors have reported similar reductions in adult survival following increased reproductive investment (e.g. Askenmo 1979; Nur 1984; Reid 1987; Deschamps *et al.* 2009). My findings suggest that in long-tailed tits, climate greatly influences the balance of the survival-productivity trade-off, as shown previously in blue tits (Thomas *et al.* 2001). This is therefore likely to be an important mechanism of passerine population change in long-tailed tits, and perhaps in other short-lived r-selected species also.

6.2.3 Increasing productivity?

In chapter four, I offered evidence suggesting that warming during the month of May increases the recruitment of juveniles into the breeding population, but that warming during March is associated with a reduction in recruitment. Climate change is therefore unlikely to lead to increased productivity in the future, particularly given the strong density dependence of recruitment in this population. Furthermore, fledgling production was impacted relatively little by weather in this population, being instead largely determined by predation rates, which are not significantly influenced by monthly weather patterns. I did however observe reduced fledgling production in years with shorter breeding seasons, suggesting that continued shortening of the breeding season in response to warming April temperatures (chapter two) could lead to a decline in fledgling production at the population level. It is possible that in this co-operative species, the positive effect of helpers on nestling mass (chapter four) and subsequent recruitment (Hatchwell *et al.* 2004; Sharp *et al.* 2008) could act as a buffer against reduced productivity with further shortening of the breeding season. Co-operation may also reduce the negative impacts of years with harsh weather, as shown in some other passerines (Shen *et al.* 2012). Whether such co-operative benefits will be sufficient to maintain productivity under future climates will require further investigation, and will depend in part on the relative changes in interacting mechanisms influencing productivity in this species.

Importantly, my finding that weather during the non-breeding season had little effect on recruitment rates at the population level suggests that, like adult survival (chapter three), juvenile survival in this population is most strongly determined by weather during the spring. Thus in years with inclement spring weather, long-tailed tits (and perhaps other species) may suffer the double whammy of reduced productivity and survival. Under future climates, the expected increase in periods of extreme weather (such as prolonged cold or wet weather) could therefore incur an increased frequency of sporadic population crashes amongst long-tailed tits. Whilst the high reproductive capacity of this species makes it relatively able to recover from such crashes if they are followed by a year or more of favourable conditions (Marchant *et al.* 1990), this situation may change in the future if consecutive inclement breeding seasons limit population recovery.

6.2.4 Altered interspecific interactions?

An effect of weather on productivity and survival could be mediated through the interaction between passerines and their caterpillar prey, which can become desynchronised due to differential phenological responses to climate change at different trophic levels. This so-called trophic mismatch effect has been suggested as a mechanism for population decline in some migratory passerines (Both *et al.* 2006; Goodenough, Hart & Stafford 2010; Both *et al.* 2011). In chapter five, I presented evidence that caterpillars are an important food resource for breeding long-tailed tits and that trophic mismatch could occur in long-tailed tits in the future, as caterpillar phenology responds to temperature during April whilst breeding initiation is influenced by March temperature. The extent of future mismatch in this and other passerine species will therefore depend on the relative rate of warming at different stages of the spring (Visser, Holleman & Gienapp 2006; Vatka, Orrell & Rytkönen 2011), potentially creating tipping points of climatic effects in the future (Thomas *et al.* 2004; Doak & Morris 2010). Disruptions to other elements of the ecosystem (e.g. the synchrony between caterpillars and their host trees; Visser & Hollemann 2001) may exacerbate such effects.

Importantly, the plasticity in timing of breeding that I have demonstrated in long-tailed tits suggests that this species may, thus far, have kept pace with advancing caterpillar phenology. Evidence for this lies in the finding that the caterpillar peak date in Wytham Woods, 200 km south of our study site, advanced by approximately two weeks during the period 1961–2007 (Charmantier *et al.* 2008), and that over a similar time period, long-tailed tits across the UK have advanced their timing of breeding by a very similar amount: 16 days during 1968–2011 (Baillie *et al.* 2014). In contrast, many other passerine species seem to be less phenologically flexible (Both & Visser 2001; Visser, Both & Lambrechts 2004; Goodenough, Hart & Stafford 2010). Consequently, long-tailed tits may benefit from the advancing caterpillar phenology by evading some of the interspecific competition for their key food source. Given the likely benefits of a caterpillar-rich diet for productivity (chapter five; Tremblay *et al.* 2003; Visser, Holleman & Gienapp 2006; Burger *et al.* 2012) and adult survival (due to reduced reproductive costs; Thomas *et al.* 2001; Tremblay *et al.* 2005), it is possible that reduced competition for food as a result of high phenological plasticity in timing of breeding could be a mechanism for past (and perhaps future) population growth in the long-tailed tit. However, the reduced recruitment I observed from years with cold March temperature (chapter four) could be indicative of negative impacts of reduced synchrony with the caterpillar peak in such years, due to breeding being initiated too early for nestlings to benefit from the caterpillar peak. It thus remains possible that the high plasticity in timing of breeding in the long-tailed tit may not prove entirely beneficial, and further study elucidating the mechanisms driving the observed effects is needed.

6.3 Unanswered questions

Whilst this thesis considers key mechanisms through which climate change could influence avian demography and population size, several other issues warrant consideration in future research. In particular, several findings of this thesis highlight the need for increased focus on understanding the role of species interactions in determining the impacts of climate change on species demography. For instance, I have suggested that the high phenotypic plasticity in timing of breeding shown by the long-tailed tit may enable it to experience reduced competition for food resources, and other alterations in competitive balance are likely to arise as species continue to diverge in their responses to climate change (Walther *et al.* 2002). Furthermore, my finding that nest predation was a key driver of fledgling production in this population identifies the need for further study of the impacts of weather on predator abundance and behaviour. I have suggested that variation in daily weather patterns could be an important determinant of daily predation patterns, such as the possible reduction in predator activity during days of heavy rainfall (Chase, Nur & Geupel 2005), and a thorough analysis of daily variation in nest predation rates would be valuable. Such effects could become more important under future climates, with sporadic weather events, such as periods of heavy rainfall, expected to become more common (Stocker *et al.* 2013). Predation rates are also dependent on nest situation and visibility (Martin & Joron 2003), which could change in the future as climate change alters vegetation development (Fitter *et al.* 1995; Sanz *et al.* 2003; Bourgault *et al.* 2010; Tøttrup *et al.* 2010).

Another important topic lies in determining the effects of garden feeding stations on passerine numbers at the regional scale, as food supplementation can improve productivity and/or survival (Jansson, Ekman & van Brömssen 1981; Lahti *et al.* 1998; Koivula, Orell & Lahti 2002; Ockendon *et al.* 2009). In the Rivelin population, rates of food supplementation are low, being limited to a few gardens around the periphery of the site. However, across the UK the provision of high-energy foods such as suet has been increasing since 1970, and the presence of long-tailed tits at such feeding stations has also increased (Chamberlain *et al.* 2005). Although the directionality of the link between increased use of garden feeders and population size is unclear, it seems likely that this species is profiting from food supplementation. In particular, although we observed no impact of winter weather on adult survival during the course of this study, exceptionally harsh weather during winter and early spring has been previously linked to population crashes (Marchant *et al.* 1990) and food provision during the winter may help to buffer long-tailed tits against such effects. Indeed, long-tailed tits spend more time at garden feeding stations during spells of particularly cold weather (Glue 2003). Given that extreme weather events are expected to become more common over the coming decades (Stocker *et al.* 2013), buffering passerines against such sporadic events could become an important component of strategies to mitigate against the negative impacts of climate change. Furthermore, food provision during the summer could reduce the strong density dependence of juvenile recruitment observed in this study, given that food competition is thought to be a key component of density dependence (Newton 1998; Robinson, Baillie & Crick 2007; Norman & Peach 2013).

Finally, a major element of climate change effects on passerines that I have not addressed here is that of disease, which can play a role in controlling and regulating bird populations (e.g. van Riper 1986; Leech & Crick 2007; Atkinson & Samuel 2010). Climate change may alter the distributions, prevalence, virulence and phenology of pathogens and parasites in various ways (Leech & Crick 2007; Brugger & Rubel 2009; Møller 2010; Slenning 2010), potentially triggering passerine population declines (Brugger & Rubel 2009). The consequences of such changes for bird populations are likely to be highly species-specific (Gaston *et al.* 2002; Møller

2010; Slenning 2010). For instance, increased abundance of feather mites *Trouessartia spp.* was found to advance timing of breeding in a population of barn swallows *Hirundo rustica*, yet increased abundance of the tropical fowl mite *Ornithonyssus bursa* was associated with delayed breeding in the same population (Møller 2010). The role that disease will play in structuring biodiversity under future climates is highly uncertain but potentially important (Leech & Crick 2007).

6.4 Methodological recommendations

The findings of this thesis offer several important recommendations for the development of more reliable assessments of climate change impacts on passerines. First, I demonstrated in chapter two that the commonly-used index of avian timing of breeding, namely population average lay date, can offer a misleading picture of phenological change if birds are terminating breeding earlier. I showed that such an index needs to be more comprehensive by incorporating timing of re-nesting and breeding termination (as well as double-brooding, in multi-brooded species), in order to act as a reliable indicator of species responses to climate change. The data used to calculate average timing of breeding at the national scale do not distinguish between first attempts and re-nests (Crick & Sparks 1999), and an index such as the 90th percentile of lay dates could therefore offer a more robust way to monitor changes in breeding season length.

An important theme running throughout this thesis is the need to consider the effects of weather throughout the entire annual cycle. Previous studies have tended to assume that weather during the breeding season is most important in determining productivity whilst survival is more dependent on winter weather (e.g. Lack 1954; Peach, Siriwardena & Gregory 1999; Sæther, Sutherland & Engen 2004). In contrast, I have shown that the breeding season is the time of greatest climatic influence on both productivity and survival. Furthermore, I have demonstrated frequently opposing effects of warming during different months, even on a single aspect of demography (e.g. the positive effect of May warming on recruitment, despite a negative effect of March warming). Given the expected divergence in warming patterns between different times of year, it is essential that investigations of species responses to climate change seek to pinpoint the precise timing of weather effects. Furthermore, the findings of this thesis support previous demonstrations of the importance of incorporating density dependence into predictive models to ensure that projections are biologically realistic (Robinson *et al.* 2007; Norman & Peach 2013).

In this thesis, I have focused mainly on a single intensively studied population, and it is important to recognise that species may show differing responses to climate change between areas and populations (Visser *et al.* 2003; Parmesan *et al.* 2011). In chapter two, I demonstrated that predictive models developed in a single population can provide useful inference at much larger spatial scales, which offers a useful method of improving the reliability of predictive models at the regional scale. However such models would be further improved by the study of more individual populations in order to validate the spatial applicability of observed responses. Comparison of climatic responses between populations could also indicate habitat features that may reduce the impacts of climate change, thereby offering useful insights into effective conservation management strategies. It is of course important to recognize the difficulty of maintaining the continuity and methodological consistency of long-term studies of individual populations. Nevertheless, inter-population comparisons could be achieved with data currently available in the form of the BTO Constant Effort Site ringing scheme, which can be used to gain an index of annual productivity by assessing the ratio of juveniles to adults in the population (Robinson, Baillie & Crick 2007). Although my attempts to use these data to calculate annual indices of productivity in long-tailed tits were unsuccessful due to low sample size, in many species this approach could offer a readily applicable tool to monitor interannual variations in productivity between populations (Robinson, Baillie & Crick 2007). Such inter-population comparisons and detailed single-populations studies can thus offer invaluable complementary insights into the processes driving long-term patterns observed at the regional scale.

6.5 Conclusion

In this thesis, I have suggested that increasing adult survival could be contributing to the two-fold increase in the UK long-tailed tit population over the past 48 years (Baillie *et al.* 2014). I have shown that adult survival increases in response to warmer and drier springs and warmer autumns, and should therefore continue to increase in the coming decades. In contrast, juvenile recruitment is unlikely to increase due to the opposing effects of March and May temperature and the strong density dependence of recruitment in the Rivelin population. Population increases are therefore likely to occur mainly via increasing adult survival, which is much less strongly regulated by population size at the moderate densities observed during this study.

Another major change observed in the UK long-tailed tit population since 1968 is that average laying date has advanced by a remarkable 16 days, from 21 April to 5 April (Baillie *et al.* 2014). However, I have shown that this advance in average lay date is at least partly attributable to an advance in the timing of the end of breeding, perhaps in response to a temporal shift in the peak abundance of caterpillars, which are a key food source for breeding long-tailed tits. Whilst I have shown that breeding starts earlier in years when March is warmer, it is likely that energetic constraints will prevent breeding initiation from advancing as rapidly as termination, and faster rates of warming in April (as observed over the past 20 years) are likely to exacerbate this. Therefore, whilst long-tailed tits seem more able to maintain pace with advancing phenology than some other woodland passerines (see Both 2010), which could initially put them at a competitive advantage during spring, there is a possibility that under continued warming long-tailed tits could become mismatched from their caterpillar food source. Indeed, this may explain the reduced recruitment from years with warm March temperatures observed in this study. Moreover continued shortening of the breeding season in response to warming April temperatures is likely to lead to reduced fledgling production, which, in combination with the high rates of nest predation in this species, could impact population size dramatically.

Ultimately, the consequences of climate change for populations of long-tailed tits and other passerines will depend on the precise nature and timing of alterations in weather patterns and the incidence of extreme weather events, as well as on how such changes affect community dynamics. Quantifying the relative importance of the various mechanisms that I have shown to influence demography will require population modelling, and more long-term data on food availability and interspecific interactions. Whilst predictions of future impacts will be inevitably fraught with uncertainties (Thomas *et al.* 2004), I hope that this thesis contributes to our understanding of the demographic mechanistic basis of weather impacts on passerine birds.

Appendix 1

The seasonal pattern of caterpillar abundance in the Rivelin Valley was assessed using the frass-fall method of Tinbergen (1960). During the long-tailed tit breeding seasons of 2009–2013, caterpillar abundance was estimated for 16 trees within the Rivelin study site, with two oak *Quercus petraea/robur* and two silver birch *Betula pendula* trees monitored at each of four sites located throughout the long-tailed tit study area. These are two of the most common tree species within the study site, and are frequently used by foraging long-tailed tits during the chick-rearing period. At each tree, we collected caterpillar frass falling from the canopy by placing a wooden frame (50 x 50 cm) covered in nylon mesh beneath the canopy centre. Traps were either hanging from a branch or standing on the ground, depending on which offered the best collection possibility for that particular tree with respect to canopy shape. Each year, sampling commenced within a few days of bud burst and continued until the amount of frass collected was one quarter or less of the maximum amount collected. Sampling was conducted only during dry periods, as rain can wash frass out of the mesh, and when wind-speed was 10mph or less, to reduce the risk that some of the collected frass originated from nearby trees rather than the focal one. Due to these constraints sampling duration and frequency varied between sampling events, but there were 10-12 sampling events per year, and on average sampling was conducted approximately every four days. We aimed to sample most frequently when caterpillars were abundant, to increase the accuracy of temporally pinpointing the peak abundance. Sampling duration was approximately 30 hours each time. Frass was removed from the traps by sweeping with a paintbrush through a glass funnel into glass collection vials. To separate frass from non-frass material, samples were passed through a series of soil sieves and sorted by hand. Frass was then dried for 24 hours at 80ºC, and weighed to an accuracy of 0.002g using a Tanita digital scale (model 1230, Tanita, Japan). Mean frass mass (hr^{-1}) was converted to caterpillar biomass using the equation derived by Tinbergen & Dietz (1994): Caterpillar biomass = $(24.38 \times F) - (0.767 \times F \times T)$, where F = frass dry mass (mg) and T = ambient temperature (ºC). Hourly temperatures during each sampling period were obtained from the Weston Park Weather Station, located 5km from the centre of the study site.

Appendix 2

Appendix 2.1 Logistic regressions of re-nesting occurrence (re-nest vs. termination) following nest failure, in response to failure date, for each year of the study used in analysis of termination date, 1995–2011. McFadden's R^2 was calculated as the difference in deviance between the null and explanatory model, divided by the deviance of the null, and is thus equivalent to D^2.

Year	*n*	Parameter estimate ± 1SE	Wald statistic	*P* value	McFadden's R^2	Dispersion parameter
1995	19	-0.19 ± 0.09	2.01	0.045	0.39	0.95
1996	40	-0.26 ± 0.09	2.87	0.004	0.62	0.56
1997	51	-0.13 ± 0.04	3.76	<0.001	0.38	0.89
1998	36	-0.01 ± 0.03	2.89	0.004	0.35	0.95
1999	38	-0.02 ± 0.05	3.24	0.001	0.47	0.77
2000	33	-0.13 ± 0.04	2.96	0.001	0.40	0.88
2002	61	-0.12 ± 0.03	3.82	<0.001	0.33	0.95
2004	57	-0.33 ± 0.11	2.97	0.003	0.70	0.43
2005	56	-0.17 ± 0.04	3.91	<0.001	0.58	0.58
2006	44	-0.42 ± 0.21	2.07	0.038	0.90	0.14
2007	53	-0.24 ± 0.07	3.26	0.001	0.74	0.35
2008	75	-0.37 ± 0.12	3.14	0.002	0.88	0.37
2009	33	-1.19 ± 0.91	1.30	0.190	0.85	0.17
2010	52	-0.69 ± 0.36	1.93	0.050	0.66	0.20
2011	57	-0.29 ± 0.09	3.39	<0.001	0.66	0.48

Appendix 2.2 Pearson correlation coefficients between monthly spring temperature (temp) and precipitation (prec) in Sheffield, UK, during 1995–2011. Data from 2001 were excluded as avian data were excluded from this year. * denotes correlations that are significant at $P < 0.05$ (where $n = 16$ years). Note that collinearity between climatic predictors was within the limits to which information theoretic methods are robust (Freckleton 2011), with variance inflation factor < 3.9 for all variables.

	March temp	April temp	May temp	Feb prec	March prec	April prec	May prec
Feb temp	+0.559*	+0.026	+0.534*	+0.275	-0.590	+0.234	+0.057
March temp		+0.212	+0.569*	+0.046	-0.408	+0.219	-0.133
April temp			+0.120	+0.210	-0.609*	-0.606*	+0.059
May temp				-0.163	+0.188	+0.319	-0.010
Feb prec					-0.512*	-0.378	-0.010
March prec						+0.313	+0.160
April prec							-0.170

Appendix 2.3 Range and temporal trends in monthly mean temperature (temp) and total precipitation (prec) at Weston Park Weather Station (5km from the Rivelin Valley), during 1995–2011 (the period of local study of long-tailed tits) and 1968–2010 (the period of national study of long-tailed tits). Linear and quadratic models were compared for each weather variable by assessing the change in AICc with respect to the null model, where a negative $\Delta\text{AICc}_{\text{null}}$ indicates evidence of a temporal trend; quadratic models were never more parsimonious than the null, and linear trends are therefore displayed below with associated statistics. * denotes variables showing evidence of a temporal trend ($P < 0.1$ and negative $\Delta\text{AICc}_{\text{null}}$). All data from 2001 are excluded to maintain consistency with long-tailed tit analyses.

Weather variable	Time period	Month	Range	Linear trend ±1SE	R^2	F_{df}	P	Linear model $\Delta\text{AICc}_{\text{null}}$
Temp (ºC)	1995–2011	Feb	2.30 – 8.15	-0.08±0.08	0.07	$0.99_{1,14}$	0.34	+1.99
		Mar	3.80 – 8.55	+0.01±0.07	<0.01	$0.03_{1,14}$	0.86	+3.04
		Apr*	7.65 – 12.30	+0.12±0.06	0.22	$4.04_{1,14}$	0.06	-0.98
		May	9.15 – 13.25	+0.04±0.05	0.05	$0.70_{1,14}$	0.42	+2.29
	1968–2010	Feb*	-1.00 – 8.15	+0.05±0.02	0.12	$5.59_{1,40}$	0.02	-3.16
		Mar*	2.35 – 8.85	+0.05±0.02	0.20	$10.08_{1,40}$	0.003	-7.11
		Apr*	5.65 – 11.60	+0.05±0.01	0.30	$17.03_{1,40}$	<0.001	-12.57
		May*	9.15 – 13.65	+0.03±0.01	0.14	$6.74_{1,40}$	0.01	-4.21
Prec (mm)	1995–2011	Feb	9.3 – 173.9	-1.15±1.98	0.02	$0.34_{1,14}$	0.57	+2.70
		Mar	12.4 – 100.2	-0.61±1.38	0.01	$0.20_{1,14}$	0.66	+2.85
		Apr	5.8 – 153.3	-1.97±2.09	0.06	$0.89_{1,14}$	0.36	+2.09
		May	17.5 – 129.8	+0.41±1.45	0.01	$0.08_{1,14}$	0.78	+2.99
	1968–2010	Feb	4.6 – 201.4	-0.28±0.51	0.01	$0.31_{1,40}$	0.58	+2.01
		Mar	15.1 – 149.9	-0.51±0.40	0.04	$1.65_{1,40}$	0.21	+0.64
		Apr	5.8 – 153.3	+0.005±0.45	<0.01	$<0.001_{1,40}$	0.99	+2.33
		May	14.4 – 129.8	-0.21±0.37	0.01	$0.34_{1,40}$	0.57	+1.98

Appendix 2.4 Two indices of predation intensity, and annual stage-specific predation risk calculated using the Mayfield method. Proportion of nests predated = total proportion of nests that were predated out of all nests known to have been predated or fledged. Mayfield predation estimate = total probability of a nest being predated at some point during the nesting period, used as the index of predation intensity in all subsequent analyses and calculated as the product of the three stage-specific risk estimates, denoted 'Pred (egg/inc/chick)'. No. nest days = total number of days during which a nest was active, summed for all nests over the entire breeding season within each year, as used in calculations of Mayfield estimates.

Year	Proportion of nests predated	Mayfield predation estimate	Pred (egg) probability	Pred (inc) probability	Pred (chick) probability	No. nest days
1995	0.65	0.59	0.04	0.43	0.26	764
1996	0.72	0.68	0.17	0.32	0.44	939
1997	0.85	0.79	0.29	0.55	0.32	919
1998	0.64	0.55	0.09	0.20	0.38	1005
1999	0.63	0.57	0.14	0.27	0.33	1279
2000	0.52	0.47	0.08	0.34	0.13	1495
2001	--	--	--	--	--	--
2002	0.79	0.75	0.14	0.50	0.42	1140
2003	0.68	0.61	0.10	0.22	0.45	1254
2004	0.59	0.54	0.06	0.25	0.34	2003
2005	0.83	0.80	0.10	0.26	0.71	1093
2006	0.73	0.66	0.04	0.31	0.49	1341
2007	0.84	0.78	0.10	0.25	0.67	1078
2008	0.81	0.76	0.16	0.45	0.49	1628
2009	0.71	0.66	0.18	0.28	0.43	1044
2010	0.77	0.68	0.04	0.27	0.54	1650
2011	0.77	0.76	0.26	0.46	0.40	1471
Mean	0.72	0.67	0.12	0.33	0.43	1256
SD	0.10	0.10	0.08	0.11	0.14	326

Appendix 3

Appendix 3.1 Annual number of (no.) breeding long-tailed tits in the Rivelin population, and number of males and females captured/sighted and resighted each year. The number of breeding adults is likely to be a very slight underestimate, since a very small percentage of nests are not found in some years (the exception to this is 2001, when a higher proportion of nests were not found due to reduced site access). Birds were occasionally observed only later in the season when they appeared as helpers, and the total number of adults caught/sighted therefore sometimes exceeds the number of breeding adults. The number of adults caught for the first time includes both (i) adults caught as unringed individuals, and (ii) individuals that were first ringed as nestlings in the Rivelin site being caught or sighted for the first time as adults.

Year	No. breeding adults	Total no. adults caught or sighted	Total no. males caught or sighted	Total no. females caught or sighted	No. adults caught for the first time	No. adults resighted from a previous year
1994	34	44	25	19	44	0
1995	48	46	25	21	27	19
1996	72	70	38	32	44	26
1997	72	70	36	34	35	35
1998	76	68	34	34	35	33
1999	78	74	40	34	47	27
2000	100	100	54	46	57	43
2001	50	42	23	19	24	18
2002	82	80	44	36	63	17
2003	90	93	52	41	65	28
2004	136	143	77	66	83	60
2005	94	99	49	50	39	60
2006	102	103	55	48	47	56
2007	98	94	48	46	62	32
2008	128	139	71	68	87	52
2009	86	84	44	40	38	46
2010	112	115	61	54	65	50
2011	114	112	62	50	64	48
2012	130	120	66	54	59	61

Appendix 3.2 Selection of a reference model for adult long-tailed tit survival in the Rivelin population, 1994–2012. Shown is the ΔAICc < 20 top subset of models from all reduced models nested within the global structural model ϕ(~time*sex*ringingAge)p(~sex*ringingAge). Also shown are the null model (final row) and the 'reference null' model ϕ(~1)p(~sex) used to calculate R^2 (proportion of temporal variation explained) of climatic models (penultimate row). Displayed for each model are the number of parameters (npar), the change in AICc with respect to the reference model (ΔAICc), the AICc weight, and the model deviance. In all models, p was fixed to 0.4 in 2001, to reflect the observed reduction in recapture/resighting probability that year. Note that ringing age showed some influence on survival/recapture probability (birds ringed as nestlings tended to show higher survival); we therefore included ringing age as a main effect in the final subset of climatic survival models, but this did not improve their AICc and we were thus confident that our reference model was suitable.

Model	npar	ΔAICc	AICc weight	Deviance
Phi(~time)p(~sex)	20	0.0	0.216	451.2
Phi(~time + ringingAge)p(~sex)	21	0.8	0.146	449.9
Phi(~sex + time)p(~sex)	21	1.6	0.095	450.8
Phi(~time)p(~sex + ringingAge)	21	1.8	0.087	451.0
Phi(~time)p(~sex * ringingAge)	22	1.9	0.082	449.0
Phi(~time + ringingAge)p(~sex + ringingAge)	22	2.3	0.070	449.4
Phi(~time + ringingAge)p(~sex * ringingAge)	23	2.4	0.066	447.4
Phi(~sex + ringingAge + time)p(~sex)	22	2.7	0.057	449.8
Phi(~sex + time)p(~sex + ringingAge)	22	3.4	0.039	450.5
Phi(~sex + time)p(~sex * ringingAge)	23	3.6	0.035	448.7
Phi(~sex + ringingAge + time)p(~sex + ringingAge)	23	4.2	0.027	449.2
Phi(~sex + ringingAge + time)p(~sex * ringingAge)	24	4.3	0.025	447.3
Phi(~time)p(~1)	19	5.7	0.013	458.9
Phi(~sex + time)p(~1)	20	6.0	0.011	457.2
Phi(~time + ringingAge)p(~1)	20	6.1	0.010	457.3
Phi(~sex + ringingAge + time)p(~1)	21	7.0	0.007	456.2
Phi(~time)p(~ringingAge)	20	7.7	0.005	458.9
Phi(~time + ringingAge)p(~ringingAge)	21	7.9	0.004	457.1
Phi(~sex + time)p(~ringingAge)	21	8.0	0.004	457.1
Phi(~sex + ringingAge + time)p(~ringingAge)	22	8.9	0.003	456.0
Phi(~1)p(sex)	3	37.9	<0.001	523.7
Phi(~1)p(~1)	2	43.8	<0.001	531.5

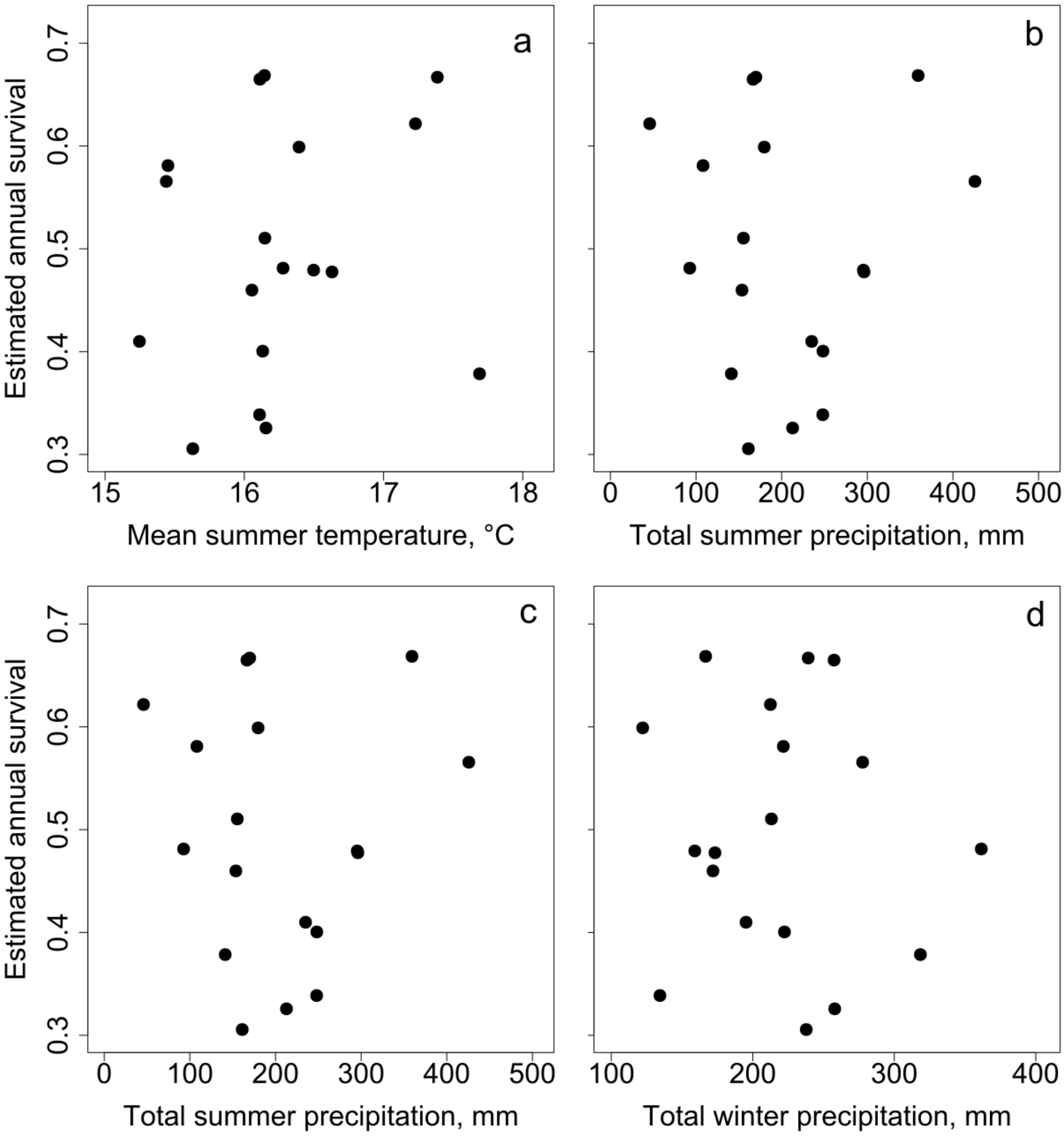
Appendix 3.3 Pearson correlation coefficients between weather variables and population size in the Rivelin study site, 1994–2012. Note that only average indices (t1-4 and p1-4) were used in survival analyses. Average indices: t = mean temperature, ºC; p = total precipitation, mm. Extreme indices: c = number of cold days (minimum temperature < 0ºC); g = number of glaze days (minimum temperature < 0ºC and total precipitation > 1mm); h = number of hot days (maximum temperature > 25ºC); r = number of rain days (total precipitation ≥ 10mm). Seasons as defined in the text: 1 = spring, 2 = summer, 3 = autumn, 4 = winter. Pop = population size at the end of the spring breeding season. Negative correlations are indicated as such, and the absence of '-' preceding a coefficient therefore indicates a positive correlation.

	t1	**t2**	**t3**	**t4**	**p1**	**p2**	**p3**	**p4**	**c1**	**c3**	**c4**	**g1**	**g4**	**h2**	**r1**	**r2**	**r3**	**r4**	**pop**
t1	1	-0.27	0.22	0.15	-0.21	0.41	-0.36	-0.15	-0.69	-0.43	-0.17	-0.42	-0.01	-0.40	-0.04	0.29	-0.20	-0.15	0.30
t2	-0.27	1	0.27	0.08	-0.02	-0.33	-0.28	0.14	0.54	0.06	-0.06	0.46	0.01	0.83	-0.31	-0.36	-0.18	0.11	-0.06
t3	0.22	0.27	1	0.24	-0.10	-0.16	-0.39	0.20	0.19	-0.32	-0.26	0.52	-0.07	0.34	-0.18	-0.04	-0.31	-0.04	0.09
t4	0.15	0.08	0.24	1	0.12	0.08	-0.22	0.46	-0.05	-0.23	-0.92	0.17	-0.81	0.03	0.07	0.11	-0.33	0.40	0.03
p1	-0.21	-0.02	-0.10	0.12	1	0.08	0.57	0.21	0.13	-0.28	-0.09	0.30	0.16	-0.04	0.84	0.15	0.66	0.16	0.28
p2	0.41	-0.33	-0.16	0.08	0.08	1	-0.19	-0.28	-0.47	-0.12	-0.10	-0.35	0.11	-0.52	0.25	0.90	-0.09	-0.26	0.13
p3	-0.36	-0.28	-0.39	-0.22	0.57	-0.19	1	0.04	0.01	0.02	0.28	-0.14	0.14	-0.23	0.47	-0.01	0.92	0.09	0.07
p4	-0.15	0.14	0.20	0.46	0.21	-0.28	0.04	1	0.16	-0.53	-0.25	0.36	-0.40	0.12	0.00	-0.27	-0.08	0.84	-0.34
c1	-0.69	0.54	0.19	-0.05	0.13	-0.47	0.01	0.16	1	0.27	0.12	0.76	-0.05	0.61	-0.08	-0.48	0.02	0.19	-0.03
c3	-0.43	0.06	-0.32	-0.23	-0.28	-0.12	0.02	-0.53	0.27	1	0.08	-0.13	-0.01	0.18	-0.34	-0.14	-0.03	-0.22	-0.06
c4	-0.17	-0.06	-0.26	-0.92	-0.09	-0.10	0.28	-0.25	0.12	0.08	1	-0.12	0.7	0.01	-0.07	-0.11	0.36	-0.14	-0.10
g1	-0.42	0.46	0.52	0.17	0.30	-0.35	-0.14	0.36	0.76	-0.13	-0.12	1	-0.11	0.65	0.15	-0.29	-0.10	0.22	-0.05
g4	-0.01	0.01	-0.07	-0.81	0.16	0.11	0.14	-0.40	-0.05	-0.01	0.70	-0.11	1	-0.04	0.18	0.09	0.35	-0.49	-0.05
h2	-0.40	0.83	0.34	0.03	-0.04	-0.52	-0.23	0.12	0.61	0.18	0.01	0.65	-0.04	1	-0.28	-0.42	-0.18	0.14	-0.21
r1	-0.04	-0.31	-0.18	0.07	0.84	0.25	0.47	0.00	-0.08	-0.34	-0.07	0.15	0.18	-0.28	1	0.31	0.59	-0.07	0.19
r2	0.29	-0.36	-0.04	0.11	0.15	0.90	-0.01	-0.27	-0.48	-0.14	-0.11	-0.29	0.09	-0.42	0.31	1	0.07	-0.29	0.04
r3	-0.20	-0.18	-0.31	-0.33	0.66	-0.09	0.92	-0.08	0.02	-0.03	0.36	-0.10	0.35	-0.18	0.59	0.07	1	-0.02	0.13
r4	-0.15	0.11	-0.04	0.40	0.16	-0.26	0.09	0.84	0.19	-0.22	-0.14	0.22	-0.49	0.14	-0.07	-0.29	-0.02	1	-0.23
pop	0.30	-0.06	0.09	0.03	0.28	0.13	0.07	-0.34	-0.03	-0.06	-0.10	-0.05	-0.05	-0.21	0.19	0.04	0.13	-0.23	1

Appendix 3.4 Climatic models of adult long-tailed tit survival in the Rivelin population, 1994–2012. Shown are the $\Delta AIC<2_{climatic}$ top subset of models, which were used to construct the climatic model average. $\Delta AICc_{time}$ and $\Delta AICc_{climatic}$ indicate, respectively, the ΔAICc of the focal model relative to the reference model ϕ(~time)p(sex) and relative to the best climatic model ϕ(~t1+p1+t3+p3+t1:p1)p(~sex); R^2 indicates the proportion of temporal variation explained. In all models, p was modelled separately for each sex, and was fixed to 0.4 in 2001. Notation for survival models follows abbreviations used previously, where t indicates mean seasonal temperature, p total seasonal precipitation, the numerals 1-4 seasons as defined in the text, and : the interaction term.

Survival model	npar	$\Delta AICc_{time}$	$\Delta AICc_{climatic}$	R^2
Phi(~t1+p1+t3+p3+t1:p1)p(~sex)	8	-5.11	0.00	0.73
Phi(~t1+p1+t3+p3+t1:p1)p(~sex)	8	-4.86	0.25	0.73
Phi(~t1+p1+t3+t1:p1)p(~sex)	7	-4.85	0.26	0.70
Phi(~t1+p1+t3+t1:p1+t3:p3+t1^2)p(~sex)	9	-4.67	0.44	0.76
Phi(~t1+p1+t3+t1:p1+t1^2)p(~sex)	8	-3.94	1.17	0.72
Phi(~t1+p1+t3+p3+t1:p1+t3:p3)p(~sex)	9	-3.66	1.45	0.74
Phi(~t1+p1+t3+t1:p1+p1^2)p(~sex)	8	-3.64	1.47	0.71
Phi(~t1+p1+t3+p3+t1:p1+t1^2)p(~sex)	9	-3.47	1.64	0.74
Phi(~t1+p1+t3+t1:p1+t1^2+p1^2)p(~sex)	9	-3.21	1.90	0.74
Phi(~t1+p1+t3+p3+t1:p1+p1^2)p(~sex)	9	-3.18	1.93	0.73
Phi(~t1+p1+t3+p3+t1:p1+p3^2)p(~sex)	9	-3.13	1.98	0.73

Appendix 3.5 The lack of relationship between adult long-tailed tit survival estimates (●) from the reference model ϕ(~time)p(sex) and four weather variables, for the Rivelin population in the years 1994-2012. Solid lines indicate survival estimated from model-averaged parameter estimates for each weather variable, calculated over the range of each variable experienced during the study. Only weather variables that do not show a univariate relationship with survival are displayed here, namely (a) mean summer temperature, (b) total summer precipitation, (c) mean winter temperature, (b) total winter precipitation. For relationships between survival and spring/autumn weather, see Fig. 3.1.



Appendix 3.6 Annual seasonal weather values and population size in the Rivelin study site, 1994–2011. Columns display seasonal means, where t = mean seasonal temperature (ºC), p = total seasonal precipitation (mm), numerals 1-4 = seasons as defined in the text, popSize = adult + fledgling population size at the end of season 1. The overall mean and standard deviation (SD) of each time series are also shown (bottom two rows).

Year	t1	t2	t3	t4	p1	p2	p3	p4	popSize
1994	8.7	16.3	10.4	5.5	199.0	92.7	309.4	361.5	73
1995	8.9	17.2	11.3	2.7	136.6	45.9	158.0	212.5	129
1996	7.4	16.1	10.1	4.0	129.7	155.4	232.0	213.2	139
1997	9.7	16.6	10.5	6.3	127.7	296.2	166.4	173.3	136
1998	9.5	15.2	10.2	5.3	241.9	235.1	296.6	195.3	163
1999	10.1	16.1	11.4	5.3	225.6	166.6	213.2	257.5	226
2000	9.2	15.6	10.3	4.1	258.7	161.2	425.3	237.8	269
2001	8.4	16.2	11.3	5.2	194.4	212.8	205.4	257.9	103
2002	9.8	16.1	10.5	4.3	137.5	248.2	306.2	222.4	177
2003	10.0	17.4	10.5	5.1	126.6	169.9	120.8	239.2	176
2004	9.7	16.5	10.9	5.4	197.4	295.4	159.1	159.1	336
2005	9.1	16.4	11.5	4.4	131.9	179.7	259.8	122.2	148
2006	8.3	17.7	12.5	6.5	234.5	141.3	228.4	318.5	210
2007	10.2	15.4	10.9	5.5	134.1	425.7	109.7	277.6	144
2008	8.9	16.1	10.2	4.0	221.5	248.0	257.6	134.4	242
2009	9.9	16.1	11.3	2.4	190.0	359.4	233.3	166.7	168
2010	8.9	16.1	9.9	3.5	102.8	153.7	250.1	171.9	191
2011	10.5	15.5	12.4	5.4	59.8	108.2	126.8	221.6	216
Mean	9.3	16.3	10.9	4.7	169.4	205.3	225.5	219.0	180
SD	0.8	0.7	0.8	1.1	55.5	95.6	79.9	61.9	63

Appendix 3.7 Future climate projections for the 25 x 25km grid square including the Rivelin Valley, for the period 2070–2099. Data on projected percentage change in climatic variables were extracted from UKCP 2009, and converted to future absolute projected values by multiplying by the recent historical mean (i.e. mean seasonal values for the period 1994–2012 at Weston Park Weather Station). CDF = cumulative distribution function, representing the percentage likelihood that the increase will be less than this projection; temp = mean seasonal temperature (ºC); prec = total seasonal precipitation (mm). Equivalent values were also calculated for the periods 2010–2039 and 2040–69, but are not shown here for the sake of clarity.

Emissions scenario	CDF	Spring temp	Autumn temp	Spring prec	Autumn prec
Historical mean	--	9.3	10.9	169.4	225.5
Low	10%	9.4	11.1	157.4	208.0
	50%	9.5	11.2	171.1	232.6
	90%	9.6	11.3	186.1	260.4
Medium	10%	9.5	11.1	158.5	213.1
	50%	9.6	11.3	171.1	234.2
	90%	9.7	11.4	184.9	257.6
High	10%	9.5	11.2	157.5	210.8
	50%	9.6	11.4	170.8	235.0
	90%	9.8	11.6	185.5	262.4

Appendix 4

Appendix 4.1 Comparison of models of (a) clutch size and (b) recruitment probability in response to weather during various lengths of (a) pre-laying and (b) post-fledging periods, respectively. For each response, the effects of daily mean temperature (ºC) and precipitation (mm) were compared for the 4, 8, 12, 14, 16 and 32 days preceding laying or following fledging, controlling for non-climatic parameters as detailed in Table 4.1. Shown is the difference in AICc of the specified weather model (both linear and quadratic equivalents) compared to the model comprising only non-climatic parameters. Note that a 14-day period was used in subsequent analyses.

Length of period (days)	Temperature		Precipitation	
	Linear	Quadratic	Linear	Quadratic
(a) Clutch size in response to pre-laying weather				
4	+0.7	+2.5	+2.0	+3.6
8	+1.5	+3.4	+2.0	+1.3
12	+1.0	+1.6	+1.2	+2.4
14	+1.1	+1.9	+1.4	+3.4
16	+1.3	+2.5	+1.9	+4.0
32	+1.9	+3.4	+1.9	+3.1
(b) Recruitment probability in reponse to post-fledging weather				
4	-0.7	+0.3	+1.8	+2.0
8	-2.6	-0.6	+1.1	-0.9
12	-0.6	+0.6	+0.9	+1.8
14	-0.7	+0.7	+1.0	+1.1
16	-0.5	+0.4	-0.6	-0.8
32	-2.3	-1.4	+2.1	+3.9

Appendix 4.2 Individual productivity outcomes in response to precipitation during nest-specific periods. Productivity was modelled in response to three indices of extreme precipitation, i.e. the presence/absence of exceptionally wet, extremely wet, or very wet days during the focal period, as defined below. Non-climatic predictors were controlled for in all models as detailed in Table 4.1. Shown is the difference in AICc of the specified precipitation model compared to the model comprising only non-climatic predictors. Note that the presence/absence of very wet days was used as the predictor in subsequent analyses; the exception was for analyses of recruitment probability, for which the presence/absence of extremely wet days was used due to sample size issues.

Productivity response (Focal weather period)	Exceptionally wet days (wettest 2.5%)	Extremely wet days (wettest 5%)	Very wet days (wettest 10%)
Fledged brood size (Nestling$_{11}$)	+1.1	+1.3	+1.2
Hatching probability (Egg)	+30.1	+29.9	+30.1
Fledging probability (Nestling)	+25.4	+10.1	-11.5
Nestling mass (Nestling$_{11}$)	+2.1	+1.9	+1.9
Recruitment probability (Post-fledging)	+1.8	-2.9	-2.8

The three indices of extreme precipitation were defined as follows. Exceptionally wet = precipitation exceeded the amount falling on the wettest 2.5% of days, i.e. ≥14.7, 16.7, 16.5, 15.7 mm during the egg, nestling$_{11}$, nestling and post-fledging periods, respectively. Extremely wet = precipitation exceeded the amount falling on the wettest 5% of days, i.e. ≥11.3, 11.2, 11.2, 10.4 mm during the egg, nestling$_{11}$, nestling and post-fledging periods, respectively. Very wet = precipitation exceeded the amount falling on the wettest 10% of days, i.e. ≥6.4, 6.0, 5.9, 6.0 mm during the egg, nestling$_{11}$, nestling and post-fledging periods, respectively.

Appendix 4.3 The effects of winter weather on population-level productivity outcomes in a population of long-tailed tits in the Rivelin Valley, 1995–2013. Productivity outcomes were (a) mean clutch size, (b) mean brood size of fledged nests, modelled in response to mean daily temperature (temp) and mean daily precipitation (prec) during each month of the winter preceding breeding, December–February. Non-climatic parameters were controlled for as detailed in Table 4.2. Model averages are displayed, showing the model-averaged R^2, and the parameter estimate (est.), standard error (SE) and partial R^2 of each variable retained. Note that 95% confidence intervals overlapped zero for all climatic parameter estimates.

Variable	Est.	SE	Partial R^2
(a) Clutch size: R^2 = 0.37; 3 models in set			
Intercept	*+8.492*	*0.533*	--
Prop 1st attempts	+1.594	0.623	0.24
Adult pop size	-0.004	0.002	0.03
Feb prec	+0.002	0.002	0.03
(b) Brood size: R^2 = 0.39; 4 models in set			
Intercept	*-2.189*	*5.241*	--
Clutch size	+1.107	0.455	0.20
Prop 1st attempts	+2.196	1.080	0.13
Dec prec	-0.005	0.003	0.01
Feb prec	+0.007	0.004	0.03

Appendix 4.4 Annual predation rate in response to weather during the breeding season and the preceding winter, in a population of long-tailed tits in the Rivelin Valley, 1995–2013. Predation was modelled in response to (a) average weather conditions, which were mean monthly temperature and precipitation during the winter (December–February) and during each month of the breeding season (March–May); (b) extreme weather conditions, which were mean temperature and total precipitation during the coldest and the wettest winter month, the number of very wet days during each month of the breeding season, and mean temperature during each month of the breeding season. Very wet days were defined as those on which precipitation exceeded 5.9 mm, which was the amount falling on the wettest 10% of days when chicks were in the nest over the course of the study. All analyses controlled for adult population size. Displayed are the model-averaged parameter estimate (est.), standard error (SE) and partial R^2 of each variable in the model average. In both analyses, four models were retained in the model average set, but note that in both cases the best model was the null.

Variable	Est.	SE	Partial R^2
(a) Average weather			
Intercept	*+3.139*	*0.956*	--
March temperature	+0.205	0.137	0.10
March precipitation	-0.013	0.008	0.14
April precipitation	-0.007	0.005	0.03
(b) Extreme weather			
Intercept	*+3.118*	*0.718*	--
March temperature	+0.161	0.123	0.10
March very wet days	-0.158	0.127	0.09
May very wet days	+0.141	0.123	0.08

Appendix 4.5 Model averages of individual-level productivity outcomes in response to weather during nest-specific periods of the breeding season, in a population of long-tailed tits in the Rivelin Valley, 1995-2013. Productivity outcomes were (a) clutch size, (b) brood size of fledged nests, (c) hatching probability, (d) fledging probability, (e) nestling mass, and (f) recruitment probability of fledged males, modelled in response to mean daily temperature (temp) and mean daily precipitation (prec) during nest-specific periods. Non-climatic parameters that could influence productivity were also included as predictors, as detailed in Table 4.1. Displayed are the model-averaged parameter estimate (est.) and standard error (SE) of each variable retained in the model average, as well as the number of models in the model average set, the D^2 of the best model, and the partial D^2 of each parameter retained in the best model, where '--' indicates variables not retained in the best model.

Variable	Est.	SE	Partial D^2
(a) Clutch size: D^2 = 0.10, 5 models in set			
Intercept	*+9.740*	*0.237*	
Relative lay date	+0.025	0.014	0.104
Relative lay date^2	-0.002	<0.001	
Pre-laying temperature	+0.029	0.040	--
Pre-laying precipitation	-0.050	0.121	--
Laying temperature	-0.009	0.028	--
Laying precipitation	+0.029	0.087	--
(b) Fledged brood size: D^2 = 0.05, 8 models in set			
Intercept	*-2.385*	*1.640*	
Relative lay date	-0.013	0.015	--
Clutch size	+1.002	0.133	0.054
Number of helpers	+0.199	0.114	0.003
Nestling$_{11}$ temperature	+0.096	0.081	--
Nestling$_{11}$ wet days	+0.274	0.015	--
(c) Hatching probability: D^2 = 0.04, 2 models in set			
Intercept	*-0.781*	*0.602*	
Relative lay date	-0.052	0.009	0.029
Predation rate	-0.408	0.109	0.008
Egg temperature	+0.266	0.052	0.020
Egg wet days	+0.141	0.208	--

---continued overleaf---

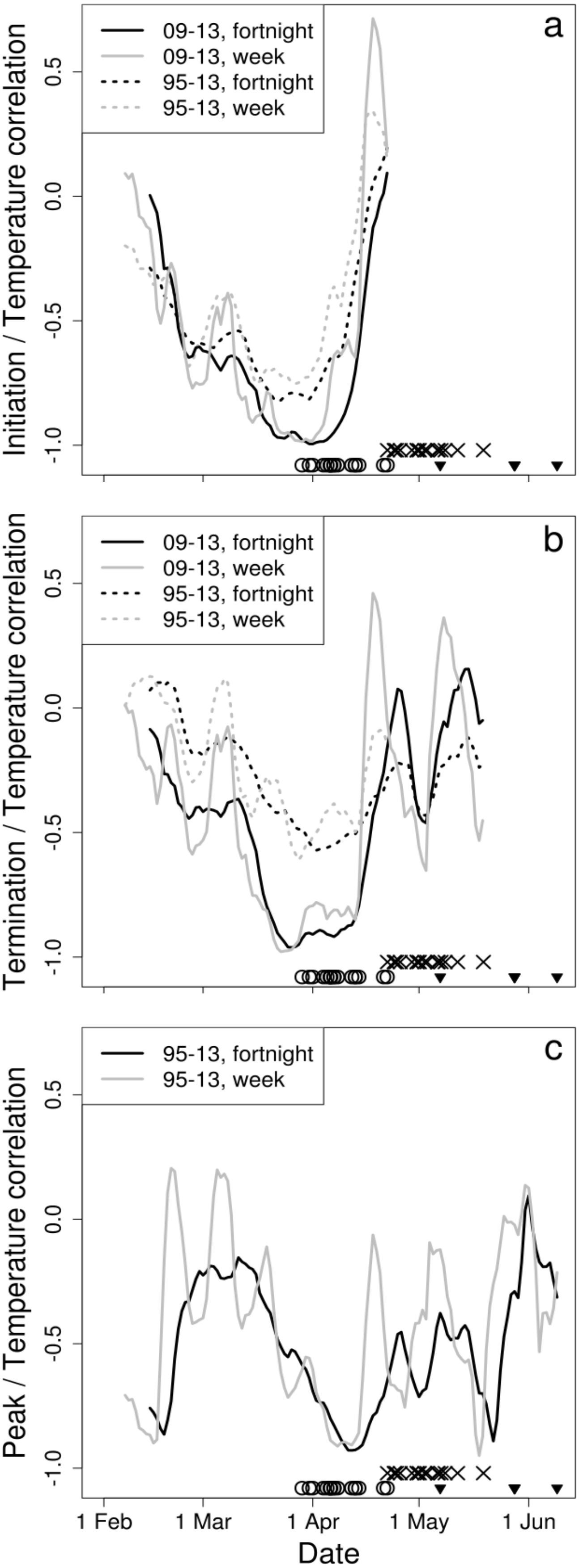
(d) Fledging probability: D^2 = 0.12, 2 models in set			
Intercept	*-4.182*	*1.080*	
Relative lay date	-0.041	0.014	0.017
Predation rate	-0.070	0.217	--
Nestling temperature	+0.366	0.089	0.038
Nestling wet days	+1.720	0.291	0.071
(e) Nestling mass: D^2 = 0.50, 7 models in set			
Intercept	*-1.060*	*0.524*	
Relative lay date	+0.004	0.002	0.008
Number of helpers	+0.057	0.021	0.024
Number of helpers^2	-0.004	0.008	
Tarsus length	+0.462	0.029	0.482
Brood size	-0.011	0.006	0.007
Nestling$_{11}$ temperature	-0.013	0.015	--
(f) Recruitment probability: D^2 = 0.07, 8 models in set			
Intercept	*-2.565*	*2.487*	--
Relative lay date	-0.052	0.014	0.035
Population size	-0.003	0.002	0.006
Mass:tarsus ratio	+7.726	5.029	0.005
Post-fledging temp	+0.128	0.085	--
Post-fledging wet days	-0.541	0.205	0.012

Appendix 4.6 The effects of weather on population-level productivity outcomes in a population of long-tailed tits in the Rivelin Valley, 1995–2013. Productivity outcomes were (a) mean clutch size, (b) mean brood size of fledged nests, (c) number of fledglings per breeding female, (d) number of recruits per breeding female, and (e) recruitment probability of fledged males, modelled in response to mean daily temperature (temp) and mean daily precipitation (prec) during each month of (a-d) the breeding season, March–May or (e) the year from hatching to recruiting, March–February. Non-climatic parameters were controlled for as detailed in Table 4.2. Best models are displayed, showing the model D/R^2, and the parameter estimate (est.), standard error (SE) and partial D/R^2 of each variable retained in the best model.

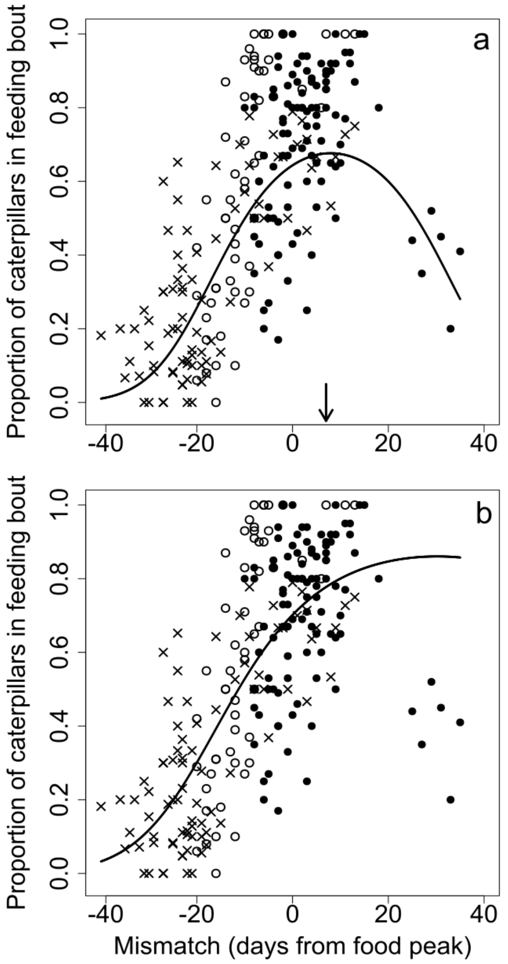
Variable	Est.	SE	Partial D/R^2
(a) Clutch size: $R^2 = 0.30$			
Intercept	*+8.365*	*0.479*	--
Proportion 1st nests	+1.672	0.633	0.30
(b) Brood size: $R^2 = 0.57$			
Intercept	*-4.350*	*3.815*	--
Clutch size	+1.080	0.399	0.23
Proportion 1st nests	+1.838	0.936	0.12
March prec	+0.009	0.004	0.14
(c) Fledglings per ♀: $R^2 = 0.53$			
Intercept	*+3.585*	*0.955*	--
Predation rate	-0.805	0.199	0.52
Season length	+0.072	0.038	0.11
(d) Recruits per ♀: $R^2 = 0.67$			
Intercept	*-6.505*	*1.733*	--
Population size	-0.009	0.003	0.28
March temp	-0.473	0.119	0.44
May temp	+0.820	0.186	0.54
(e) Recruitment probability: $D^2 = 0.77$			
Intercept	*-4.370*	*1.359*	--
Population size	-0.009	0.002	0.64
March temp	-0.298	0.089	0.27
May temp	+0.575	0.141	0.42

Appendix 5

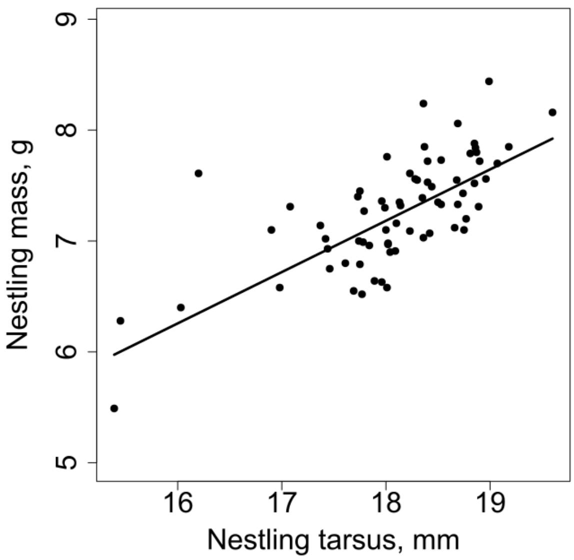
Appendix 5.1 ---displayed overleaf--- The correlation between temperature (ºC) during overlapping fortnightly (black lines) and weekly (grey lines) periods and three phenological responses: (a) breeding initiation, (b) breeding termination, (c) caterpillar peak date. Data are from the Rivelin Valley during two time periods: 2009–2013 (solid lines) and 1995–2013 (dotted lines), because caterpillar peak data were only available for the shorter time period. Mean daily temperature was calculated for fortnightly periods starting at 1-day intervals from 14 February and weekly periods from 7 February, ending with the fortnight or week preceding the latest date of the focal phenological response over the course of the study. Date on the *y* axis indicates the temperature during the fortnight preceding the date shown (e.g. 1 April indicates the period from 17 March to 1 April inclusive). The annual timing of each response is shown just above the *x* axis, where breeding initiation = ○, breeding termination = ×, and caterpillar peak date = ▼. Note that in three years, caterpillar peak date occurred on the same date (28 May).


a
09-13, fortnight
09-13, week
95-13, fortnight
95-13, week
Initiation / Temperature correlation
b
09-13, fortnight
09-13, week
95-13, fortnight
95-13, week
Termination / Temperature correlation
c
95-13, fortnight
95-13, week
Peak / Temperature correlation
0.5
0.0
-0.5
-1.0
1 Feb
1 Mar
1 Apr
1 May
1 Jun
Date

Appendix 5.2 The relationship between mismatch and the caterpillar content during an individual feeding bout, where a negative mismatch value indicates a date before the caterpillar peak. Data are from the Rivelin population of long-tailed tits over three years: 2011 (●), 2012 (○) and 2013 (×). The plotted lines show the relationship when controlling for either (a) year as a categorical fixed effect or (b) nest as a random effect, because there were insufficient degrees of freedom to control for both year and nest in a single model ($n = 242$ provisioning bouts at 43 nests). Both models were generalized linear mixed-effects models with binomial error structure and logit link function, controlling for nestling age as a fixed effect, where the quadratic effect of mismatch was highly significant. (a) Linear term est. ± 1SE = +0.221 ± 0.013, $P < 0.0001$; quadratic term = -0.002 ± 0.0002, $P < 0.0001$; $D^2 = 0.54$; the inflection point of the curve (↓) indicates the degree of late-mismatch beyond which dietary caterpillar content is expected to decline. (b) Linear term est. ± 1SE = +0.148 ± 0.024, $P < 0.0001$; quadratic term = -0.001 ± 0.0003, $P = 0.001$; $D^2 = 0.13$; note that the number of samples per nest was on the limit of suitability for inclusion as a random effect (range = 1 to 9, mean ± 1SD = 4.3 ± 2.1; see Bolker *et al.* 2009) and that all data points with a mismatch of >20 days come from a single nest.



Appendix 5.3 The correlation between brood-mean nestling mass and tarsus length during 2009–2013, controlling for brood size, number of helpers, relative lay date and year. The plotted line is the relationship in a general linear model (est. ± 1SE = +0.463 ± 0.061, $P < 0.0001$, partial $R^2 = 0.45$), with non-focal parameters held at their median value.



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