Impacts of climate changes on a long-distance migratory bird, the northern wheatear

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Summary

Climate-driven changes in the overall abundance or phenology of food resources may be critical factors affecting migratory populations, which depend on suitable conditions at widely-spaced locations across the planet. Numerous studies have described associations between climatic change and breeding success, survival and the timing of migration among migrant birds, but we used an experimental approach to investigate the causal mechanisms underlying these widely-reported correlations. Specifically, we used food-supplementations to simulate experimentally the impact of changes in food availability across the annual cycle of a model species of long-distance migrant bird, the northern wheatear (*Oenanthe oenanthe*). Food supplementation modified migratory schedules of wheatears by affecting migratory fuelling, but the strength of this impact varied between stages of the annual cycle and between two subspecies with contrasting migration strategies. Food supplementation advanced hatching date of wheatears in the UK, and led to some supplemented individuals increasing their reproductive output through multiple breeding attempts. Food-supplemented wheatears exhibited higher rates of annual survival than control wheatears, and the strength of this effect was most pronounced on survival of young immediately following fledging. These experiments highlight aspects of wheatear performance that are currently limited by food availability and are thus most sensitive to climate-driven changes in food supply (primarily migratory fuelling, number of breeding attempts and survival). We used experimental manipulations of temperature and soil moisture of upland grassland turfs to simulate the impact of climate change on the abundance and emergence phenology of the wheatear's arthropod prey. Warming by 2 ºC and low soil moisture levels led to a reduction in arthropod abundance later in the season, indicating how such climate-driven changes would affect food availability to wheatears across the breeding season. These studies together provide experimental evidence for the mechanisms by which climate change is expected to influence population changes in migratory taxa.

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CHAPTER 1. Introduction

INTRODUCTION

Climate change has major implications for ecosystems and populations. The spatial and temporal heterogeneity of changes in temperature and rainfall present particular challenges to long-distance migratory taxa because they have to time their migrations to coincide with food availability at locations many kilometres apart. A multitude of studies have described how a variety of ecological changes have occurred that correlate with long-term trends in climate warming, or with large-scale climate fluctuations (e.g. see reviews by Root et al. 2003, Walther et al. 2005, Parmesan 2006). Due to the complexity of ecological and climatic systems, an approach based on observations and correlations is limited in the extent to which the underlying causes of ecological change can be identified. To begin to understand the mechanisms linking climate change and ecological change, an experimental approach has been advocated (Helmuth et al. 2005), but has yet to be fully exploited. Birds undergoing long-distance migration are a very suitable study system for such research, as climate change can have major consequences at all stages of their life cycle. These birds also rely on habitats in widely-spaced locations that may not experience the same rates or direction of climate change, which may limit their ability to adapt to change. The impact of temperature on arthropod abundance and phenology is a candidate mechanism underpinning changes in the migration strategies and population dynamics of migratory birds, for which arthropods are often the most important component of diet.

In this study I use food supplementation experiments to simulate climate-linked increases in food availability across the annual cycle of a long-distance migratory bird, the northern wheatear (*Oenanthe oenanthe*) (Fig. 1.1). These food supplementations are linked to projections of climatic change by experimental manipulations of temperature

Fig. 1.1. Male northern wheatear *Oenanthe oenanthe* at entrance to nesting burrow, with grub for nestlings on Fair Isle, Shetland.

and moisture on the emergence phenology and abundance of the arthropod prey of northern wheatears. These experiments indicate the likely effect of climate warming and altered rainfall on the food availability of a long-distance migratory bird and, in turn, the impact of changes in food availability on the bird's body mass regulation, breeding productivity and survival. This chapter summarises our current knowledge on impacts of climate change on migratory taxa and provides justification for the novel research described in the remainder of the thesis. The observed associations between recent climate change and aspects of the biology of migratory species have already been reviewed extensively (Gordo 2007, Jonzén et al. 2007a, Robinson et al. 2009). Rather than repeating such a review, here I focus on an area in which our understanding remains very limited, namely the underlying mechanisms by which climate change may affect migratory species. In this way, I highlight the need and opportunity for the experimental investigations described in the subsequent chapters.

Impacts of climate change on migratory organisms

Climate change is already altering the world's ecosystems, and the rate of change is likely to accelerate over the coming decades (IPCC 2007). Global mean surface temperature increased by 0.76˚C between 1906 and 2005 and the best estimates of climate change models predict that a further increase of between 1.8 and 4.0˚C will be recorded by 2099, depending on the scenario of future greenhouse gas emissions (IPCC 2007). Global temperature changes have not been uniform, with heterogeneity evident at a range of temporal and spatial scales. For example, daily minimum temperatures have increased approximately twice as much as daily maxima (Easterling et al. 2000a), while temperature has increased at a faster rate in the Arctic than elsewhere (IPCC 2007). Rainfall patterns have also changed, and the incidence of extreme weather events (e.g. heavy precipitation, droughts and heat waves) has increased (IPCC 2007). There is now compelling evidence that climate change is causing changes in the phenology, abundance and distribution of different plant and animal taxa (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Warren et al. 2011). Long-distance migratory taxa are likely to be especially vulnerable to the effects of climate change, as their ability to complete their annual cycle depends on environmental conditions (including weather, habitat quality and food availability) at locations hundreds or thousands of kilometres apart.

Climate change has fitness implications for migrants at their breeding grounds (e.g. affecting fecundity), wintering grounds (affecting survival) or during migration (affecting both survival and subsequent fecundity). It is, however, over-simplistic to view life cycle stages in isolation; events throughout an organism's annual cycle are fundamentally interlinked (Marra et al. 1998, Norris et al. 2004). Travelling many kilometres on migration requires a large intake of energy, and migrants are dependent on high quality foraging resources to undertake these journeys. Thus, the quality of foraging resources at stopover sites affects the condition of migrants on arrival. Arriving in poor condition may, in turn, result in lower survival or fecundity at subsequent life-cycle stages. Such carry-over effects on individual fitness can even extend beyond one annual cycle. For example, late arrival at breeding grounds can result in an individual obtaining a low quality territory, leading to lower body condition at the end of the breeding season. This, in turn, may result in delayed or slower post-breeding migration and settlement on a poor quality territory on arrival back at the wintering area (Marra et al. 1998, Gill et al. 2001). Arriving late at breeding grounds relative to seasonal peaks in food abundance may in turn have negative consequences for reproductive success (Stenseth and Mysterud 2002, Both 2010).

Higher spring temperatures at high- and mid-latitudes over recent decades have resulted in shifts in abundance of primary producers (e.g. plants and phytoplankton) in space and time (Root et al. 2003, Winder and Schindler 2004, Hays et al. 2005, Menzel et al. 2006). Consequently, the abundance and phenology of the consumers (e.g. arthropods and zooplankton) that feed on these primary producers have altered, with knock-on effects on higher trophic levels (Edwards and Richardson 2004, Visser et al. 2006, Pearce-Higgins et al. 2010). Temperature may also have direct effects on arthropod development, which is generally accelerated by warming (Bale et al. 2002). Experimental evidence of the nature of the links between climate variables and phenological change is relatively lacking compared to the wealth of observational data. Experiments have confirmed that the phenology of primary producers responds to warming temperatures; in terrestrial plants usually by advancing timing of bud burst, flowering and fruiting (Strathdee et al. 1993, Sherry et al. 2007, De Frenne et al. 2011), although experimental warming may also delay plant reproductive phenology in late-flowering plants (Sherry et al. 2007). Animal populations generally respond to climatic fluctuations by adjusting their phenology to track that of lower trophic levels (even if they rarely actually match it). For example, the phenology of herbivorous arthropods appears to track that of their host plants (Strathdee et al. 1993). The timing of spring migration into Europe of many bird species is earlier in warmer springs, in accordance with the earlier phenology of European plants and invertebrates (Forchhammer et al. 2002, Hüppop and Hüppop 2003, Cotton 2003, Gordo 2007). Among the few organisms in which shifts in phenology have been compared between trophic levels, however, in the majority of cases, consumers have either advanced their phenology too much or not enough, relative to the lower trophic levels on which they depend (Visser and Both 2005).

The ability of migratory species to respond to changes in the timing of food supply will be affected by ability to change the timing of migration. Short-distance migrants are likely to be able to adjust the timing of spring departure according to local weather conditions, since these are likely to correlate broadly with weather conditions at the destination (Forchhammer et al. 2002). In contrast, for long-distance migrants, local weather conditions in the wintering grounds are unlikely to be an adequate indicator of conditions at the breeding grounds thousands of kilometres away. Hence, many long-distance migrants may be constrained in their ability to match migration timing with phenological shifts of their food supplies at their breeding grounds (Stenseth and

Mysterud 2002, Both and Visser 2005, Post and Forchhammer 2008, Thackeray et al. 2010).

The inability to track advancing phenology of food supplies leads to trophic mismatches between migratory predators and their prey, with demographic consequences (Visser and Both 2005). For example, recruitment of Atlantic cod (*Gadus morhua*) in the North Sea, which migrate to specific spawning locations, has been affected due to reduced food availability at the appropriate time for cod larvae (Beaugrand et al. 2003). Mismatching of breeding and foraging resource availability due to climate warming has resulted in a decline in breeding productivity and offspring survival of migratory caribou (*Rangifer tarandus*) in Greenland (Post and Forchhammer 2008). Migratory bird species breeding in Europe that have not advanced their phenology in relation to climatic warming have declined in abundance (Møller et al. 2008). Declines of pied flycatchers (*Ficedula hypoleuca*) in Europe have occurred in populations that have not advanced migration phenology sufficiently to maintain synchrony of breeding with peak abundance of caterpillars, the main prey delivered to nestlings (Both et al. 2006). For some insectivorous bird species populations, spring arrivals may be actually becoming later, for example common nightingale (*Luscinia megarhynchos*) and common cuckoo (*Cuculus canorus*) in parts of southern Europe (Peñuelas et al. 2002, Gordo et al. 2005). The mismatch between arrival of these species and the timing of food availability is particularly great, as insect phenology has generally advanced in their breeding areas. Nightingales in Croatia have advanced their spring arrivals, however (Kralj and Dolenec 2008), so the effects of climate change on these species' migration phenology is unclear. A mechanistic approach, particularly investigating the role of changes in food supplies in the wintering grounds and *en route* during migration, are likely to be of greater value in explaining such patterns, than correlations with temperatures trends alone.

Changes in the timing of arrival of migrants at their breeding grounds could be due to changes in departure timing from the tropical winter grounds and / or altered speed of migration. The speed of migration is affected by a combination of fuelling conditions (availability of food) experienced *en route*, wind direction and speed, and other aspects of weather conditions, such as rain or snowfall (Dänhardt and Lindström 2001). Departure timing appears to be predominantly governed by endogenous circannual rhythms (Hagan et al. 1991), but may be modified by other environmental factors such as photoperiod (Berthold and Terrill 1991, Gwinner 1996). There is empirical evidence that both departure timing and migration speed are associated with climatic and ecological conditions. Climate-driven changes in winter foraging may be a proximate cue for both short- and long-distance migrants to leave their winter grounds earlier, and / or may release a constraint on earlier departure. For example, rainfall in the tropical wintering grounds of American redstarts (*Setophaga ruticilla*) affects food (arthropod) availability, which in turn influences body condition and spring-departure timing (Studds and Marra 2011). Similarly, faster spring migration in pied flycatchers (*Ficedula hypoleuca*) is associated with warmer conditions close to the breeding grounds (Ahola et al. 2004).

Although there exists a vast literature on the associations between climate variables and the phenology and populations of migratory birds, the ecological and behavioural mechanisms underlying these changes remain poorly understood. The main drawback of correlative studies (e.g. climate envelope modelling (Pearson and Dawson

2003) and trends based on fluctuations in large-scale climate cycles (Hüppop and Hüppop 2003)) is the difficulty in ascribing causation to climate change. The potential of climate envelope models to predict future distributions and abundances is limited because they largely ignore the potential for biotic interactions, genetic adaptability and dispersal limitations to modify the relationship between species and climate change (Hampe 2004, Van der Putten et al. 2010). By understanding the underlying mechanisms, it may be possible to appreciate the reasons for species-level variation in adaptation to climate change (Wingfield et al. 2011). I use experimental manipulations of food supply to simulate climate-driven increases in food availability at breeding, wintering and stopover sites of a long-distance migratory bird. The food supplementation that I have used was not designed to mimic directly the expected ecological response to climate change, which, in seasonal environments, is predicted to involve a shift in distribution of peaks in resource availability, as well changes in overall abundance. By supplementing food across whole breeding seasons and migratory fuelling periods, I aim to highlight aspects of the bird's performance that are currently limited by food availability and thus are phenotypically flexible to climate-linked alterations in food supply.

A common migratory strategy of passerine birds is to breed in temperate and Arctic regions during the relatively short period of high productivity in spring and early summer, departing these areas when conditions become hostile (Moreau 1972, Alerstam and Högstedt 1982). Long-distance migratory birds may depend on a few specific stopover sites, as their migration is under the control of a sophisticated timing system, composed of both endogenous (circadian and circannual biological clocks) and exogenous (environmental variables, particularly photoperiod) components (Gwinner

1996, Bairlein and Hüppop 2004). The birds depend on suitable habitats and food at these stopover sites to fuel sufficiently for the next stage of migration. Climate change may affect the predictability and spatial distribution of foraging resources for stopover. Long-distance migrants could, therefore, be more affected by climate change than short- or medium-distance migrants, as the latter may be more flexible in their stopover decisions. Furthermore, short-range migrants rely on fewer intermediate migratory-stopover locations, which are more likely to correlate in their phenology with conditions at the breeding grounds.

Climate can impact on the reproductive success and survival of organisms by affecting the lower trophic levels on which they depend for food (White 2008). For example, climate-driven fluctuations in arthropod prey abundance have been shown to relate to the productivity of migratory birds in Europe (e.g. European golden plover *Pluvialis apricaria*, Pearce-Higgins et al. 2009) and North America (e.g. black-throated blue warbler *Dendroica caerulescens*, Sillett et al. 2000). In the case of the golden plover, reduced abundance of their key prey, craneflies (Tipulidae), was associated with warmer summer temperatures at their southern range margin the preceding year. This in turn was associated with reduced recruitment of plovers in the following year (Pearce-Higgins et al. 2010).

Climate change can have direct impacts on arthropods by affecting their physiology and behaviour, or indirect impacts by affecting other factors, such as the phenology and growth of their host plants (Bale et al. 2002). Changes in temperature, CO_2 and rainfall can each affect arthropod abundance and phenology. Modest increases in temperature can cause dramatic increases of some insect taxa, such as species of

Hemiptera (Strathdee et al. 1993, Miles et al. 1997). Climate warming can also cause declines of cold-adapted insects, such as Tipulidae (Pearce-Higgins et al. 2010, Carroll et al. 2011), probably because of increased mortality due to drying of the soil (Coulson 1962, Coulson et al. 1976). Elevated CO_2 can influence insect-plant interactions in a number of ways, for example by reducing insect herbivore performance (by chemical changes in leaf tissues), although elevated temperature can buffer this effect (Veteli et al. 2002, El Zvereva 2006). The increase in occurrence of extreme events associated with climate change (Easterling et al. 2000b) may have greater impacts on survival and performance than increases in mean temperature. For example, drought, flooding and late frosts may all have severe impacts on insect abundance (Parmesan et al. 2000). Experimental simulations of winter warming events in the Arctic – which are predicted to become more frequent – had large negative effects on plant productivity, with delayed spring bud burst and reduced growth and fruit production (Bokhorst et al. 2011). Such effects will inevitably affect higher trophic levels. Most research has focused on individual environmental factors, primarily temperature, but the interaction between climate change factors has not received enough attention (Bale et al. 2002). For example, changes in rainfall could mitigate the effect of temperature or act in combination to produce a stronger ecological response.

The study system

The study species, the northern wheatear, is a small insectivorous passerine bird of the family Turdidae. It was chosen for its extreme long-distance migrations, its tractability for field experiments, and the fact that a series of recent studies have paved the way for the proposed work (Pärt 2001a, 2001b, Schmaljohann and Dierschke 2005, Delingat et al. 2006). I focus on two subspecies of northern wheatear: *O. o. oenanthe* and *O. o.*

leucorhoa, both of which winter in the Sahel region in sub-Saharan Africa but which have contrasting migratory journeys. By focusing on these two closely-related and ecologically similar taxa, phylogenetic and ecological differences could be controlled while examining how differences in migration strategy might affect the response to climate change. Northern wheatears are mainly insectivorous, in common with most other long-distance migratory songbirds. Their reproductive success probably depends, to a large extent, on timing their breeding to match peak emergences of their arthropod prey, as has been shown in other species (Van Noordwijk et al. 1995, Both and Visser 2005). Wheatears inhabit open areas, facilitating observation in the field. Recent studies have revealed much about the factors that influence reproductive success and migration strategy of wheatears. It has been shown, for example, that territory quality is the most important variable determining reproductive success of wheatears, not individual quality, and that early arriving, usually older, birds were able to settle on the best territories (Currie et al. 2000, Pärt 2001a, 2001b). There is therefore likely to be selection pressure for early arrival on breeding grounds. Accordingly, northern wheatears appear to follow a time-minimisation spring migration strategy (Delingat et al. 2006).

The northern wheatear has a very large breeding distribution that stretches from eastern Canada, Greenland and Iceland, eastward through most of Europe, much of central and northern Asia and into Arctic North America. The winter quarters of the entire world population, including those birds breeding in the Nearctic, lies in Africa in a broad belt south of the Sahara extending from the west to east coasts (Cramp 1988). The global population numbers approximately 2,900,000 individuals (BirdLife International, 2004). There has been a marked decline in abundance of wheatears and a retraction of their breeding range in NW Europe over recent decades, particularly in lowland grassland, but also in marginal upland areas (Cramp 1988, Baillie et al. 2010, PECBMS 2010). This decline has been attributed mainly to agricultural intensification that reduces habitat diversity and abundance of invertebrates, but also coincides with recent climate warming.

Four subspecies of northern wheatear are recognised (Cramp 1988): *O. o. oenanthe*, *O. o. libanotica*, *O. o. leucorhoa* and *O. o. seebohmi*, all of which winter in sub-Saharan Africa. The latter subspecies breeds in North Africa, while *O. o. libanotica* breeds from southern Europe east to Mongolia (Cramp 1988, Wernham et al. 2002). *O. o. oenanthe* and *O. o. leucorhoa* are the focus of the present study; both are long-distance migrants which migrate from or through NW Europe, but they contrast markedly in their migration strategies. *O. o. oenanthe* is widespread, breeding across NW Europe, including Scandinavia and the UK. This subspecies migrates in short flight-stages, south from the breeding grounds through France, Spain/Portugal and North Africa, before crossing the Sahara. These short flight stages require relatively small fuel reserves to be accumulated before each migration flight (Dierschke and Delingat 2001). *O. o. leucorhoa*, on the other hand, breeds in eastern Canada, Greenland and Iceland. This subspecies therefore makes trans-oceanic crossings in excess of 1,000 km, which require very large fuel reserves to be accumulated prior to departure (Ottosson et al. 1990, Delingat et al. 2008). It has even been suggested that *O. o. leucorhoa* may sometimes fly non-stop from Greenland and Canada to northwest Africa during autumn migration, a journey of over 4,000 km (Snow 1953, Thorup et al. 2006).

Wheatears seem to follow a time-minimisation migration strategy, which is common amongst migratory passerines, although this is modified by the distance that must be travelled to cross barriers (Dierschke and Delingat 2001). Higher fuel loads are accumulated before departure across large ecological barriers, such as the Atlantic ocean or Sahara desert (Delingat et al. 2008, Boström et al. 2010). Environmental factors such as predation risk and local weather conditions also affect stopover decisions (Dierschke and Delingat 2001, Schmaljohann and Dierschke 2005), yet little is known about the impacts of climate- and ecological-changes on wheatears at their migration stopover sites.

Wheatears require ready-made rock or burrow nest sites immediately adjacent to insect-rich patches of bare ground or short swards. Within these constraints, they occur in a wide variety of different habitats, including arctic tundra, moorland, heaths, unimproved and improved grasslands, sand-dunes, and even forest clearings (Cramp 1988). Breeding site selection is thought to be made mainly on arrival, but may also be influenced by information collected the previous breeding season, on prior reproductive success and the distribution of conspecifics (Arlt and Pärt 2007). Territory quality (largely determined by vegetation height, which affects wheatear foraging success) appears to be more important than individual quality in determining reproductive success (Currie et al. 2000, Pärt 2001a, 2001b). Experimental manipulations of vegetation height show that northern wheatears holding territories with a short field layer rear young much more successfully than those in which the vegetation grows taller (Pärt 2001b). Adult survival rates are also higher in wheatears breeding in territories with short field layers (Low et al. 2010). Date of arrival on the breeding grounds is an important determinant of breeding success. Early arriving males, which are usually older, settle on territories first and are more likely to pair than later arriving males (Currie et al. 2000).

Breeding northern wheatears usually occur at densities between 5-20 pairs km^{-2} but may reach densities of up to 23 pairs km^{-2} in prime habitat (Cramp 1988). Densities are low in areas of intensive agriculture, although wheatears often breed in areas of low intensity cultivation and sheep grazing. They form a mainly monogamous pair bond during the breeding season, but polygynous situations sometimes occur in which paired males mate with females outside of the pair bond. The monogamous pair bond only lasts for the breeding season, but pairing between the same individuals is often renewed annually because of fidelity to territories by both sexes (Cramp 1988).

Detecting trends in the global population of the northern wheatear has been difficult because of the vast area occupied by the species in summer. The wheatear’s range has recently extended into eastern Canada, possibly due to increases in summer temperatures. Similar expansions in range may have occurred along the tundra of northern Scandinavia and arctic Russia (Cramp 1988). Further south, declines have occurred in central and western Europe, mainly due to agricultural intensification of former habitat (Kneis 1982). Eutrophication-linked rich grass growth in formerly sparsely vegetated areas has also contributed to declines (Osieck and Hustings 1994) because wheatears need short field layers to forage successfully (Arlt and Pärt 2007). The northern wheatear has declined rapidly in Europe since 2008 (PECBMS 2010). Wide fluctuations in the wheatear population of Britain have been recorded since monitoring began in 1994, and the species is considered likely to have declined (Baillie et al. 2010).

Little is known of wheatear ecology in their wintering grounds. Wheatear densities in northern Nigeria are negatively correlated with tree density, except at very low tree densities, which predict low numbers of wheatears (Wilson and Cresswell 2010). They are mainly solitary outside of the breeding season. They defend relatively stable territories in their winter quarters (Leisler et al. 1983) and some also establish temporary territories on stopover sites during migration. The Sahelian droughts of the 1960s, 1972 and 1983 are thought to have reduced the number of birds returning to their breeding grounds (Cramp 1988, Clement 1997).

Wheatears spend a large proportion of daylight hours searching for food (e.g. 51–67% for migrants stopping over on Helgoland Island, Germany) (Conder 1989, Dierschke et al. 2003). A large diversity of prey items have been recorded for the wheatear, which is unsurprising considering it has both a very large breeding distribution and winters south of the Sahara in Africa (Conder, 1989). Arthropods are particularly important, including beetles (Coleoptera), ants (Hymenoptera), craneflies (Tipulidae), caterpillars of butterflies and moths (Lepidoptera) and spiders (Araneae) (Cramp 1988). Plant berries are also eaten extensively at the end of the breeding season (Cramp 1988), probably to fatten up as partial frugivory allows birds to assimilate energy faster than insectivory alone (Parrish 1997). For nestlings, larvae of Lepidoptera and Tipulidae appear to be very important (Cramp 1988). The impact of climate change on the vast majority of these individual prey taxa is largely unknown, as is the net effect of climate change on the arthropod community as a whole, which influences the overall abundance and phenology of food availability to wheatears.

Independently of impacts on food abundance, climate change may also modify food availability to wheatears by modifying the birds' foraging success. For example, the foraging success of wheatears is affected directly by effects of the immediate local weather conditions on the birds' ability to find and capture arthropods; in wet and windy conditions foraging success is reduced, whereas in warm and still conditions foraging success is relatively high (Conder 1989).

The focus of the present study is on the ecological and individual-based mechanisms that underlie population level responses to climate change. Observed changes in phenology, survival and reproduction associated with climate change could be due to one or both of rapid evolution or phenotypic plasticity (Jonzén et al. 2006, 2007b, Both and te Marvelde 2007). By monitoring individually-marked individuals at breeding, wintering and stopover sites, I aim to determine the extent of phenotypic plasticity to changing food availability at different stages of the annual cycle.

Chapter organisation

Chapters 2 through to 5 are written as self-contained papers, for eventual publication. As such, there is some unavoidable repetition of aspects of research methods, while references, acknowledgements and appendices follow each of these chapters. Chapter 5 is based on material from the MRes theses of two Cardiff University MRes graduates, Amy Hicks and Scott McKenzie. As well as being involved in the planning of these projects and undertaking extensive re-analyses, I have also synthesised the studies for eventual submission as a peer-reviewed paper.

Aims and objectives

Aim 1. Simulating the impact of climate-driven changes in food supply, on the breeding performance, annual survival rates, and migration fuelling decisions of wheatears.

Experimental manipulations of food availability (simulating a key effect of changes in temperature and rainfall) were used to evaluate the potential role of climate-driven changes in food supply on the body mass regulation and migration fuelling strategies of wheatears along their migration route between Greenland (for *O. o. leucorhoa*) or northwest Europe (for *O. o. oenanthe*) and the Sahel zone of Africa (Chapter 2). The impacts of these manipulations of food availability on breeding productivity (Chapter 3) and annual survival rates and population growth (Chapter 4) were also measured.

Aim 2. Simulating the impact of climate warming on food availability at a breeding and stopover site.

A major gap in our understanding of how climate change will affect migratory birds is the lack of information about the net impact of climate changes on their food availability. This study therefore investigated the effect of elevated temperatures on the productivity and timing of emergence of the major arthropod taxa on which northern wheatears feed (Chapter 5).

In this study, I set out to:

1. Determine the impact of changes in food supply on body mass regulation (including migration fuel deposition rates and departure fuel loads) and timing of departure, at a breeding and stop-over location and a wintering site (Chapter 2)

2. Determine the impact of changes in food supply at the breeding grounds on nesting phenology (laying/hatching dates), and aspects of reproductive investment (clutch size, number of nesting attempts) and reproductive success (hatching success, number of offspring fledged per breeding season) of wheatears (Chapter 3).
3. Determine the impact of changes in food supply at the breeding grounds, on annual survival of juvenile and adult wheatears (Chapter 4).
4. Simulate climate warming and variation in rainfall by experimentally elevating temperature and soil water content of grassland sward in the laboratory, to predict the impact of climate changes on arthropod phenology and abundance (Chapter 5).

I conclude the thesis with a synthesis of the likely impacts of projected climate changes on population change in the northern wheatear, across the species' annual cycle. I place these findings within the wider context of climate change impacts on migratory taxa, and identify future research directions.

REFERENCES

Alerstam, T., and G. Högstedt. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. Ornis Scandinavica 13:25-37.

Arlt, D., and T. Pärt. 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. Ecology 88:792-801.

Baillie, S. R., J. H. Marchant, D. I. Leech, A. R. Renwick, A. C. Joys, D. G. Noble, C. Barimore, G. J. Conway, I. S. Downie, K. Risely, and R. A. Robinson. 2010. Breeding Birds in the Wider Countryside: their conservation status 2010. BTO Research Report No. 565. Thetford.

Bairlein, F., and O. Hüppop. 2004. Migratory fuelling and global climate change. Pages 33-47 *in* A. P. Møller, W. Fiedler, and P. Berthold, editors. Birds and Climate Change. Elsevier, Oxford.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8:1–16.

Beaugrand, G., K. M. Brander, J. A. Lindley, S. Souissi, and P. C. Reid. 2003. Plankton effect on cod recruitment in the North Sea. Nature 426:661-664.

Berthold, P., and S. B. Terrill. 1991. Recent advances in studies of bird migration. Annual Review of Ecology and Systematics 22:357-378.

Bokhorst, S., J. W. Bjerke, L. E. Street, T. V. Callaghan, and G. K. Phoenix. 2011. Impacts of multiple extreme winter warming events on sub-Arctic heathland: phenology, reproduction, growth, and CO_2 flux responses. Global Change Biology 17:2817-2830.

Boström, J. E., T. Fransson, I. Henshaw, S. Jakobsson, C. Kullberg, and S. Åkesson. 2010. Autumn migratory fuelling: a response to simulated magnetic displacements in juvenile wheatears, *Oenanthe oenanthe*. Behavioral Ecology and Sociobiology 64:1725-1732.

Both, C. 2010. Food availability, mistiming, and climatic change. Pages 129-147 *in* A. P. Møller, W. Fiedler, and P. Berthold, editors. Effects of Climate Change on Birds. Oxford University Press, Oxford.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81-3.

Both, C., and L. te Marvelde. 2007. Climate change and timing of avian breeding and migration throughout Europe. Climate Research 35:93-105.

Both, C., and M. E. Visser. 2005. The effect of climate change on the correlation between avian life-history traits. Global Change Biology 11:1606-1613.

Carroll, M. J., P. Dennis, J. W. Pearce-Higgins, and C. D. Thomas. 2011. Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. Global Change Biology 17:2991-3001.

Conder, P. 1989. The Wheatear. Christopher Helm, London.

Cotton, P. A. 2003. Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences 100:12219-22.

Coulson, J. C. 1962. The Biology of Tipula subnodicornis Zetterstedt, with Comparative Observations on *Tipula paludosa* Meigen. Journal of Animal Ecology 31:1-21.

Coulson, J. C., J. C. Horobin, J. E. C. Butterfield, and G. R. J. Smith. 1976. The maintenance of annual life-cycles in two species of Tipulidae (Diptera); a field study relating development, temperature and altitude. Journal of Animal Ecology 45:215-233.

Cramp, S. (Ed.). 1988. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Volume V: Tyrant flycatchers to thrushes. Oxford University Press, Oxford.

Currie, D., D. B. A. Thompson, and T. Burke. 2000. Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. Ibis 142:389-398.

Delingat, J., F. Bairlein, and A. Hedenström. 2008. Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in northern wheatears (*Oenanthe oenanthe*). Behavioral Ecology and Sociobiology 62:1069-1078.

Delingat, J., V. Dierschke, H. Schmaljohann, B. Mendel, and F. Bairlein. 2006. Daily stopovers as optimal migration strategy in a long-distance migrating passerine: the northern wheatear *Oenanthe oenanthe*. Ardea 94:593–605.

Dierschke, V., J. Delingat, and H. Schmaljohann. 2003. Time allocation in migrating Northern Wheatears (*Oenanthe oenanthe*) during stopover: is refuelling limited by food availability or metabolically? Journal of Ornithology 144:33–44.

Dierschke, V., and J. Delingat. 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50:535-545.

Dänhardt, J., and Å. Lindström. 2001. Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Animal Behaviour 62:235-243.

Easterling, D. R., T. R. Karl, K. P. Gallo, D. A. Robinson, K. E. Trenberth, and A. Dai. 2000a. Observed climate variability and change of relevance to the biosphere. Journal of Geophysical Research 105:101-114.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000b. Climate extremes: observations, modeling, and impacts. Science 289:2068.

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881-884.

El Zvereva, M. V. K. 2006. Consequences of simultaneous elevation of carbon dioxide and temperature for plant–herbivore interactions: a metaanalysis. Global Change Biology 12:27–41.

Forchhammer, M. C., E. Post, and N. C. Stenseth. 2002. North Atlantic Oscillation timing of long-and short-distance migration. Journal of Animal Ecology 71:1002–1014.

De Frenne, P., J. Brunet, A. Shevtsova, A. Kolb, B. J. Graae, O. Chabrerie, S. A. O. Cousins, G. Decocq, A. De Schrijver, M. Diekmann, R. Gruwez, T. Heinken, M. Hermy, C. Nilsson, S. Stanton, W. Tack, J. Willaert, and K. Verheyen. 2011. Temperature effects on forest herbs assessed by warming and transplant experiments along a latitudinal gradient. Global Change Biology 17:3240–3253.

Gill, J. A., K. Norris, P. M. Potts, T. G. Gunnarsson, P. W. Atkinson, and W. J. Sutherland. 2001. The buffer effect and large-scale population regulation in migratory birds. Nature 412:436-438.

Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. Climate Research 35:37.

Gordo, O., L. Brotons, X. Ferrer, and P. Comas. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? Global Change Biology 11:12–21.

Gwinner, E. 1996. Circannual clocks in avian reproduction and migration. Ibis 138:47–63.

Hagan, J. M., T. L. Lloyd-Evans, and J. L. Atwood. 1991. The relationship between latitude and the timing of spring migration of North American landbirds. Ornis Scandinavica 22:129-136.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. Global Ecology and Biogeography 13:469–471.

Hays, G. C., A. J. Richardson, and C. Robinson. 2005. Climate change and marine plankton. Trends in Ecology and Evolution 20:337-344.

Helmuth, B., J. G. Kingsolver, and E. Carrington. 2005. Biophysics, physiological ecology, and climate change: does mechanism matter? Physiology 67:177-201.

Hüppop, O., and K. Hüppop. 2003. North Atlantic Oscillation and timing of spring migration in birds. Proceedings of the Royal Society B: Biological Sciences 270:233-240.

IPCC. 2007. Summary for policymakers. Page *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate Change 2007: The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge.

Jonzén, N., T. Ergon, A. Linden, and N. C. Stenseth. 2007a. Bird migration and climate: the general picture and beyond. Climate Research 35:177.

Jonzén, N., A. Hedenström, and P. Lundberg. 2007b. Climate change and the optimal arrival of migratory birds. Proceedings of the Royal Society B: Biological Sciences:269-274.

Jonzén, N., A. Linden, T. Ergon, E. Knudsen, J. O. Vik, D. Rubolini, D. Piacentini, C. Brinch, F. Spina, L. Karlsson, M. Stervander, A. Andersson, J. Waldenström, A. Lehikoinen, E. Edvardsen, R. Solvang, and N. C. Stenseth. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. Science 312:1959-1961.

Kneis, P. 1982. Zur verbreitung und bestandsentwicklung, habitatund und nistplatzwahl sowie reproduktion des steinschmatzers *Oenanthe oenanthe* in der DDR: analyse der beringungsdaten 1964 bis 1978. Berichte aus der Vogelwarte Hiddensee 3:55-81.

Kralj, J., and Z. Dolenec. 2008. First arrival dates of the Nightingale (*Luscinia megarhynchos*) to Central Croatia in the early 20th century and at the turn of the 21st century. Central European Journal of Biology 3:295-298.

Leisler, B., G. Heine, and K.-H. Siebenrock. 1983. Patterns of interspecific interactions among wintering Wheatears (*Oenanthe isabellina*, *O. oenanthe*, *O. pleschanka*) and resident Chats in Kenya. Journal of Ornithology 124:393-413.

Low, M., D. Arlt, S. Eggers, and T. Pärt. 2010. Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. Journal of Animal Ecology 79:214–224.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884-1886.

Menzel, A., T. H. Sparks, E. Koch, A. Aasa, R. Ahas, K. Alm-Kübler, P. Bissolli, O. Braslavská, A. Briede, F. Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Defila, A. Donnelly, Y. Filella, K. Jatczak, F. Måge, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová, H. Scheifinger, M. Striz, A. Susnik, A. J. H. Van Vliet, F.-E. Wielgolaski, S. Zach, and A. Zust. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12:1969-1976.

Miles, J. E., J. S. Bale, and I. D. Hodkinson. 1997. Effects of temperature elevation on the population dynamics of the upland heather psyllid *Strophingia ericae* (Curtis) (Homoptera: Psylloidea). Global Change Biology 3:291–297.

Moreau, R. E. 1972. Palaearctic-African bird migration systems. Academic Press, London & New York.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences 105:16195-16200.

Van Noordwijk, A. J., R. H. McCleery, and C. M. Perrins. 1995. Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. Journal of Animal Ecology 64:451-458.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society B: Biological Sciences 271:59-64.

Osieck, E. R., and F. Hustings. 1994. Red List of Threatened and Vulnerable Bird Species in the Netherlands. Technical Report 12. Zeist.

Ottosson, U., B. Y. R. Sandberg, and J. Pettersson. 1990. Orientation cage and release experiments in Scandinavia and Greenland: the importance of visual cues. Ethology 70:57-70.

PECBMS. 2010. Trends of common birds in Europe, 2010 update. European Bird Census Council, Prague.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology and Systematics 37:637-669.

Parmesan, C., T. L. Root, and M. R. Willig. 2000. Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society 81:443-450.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Parrish, J. D. 1997. Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. The Condor 99:681-697.

Pärt, T. 2001a. The effects of territory quality on age-dependent reproductive performance in the northern wheatear (*Oenanthe oenanthe*). Animal Behaviour 62:379-388.

Pärt, T. 2001b. Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. Proceedings of the Royal Society B: Biological Sciences 268:2267-2271.

Pearce-Higgins, J. W., P. Dennis, M. J. Whittingham, and D. W. Yalden. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. Global Change Biology 16:12-23.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Peñuelas, J., I. Filella, and P. E. Comas. 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. Global Change Biology 8:531–544.

Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2369-2375.

Robinson, R., H. Crick, J. Learmonth, I. Maclean, C. Thomas, F. Bairlein, M. Forchhammer, C. Francis, J. Gill, B. Godley, J. Harwood, G. Hays, B. Huntley, A. Hutson, G. Pierce, M. Rehfisch, D. Sims, B. Santos, T. Sparks, D. Stroud, and M. Visser. 2009. Travelling through a warming world: climate change and migratory species. Endangered Species Research 7:87-99.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Schmaljohann, H., and V. Dierschke. 2005. Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*. Journal of Animal Ecology 74:131-138.

Sherry, R. A., X. Zhou, S. Gu, J. A. Arnone, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Luo. 2007. Divergence of reproductive phenology under climate warming. Proceedings of the National Academy of Sciences of the United States of America 104:198-202.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040-2042.

Snow, D. W. 1953. The migration of the Greenland wheatear. Ibis 95:376-378.

Stenseth, N. C., and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: nonlinearity and match–mismatch to the environment. Proceedings of the National Academy of Sciences 99:13379-13381.

Strathdee, A. T., J. S. Bale, W. C. Block, S. J. Coulson, I. D. Hodkinson, and N. R. Webb. 1993. Effects of temperature elevation on a field population of *Acyrthosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen. Oecologia 96:457–465.

Thackeray, S. J., T. H. Sparks, M. Frederiksen, S. Burthe, P. J. Bacon, J. R. Bell, M. S. Botham, T. M. Brereton, P. W. Bright, L. Carvalho, T. Clutton-Brock, A. Dawson, M. Edwards, J. M. Elliott, R. Harrington, D. Johns, I. D. Jones, J. T. Jones, D. I. Leech, D. B. Roy, W. A. Scott, M. Smith, R. J. Smithers, I. J. Winfield, and S. Wanless. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology 16:3304-3313.

Thorup, K., T. E. Ortvad, and J. Ø. Rabøl. 2006. Do Nearctic northern wheatears (*Oenanthe oenanthe leucorhoa*) migrate nonstop to Africa? The Condor 108:446–451.

Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2025-2034.

Veteli, T. O., K. Kuokkanen, R. Julkunen-Tiito, H. Roininen, and J. Tahvanainen. 2002. Effects of elevated CO2 and temperature on plant growth and herbivore defensive chemistry. Global Change Biology 8:1240–1252.

Visser, M. E., L. J. M. Holleman, and P. Gienapp. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164-72.

Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B: Biological Sciences 272:2561-9.

Walther, G.-R., L. Hughes, and P. Vitousek. 2005. Consensus on climate change. Trends in Ecology & Evolution 20:648-649.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Warren, R., J. Price, A. Fischlin, S. Nava Santos, and G. Midgley. 2011. Increasing impacts of climate change upon ecosystems with increasing global mean temperature rise. Climatic Change 106:141-177.

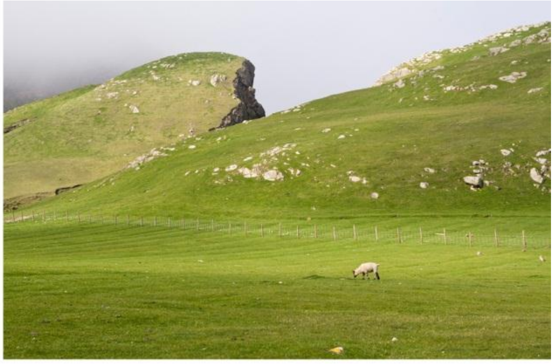
Wernham, C. V., M. P. Toms, J. H. Marchant, J. A. Clark, G. M. Siriwardena, and S. R. Baillie. 2002. The Migration Atlas: movements of the birds of Britain and Ireland. T & A.D. Poyser, London.

White, T. C. R. 2008. The role of food, weather and climate in limiting the abundance of animals. Biological Reviews 83:227-248.

Wilson, J. M., and W. Cresswell. 2010. The Northern Wheatear *Oenanthe oenanthe* in the Sahel of West Africa: distribution, seasonal variation in abundance and habitat associations. Ostrich 81:115-121.

Winder, M., and D. E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology 85:2100-2106.

Wingfield, J. C., J. Patrick Kelley, F. Angelier, O. Chastel, F. Lei, S. E. Lynn, B. Miner, J. E. Davis, D. Li, and G. Wang. 2011. Organism–environment interactions in a changing world: a mechanistic approach. Journal of Ornithology:1-10.



CHAPTER 2. Increased food availability affects body condition across the annual cycle of two subspecies of a long-distance migratory bird, the northern wheatear

ABSTRACT

Long-distance migratory birds depend on foraging resources at widely-spaced locations across the planet. Climate change may affect these resources in spatially and temporally variable ways, which may in turn affect body reserves and migration strategies, with subsequent effects on breeding success and survival. Climate-driven change in food availability is therefore a key mechanism by which climate may affect migratory populations. Food-limitation of migratory birds can occur in both breeding and non-breeding seasons, with carry-over effects between life cycle stages. Here, we test the sensitivity of body mass regulation of long-distance migratory birds to changes in food availability across the annual cycle. We used food-supplementations to simulate experimentally the impact of climate-driven changes in food availability on body mass regulation and migration fuelling strategies across the annual cycle of two subspecies of northern wheatear (*Oenanthe oenanthe oenanthe* and *O. o. leucorhoa*) which exhibit contrasting migration strategies. Food-supplementation led to overall increases in body mass of both subspecies, but the effect of increased food availability on migratory fuelling varied between season, site and subspecies. Fuelling of food-supplemented *O. o. oenanthe* was more extensive in autumn than spring, while the reverse was true in *O. o. leucorhoa*. Departure fuel loads of food-supplemented birds increased with date in *O. o. leucorhoa* leaving a wintering site in West Africa, and in *O. o. oenanthe* leaving a breeding site in northwest Europe. The annual schedules of migratory birds are already known to be organised by endogenous controls that respond to changes in day length and geomagnetic fields. In this study, we show that changes in food availability as may occur under climate change are expected to modify these schedules by affecting the migratory fuelling of wheatears, and that the strength of this impact varies by migration strategy and stage of the annual cycle.

INTRODUCTION

The spatial and temporal heterogeneity of climate change across the planet may limit the ability of long-distance migratory organisms to respond optimally to climate change because they utilise habitats at widely-spaced locations for breeding, wintering and stopping-over on migration (Stenseth and Mysterud 2002, Jones and Cresswell 2010). The environmental conditions at each stage of the annual cycle of migratory organisms may have physiological effects on individuals that carry-over into subsequent stages (Norris et al. 2004, Saino et al. 2004, Brown and Sherry 2006, Saino and Ambrosini 2008, Reudink et al. 2009b). Understanding population changes of migratory taxa therefore demands investigation of all stages of the annual cycle (Marra, Hobson & Holmes 1998; Post et al. 2008), including at the breeding, stopover and wintering areas.

Recent evidence suggests that temperature- and rainfall-linked fluctuations in food supply may be the key mechanism by which climate change affects the biology of migrant songbirds (Both and Visser 2005, Pearce-Higgins et al. 2010, Studds and Marra 2011). Changes in temperature and rainfall affect primary productivity, which in turn affects arthropod abundance and phenology (Bale et al. 2002; Dell, Sparks & Dennis 2005). Impacts of climate on arthropod food supplies are expected to have an important effect on migration strategies and breeding productivity of the primarily insectivorous migrant songbirds. Food supply can alter the birds' body condition, leading to carry-over effects into the subsequent breeding season (Brown & Sherry 2006; Reudink, Marra, et al. 2009; Smith, Reitsma & Marra 2010; Studds & Marra 2005). Furthermore, body condition can affect the timing of departure on migration (Fransson 1998, Brown and Sherry 2006, Stutchbury et al. 2011) and, in turn, the timing of arrival at the breeding or wintering grounds (Brown and Sherry 2006).

Early arrival at breeding grounds can enable an individual to obtain a higher quality territory, leading to improved reproductive success and body condition (Currie et al. 2000, Pärt 2001a, 2001b, Norris et al. 2004). Synchrony of timing of arrival at breeding grounds with the period of highest food availability can also be an important factor (Both and Visser 2001, Both et al. 2006). Timing of arrival at the breeding grounds depends on when birds depart the wintering grounds and on the duration of migration. A long-distance migratory journey typically consists of flight periods interspersed with stopover periods for rest and/or refuelling, with refuelling periods accounting for most of the overall duration of the migratory journey (Newton 2008). The timing of departure from the wintering grounds is controlled mainly by photoperiod and endogenous rhythms (Berthold and Terrill 1991), but also correlates with rainfall and food availability at the wintering areas (Studds and Marra 2011) and with body condition (Stutchbury et al. 2011). For example, female American redstarts (*Setophaga ruticilla*) wintering in high quality habitat have better body condition, depart wintering grounds earlier and fledge more offspring on their breeding grounds than female redstarts that share the same breeding grounds but winter in poorer quality habitat (Norris et al. 2004, Studds and Marra 2007). The decision to leave a stopover location is related to the rate of fat and muscle accumulation (fuel deposition rate) and the size of fuel reserves already accumulated. Birds tend to leave stopover sites early if they have especially high or low levels of fuel deposition rate, or if their fuel reserves become sufficient to make the next stage of their migration route, which may, for example, involve crossing a desert or sea, with no opportunity for refuelling (Dierschke and Delingat 2001, Schaub et al. 2008, Goymann et al. 2010). Fuel deposition rate varies with habitat type, with food availability likely to be the underlying factor (Dierschke, Delingat & Schmaljohann 2003).

Climatic effects on ecological conditions in the non-breeding areas can therefore have effects on performance in the breeding season by affecting migration timing and speed and the acquisition of favourable territories. Similarly, life-history events (e.g. late breeding) and environmental conditions during the breeding season may affect post-breeding body condition, speed of moult (Morton and Morton 1990) and the timing of autumn migration (Jenni-Eiermann and Jenni 1996, Pärt 2001b, Stutchbury et al. 2011), with carry-over effects into the non-breeding season (Linden and Møller 1989, Dawson et al. 2000).

Our central aim was to test the sensitivity of body mass regulation to changes in food availability during breeding, wintering and migration periods. To evaluate the impact of climate change on body mass regulation and migration strategy across the annual cycle, we experimentally manipulated food availability of the northern wheatear (*Oenanthe oenanthe*), a long-distance migratory songbird, to simulate climate-driven changes in food supply. We focused on two subspecies of northern wheatear: *O. o. oenanthe* and *O. o. leucorhoa,* both of which winter in the Sahel region in sub-Saharan Africa but which have contrasting migratory journeys. By focusing on these two closely-related and ecologically similar taxa, we could control for phylogenetic and ecological differences while examining how migration strategy might affect the response of migratory birds to climate change.

O. o. oenanthe has a very large breeding distribution extending from western Europe, through Scandinavia and Russia to Alaska. This subspecies migrates in short flight-stages; the Sahara presenting the largest barrier to be crossed with little opportunity for refuelling. These short flight stages require relatively small fuel reserves to be accumulated before each migration flight (Dierschke and Delingat 2001). In contrast, *O. o. leucorhoa* breeds in eastern Canada, Greenland and Iceland and must therefore cross large expanses of the North Atlantic between its breeding grounds and West Africa, via northwest Europe (Snow 1953). It has even been suggested that *O. o. leucorhoa* flies non-stop from Greenland and Canada to northwest Africa during autumn migration, a journey of over 4,000 km (Thorup, Ortvad & Rabøl 2006). These trans-oceanic flights of *O. o. leucorhoa* require very large fuel reserves to be accumulated prior to departure (Delingat, Bairlein & Hedenström 2008; Thorup et al. 2006). Both subspecies occupy a variety of open habitats, forage for arthropods mainly on the ground and establish territories in both breeding and non-breeding areas, including at stopover sites (Conder 1989, Panov 2005).

In common with most migratory songbirds, northern wheatears appear to follow a strategy of migratory fuelling and flights that minimises the total duration of the migratory journey (Delingat et al. 2006, 2008). This strategy appears to be based on the foraging and weather conditions experienced at fuelling and stopover sites (Dierschke and Delingat 2001, Dierschke et al. 2003). In a related study we showed that food availability affects the breeding productivity of northern wheatears (Chapter 3). We therefore anticipated that wheatears may also be highly sensitive to climate-driven changes in food availability at other stages of the annual cycle. To test this, we used food-supplementation at breeding sites, a stopover location and a wintering area in West Africa, thereby experimentally simulating the effects of climate-driven changes in arthropod food resources across the annual cycle. While climate change may increase food availability at breeding and stopover sites (Strathdee et al. 1993, Miles et al. 1997), the direction of change in food availability in sub-Saharan Africa is unclear (Hulme et al. 2001). If food availability in sub-Saharan Africa declines (e.g. due to drought), wheatears would become even more food-constrained than the control birds in the present study.

We hypothesised that increased food availability would (1) lead to improved body condition of northern wheatears in all stages of the annual cycle; (2) have the greatest impact on body condition in the post-breeding period and autumn migration, when natural arthropod abundance is likely to be most limiting; and (3) have a greater effect on spring departure fuel loads of *O. o. oenanthe* than *O. o. leucorhoa*, because *O. o. leucorhoa* must anyway reach the minimum fuel loads required to perform Atlantic crossings. In addition, amongst food-supplemented individuals of both subspecies, we tested the hypotheses that late birds attempt to accumulate fuel (fat and muscle) at faster rates and departure with greater fuel loads than birds leaving a site earlier. This is because birds departing later are expected to fuel more extensively if foraging resources allow, thus compensating for late departure by carrying higher fuel loads, which will increase potential flight distance and hence overall migration speed, (e.g. Ellegren 1993, Fransson 1998).

MATERIALS AND METHODS

Study locations and stages of the annual cycle

The study was conducted at three locations: (a) a breeding location of *O. o. oenanthe* (Fair Isle, UK) that is also a spring- and autumn stopover location for *O. o. oenanthe* breeding further north and for *O. o. leucorhoa*, (b) a breeding location of *O. o. leucorhoa* (Qeqertarsuaq, Greenland) and (c) a wintering location of both *O. o. oenanthe* and *O. o. leucorhoa* (Parc National des Oiseaux du Djoudj, Senegal, henceforth “PNOD”) (Fig. 2.1). Fair Isle (59°32'N, 1°39'W) is one of the Shetland Islands, off the north coast of Scotland. Qeqertarsuaq (69°15'N, 53°34'W) is an island in Disko Bay off the west coast of Greenland. PNOD (16°10'N, 16°18'W) is in northwest Senegal, close to the Senegal River Delta.

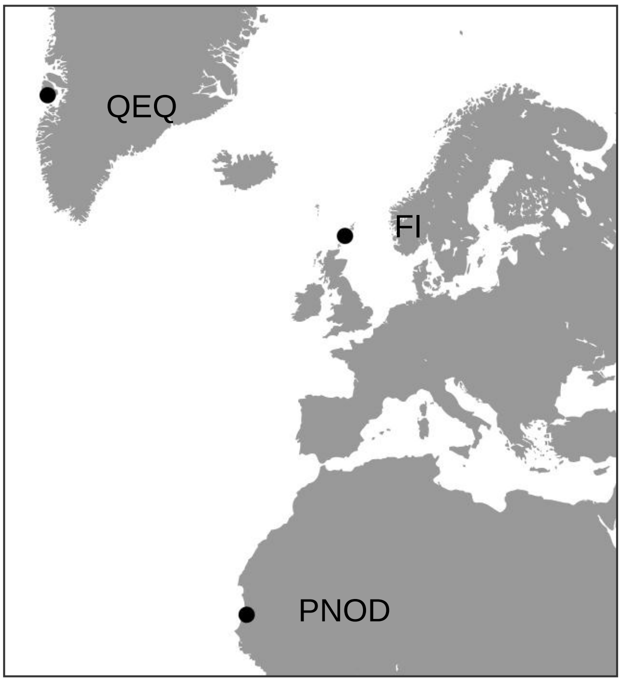


Fig. 2.2. Study sites in Greenland, Europe and Africa. QEQ = Qeqertarsuaq, FI = Fair Isle, PNOD = ‘Parc National des Oiseaux du Djoudj’.

Food supplementation experiments and remote weighing of wheatears (see Food supplementation experiment, below) were used to study the effect of increased food availability on fuel deposition rates and body reserves in all three locations. These experiments were carried-out on wheatears during five stages of the annual cycle (a) wintering and pre-migratory fuelling in PNOD in January–February 2009 and February–April 2010, (b) stopping-over on Fair Isle in April–May and August–September 2008–2009, (c) pre-migratory fuelling on Fair Isle in July–September 2008–2009, (d) pre-migratory fuelling in Qeqertarsuaq in August–September 2010 and (e) breeding on Fair Isle in April–July 2008–2010. We captured and measured additional non-supplemented wheatears in the study areas during 2008–2011, while further non-supplemented wheatears were captured and measured on Fair Isle across the period 1956–2011 by staff of Fair Isle Bird Observatory.

Bird measurements and subspecies identification

Fully-grown wheatears were captured with spring traps (www.moudry.cz, model SB30) baited with mealworms (*Tenebrio molitor*) and, on Fair Isle, additionally with large funnel (Heligoland) traps. Plumage features were used to sex and age captured birds as fledged in the current year (juvenile), in the previous year (young adult), before the previous year (old adult) or fledged before the current year (adult, but unknown if young or old) (Svensson 1992). All adult males, but only a minority of adult females, could be aged with confidence as young or old. All captured birds were measured (wing length: maximum wing chord to 1 mm) and weighed on an electronic balance (to 0.1 g). Flight muscle score was estimated on a four-class scale (0 = emaciated, 3 = large muscle mass) following Kaiser (1993) and fat score was estimated on a nine-class scale (0 = no fat, 8 = fat covering whole ventral area) following Bairlein (1994). Each bird was fitted with a unique combination of three plastic colour rings and a numbered metal ring to enable individual identification in the field. Some nestlings on Fair Isle were colour ringed before fledging and 28 wheatears at Qeqertarsuaq were also fitted with geolocators (weighing 1.2 g) as part of a separate study. Wing length was used to assign birds in PNOD and stopping-over on Fair Isle to subspecies; males with wing length less than 99 mm and females and juveniles with wing length less than 96 mm were classed as *O. o. oenanthe*, while males and juveniles with wing length greater than 102 mm and females with wing length greater than 97 mm were classed as *O. o. leucorhoa* (Svensson 1992). Individuals with intermediate wing-lengths at these locations could not be assigned to subspecies and were excluded from analysis. All wheatears breeding and stopping-over in Qeqertarsuaq were *O. o. leucorhoa*, whereas all wheatears breeding on Fair Isle were *O. o. oenanthe*.

Food supplementation experiment

Prey availability for wheatears was experimentally increased by providing live or dried mealworms (live: Fair Isle, obtained from Live Foods Direct, www.livefoods.co.uk; dried: PNOD and Qeqertarsuaq, obtained from Wild Bird Direct, http://www.wildbirddirect.com) in plastic bowls placed directly on the ground. The bowls were temporarily attached to electronic weighing balances (myweigh.co.uk; model i500), when required, to weigh birds attending them (Fig. 2.2). Small stones were placed in the bowls to weigh them down and larger rocks were positioned around the bowls to reduce the effect of wind on readings from weighing balances (Fig. 2.2). The rocks also encouraged wheatears to investigate the feeding bowls; they frequently make use of such objects as look-out posts (Conder 1989).

Fig. 2.3. Second-year (young) male wheatear (*O. o. leucorhoa*) with colour rings (right leg: dark blue/ metal, left leg: white/white/dark blue) using remote weighing set up in PNOD. The rocks and cattle dung positioned around the balance and bowl of dried mealworms are to reduce the effect of wind on the balance readings. Cardboard is attached to the front of the balance to shade the LCD from the sun, increasing its visibility. The balance reading is 29.8 g.

Dried mealworms were used in Qeqertarsuaq and PNOD because of the logistical difficulties of transporting, importing and maintaining large numbers of live mealworms in these remote locations. Only water had been removed from the dried mealworms; we assumed that there was no difference in the protein and fat content of dried and live mealworms. Water availability affects fuel deposition of blackcaps (*Sylvia atricapilla*) but not lesser whitethroats (*S. curruca*) stopping-over in Israel, the species-specific difference being attributed to contrasting adaptation to arid environments (Sapir et al. 2004). Blackcaps winter in humid forests while lesser whitethroats winter in more arid habitats. As wheatears also winter in arid environments, the results obtained in PNOD and Qeqertarsuaq are unlikely to have been substantially different if live mealworms had been offered, as on Fair Isle.

In all three locations, feeders were put out in areas with the highest relative densities of wheatears. Captures of control birds were made at the same locations. Feeders were in place for breeding pairs and their offspring at (a) Fair Isle from territory establishment in April until autumn departure (August–September) 2008–2010 and (b)

Qeqertarsuaq at the end of the breeding season until autumn departure in 2010. Feeders were positioned for wintering birds at PNOD during the late wintering period (January–February) in 2009 and from the late wintering period until spring departure (February–April) in 2010. Feeders for wheatears on migration stopover were put out on Fair Isle in spring (April–May) and autumn (August–September) 2008-2009.

Feeders intended for breeding pairs on Fair Isle were filled with at least 200 mealworms (mean weight ± SD of mealworms = 0.112 ± 0.026 g, n = 100, Thomas 1997). These feeders were refilled on at least five of every seven days, until the departure on autumn migration of all of the breeding birds and their offspring that were using the feeders (which begins in August, latest departures occurring in early September, this study). A standard route through the study site on Fair Isle was walked almost daily from mid-April until the end of May, and pairs of wheatears (determined by behavioural signs of territory establishment and pair bonding, Conder 1989) were selected alternately as fed and control (i.e. unfed) pairs. Thus, fed and control pairs were stratified both spatially and with respect to arrival date. Additional feeders for stopover migrants were positioned in locations on Fair Isle where stopover wheatears were observed. These feeders were filled with a minimum of 200 mealworms and topped up at least twice every day until departure of any wheatears using them. Feeders in PNOD and Qeqertarsuaq were put out in areas where wheatears were observed, filled with at least 200 dried mealworms (each weighing a mean of 0.0357 g) and topped up twice every day. In all three locations, feeders with higher depletion rates were filled with greater numbers of mealworms.

Feeding bowls offered to wheatears breeding on Fair Isle were covered with metal wire mesh cages to prevent the mealworms being taken by European starlings

(*Sturnus vulgaris*). These cages permitted wheatears to enter through a small hole cut at the bottom of the wire mesh (lined with strong insulating tape to prevent injury) or via a hinged weighted walkway that swung shut when starlings (approximately three to four times heavier than wheatears) attempted to enter, swinging back open again when they stepped off the platform. No cages were used on feeders in Qeqertarsuaq, PNOD or feeders for stopover wheatears on Fair Isle (when starlings were not feeding chicks and therefore mealworm-depletion rates by starlings were low). Other species did occasionally attend these feeders, but mealworms were always available for wheatears using them.

Remote-measurement of body mass

We monitored the body masses of wheatears visiting feeders at the same times of day within each study site, to enable daily body mass regulation to be studied at each location. We temporarily attached the food bowls to electronic weighing balances (My Weigh iBalance 500, My Weigh, http://myweigh.com) (Fig. 2.2) and used small video cameras (Sony Handycam DCR-SR32, Sony Corporation, http://sony.co.uk) to record the weights (to 0.1 g) of wheatears visiting the feeders. Most individuals using feeders were captured and colour-ringed for identification. Some wheatears using feeders that were not colour-ringed could be identified on the videos with a combination of some of the following characteristics: presence/absence of metal ring, sex, age, plumage differences and large individual differences in body mass (> 2 g). 1.2 g was subtracted from the weights of any wheatears that were carrying geolocators (n = 3 individuals) at Qeqertarsuaq prior to analysis. Weights of wheatears that could not be confidently identified to individual level were excluded from the analyses.

Fuel deposition rate and departure fuel load

Fuel deposition rate and body reserves were calculated for the fed wheatears that used the remote weighing set up described above. Only birds that could be categorised as either *O. o. oenanthe* or *O. o. leucorhoa* by wing length were included in this analysis. To control for the relatively large size differences between the two subspecies, we modelled fuel deposition rate and body reserves based on lean body mass. To calculate fuel deposition rate and body reserves, we first calculated for each individual bird as follows. Fully-grown wheatears (including both fed and control individuals, but excluding breeding females in May on Fair Isle, birds in moult and birds with juvenile plumage) captured between 2007 and 2010 at Fair Isle, PNOD and Qeqertarsuaq were used in the calculation of lean body mass. Lean birds were selected from this dataset, defined as birds with muscle score < 2 and fat score < 2. From this group, a subset of lean birds with mass below the 50 % quartile at each wing length was selected using quantile regression to ensure that individuals developing eggs or in moult (and not noted at the time of capture) did not elevate the estimate. We followed Schmaljohann et al. (2011), regressing body mass (g) of birds in this lean subset on wing length (mm), providing the following equations to (1) calculate lean body mass for wheatears of a given wing length (Fig. S2.1), (2) body reserves and (3) daily fuel deposition rate:

$$\text{lean body mass [g]} = 0.182 \times \text{wing length [mm]} + 4.445 \qquad (1)$$

$$\text{body reserves} = (\text{body mass [g]} - \text{lean body mass [g]}) / \text{lean body mass [g]} \qquad (2)$$

$$\text{daily fuel deposition rate} = (\text{body mass change [g] between first and last day} / \text{days between measurements}) / \text{lean body mass [g]} \qquad (3)$$

As there was variation in the times that particular individuals visited feeders and were weighed, we interpolated body masses for standardised times of day. Daily mass change was modelled using Generalised Additive Models (GAM) with three knots, fitted using the mgcv package (Wood 2008) within R (version 2.10.1, R Development Core Team 2009) to the available data points on each day (using only days with ≥ 3 weight measurements) for each individual. These fitted body mass trajectories were then used to interpolate weights for each hour between 08:00 and 19:00 (except 12:00 and 13:00). This gave a set of predicted weights at different times for each day that an individual was weighed. For each individual, one of these times was used for the calculation of daily fuel deposition rate, by selecting the time that gave the greatest span of days between first and last day, choosing the latest dates and latest times for any ties, as these were likely to be closer to the departure fuel load. For example, if weights for an individual were available at 14:00 over the period 10–15 August, and 17:00 over the period 11–16 August (both 5 day periods), 17:00 was chosen to calculate daily fuel deposition rate for that individual. A similar approach has been used in other studies of fuel accumulation (Fransson 1998, Bayly 2006, Delingat et al. 2008). Daily fuel deposition rate was calculated over a period of a maximum of 7 days (to ensure that only birds actively fuelling were included) ending on the day of departure (wheatears depart on migration at night). Box plots of daily fuel deposition rate on time of day revealed no systematic difference between times of day. Departure fuel load was the last recorded measurement of body reserves for each individual that was not subsequently observed at the location.

Flight range estimates

The amount of fuel carried by migrating birds, in combination with weather conditions, determines how far they can fly without stopping, and therefore whether barriers such as expanses of ocean can be crossed. In addition, depending on rates of fuel accumulation, birds might be able to increase overall migration speed by carrying larger fuel loads, thereby reducing the number of required stopovers (Alerstam and Lindström 1990). Maximum fuelling is rarely optimal, however, due to the rising energy costs with fuel load (Lindström and Alerstam 1992). To estimate the potential flight range (Y km) of wheatears with different departure fuel load, we used the equation developed by Delingat et al. (2008), where U is the average airspeed of a northern wheatear (47 km h^{-1}, Bruderer & Boldt 2008): $Y = 100 * U * \ln(1 + \text{departure fuel load})$. As this equation is based on observed (i.e. empirically measured) rates of mass loss in wheatears, it is considered to be more robust than calculations based on aerodynamic theory, which make a large number of assumptions (Schmaljohann et al. 2011). The flight range equation refers to distance in relation to the surrounding air; thus tail winds or head winds will modify the potential flight range (Delingat et al. 2008). Likely destinations and flight paths of departing wheatears were inferred from the literature (Snow 1953, Cramp 1988, Dierschke and Delingat 2001). We used Google Earth (Google, Mountain View, USA) to measure approximate distances from the study locations to likely stopover areas and distances across major barriers (e.g. sea and desert).

Data analysis

In each location, our samples consisted of wheatears that were food-supplemented (“fed”) and wheatears that were not using feeders (“control”). In our analyses, experimental treatment (fed or control) is referred to as “treatment”. Fed birds were weighed multiple times by remote weighing at feeding stations, whereas control birds were only weighed when they were captured – often only once. To account for this difference in sampling effort between treatment groups, we randomly selected one weight per individual wheatear from each stage of the annual cycle in which they were measured. This reduced dataset was then used in our analyses of the effects of treatment on body reserves. Stage of the annual cycle was treated as a factor in analyses and referred to as "stage". To consider the hypothesis that body reserves vary over time within each stage, we created a variable "stage-specific day", where 1 = the first day within each stage.

Based on the hatching dates that we recorded on Fair Isle during 2008–2010, all females had finished laying eggs of first clutches before the end of May. We excluded all weights of females recorded in April and May on Fair Isle due to the potentially confounding effects of different stages of egg development on comparisons of body mass between fed and control birds. Four females had second broods over the course of the study; weights of these individuals measured in the two weeks preceding and during egg-laying were also excluded.

Examining the effect of food supplementation on body reserves of wheatears stopping over on Fair Isle in spring was not possible, because in the spring dataset there were no food-supplemented *O. o. oenanthe* (with wing lengths below the overlap range of *O. o. oenanthe* and *O. o. leucorhoa*) for comparison with control *O. o. oenanthe*, and only two food supplemented *O. o. leucorhoa*. Sample sizes of fed and control *O. o. oenanthe* in the remaining stages of the annual cycle were: wintering at PNOD – 7 fed, 6 control; breeding on Fair Isle – 51 fed, 172 control; autumn migration on Fair Isle – 62 fed, 423 control. Sample sizes of fed and control *O. o. leucorhoa* in the remaining stages of the annual cycle were: wintering at PNOD – 11 fed, 9 control; autumn migration at Qeqertarsuaq – 10 fed, 117 control; autumn migration (stopover) on Fair Isle – 14 fed, 183 control.

We fitted a series of models using R to investigate (1) the effects of treatment on body reserves across the annual cycle and (2) variation in fuel deposition rate and departure fuel load between subspecies and stages of the annual cycle. We fitted linear models for the analyses of body reserves across the annual cycle and departure fuel load. We fitted variance models in the analysis of fuel deposition rate, using maximum likelihood and generalised least squares within the R nlme package (gls: Pinheiro et al. 2011), because of a large difference in the variance of fuel deposition rate between subspecies. Datasets were reduced so that there were no missing data for any of the factors in full models, to enable direct comparisons between models. The explanatory variables we included in our analyses are described in Table 2.1 and Table 2.3.

The performance of competing models was compared using Akaike's Information Criterion, corrected for small sample size (AICc; Burnham & Anderson 2002). Decreasing values of AICc indicate better statistical fits. Two statistics were obtained for each model: $\Delta AICc_i$ (the difference in AICc between model *i* and the best model) and $wAICc_i$ (Akaike weight), which indicates the likelihood that each model is the best approximation relative to all the other models in the model set. The models were ranked by $\Delta AICc_i$ and the most plausible models were defined as those with $\Delta AICc_i \leq 2$, following Burnham and Anderson (2002). Model averaging was carried out to derive parameter estimates and confidence intervals, based on the AICc weight ($AICc_{wi}$) of each model *i* (Burnham and Anderson 2002). $AICc_{wi}$ determines the contribution of each parameter estimate within model *i* to the average of that parameter across all considered models.

RESULTS

Effects of food supplementation on body reserves across the annual cycle

To determine the effect of food supplementation on body reserves, we analysed the two subspecies separately because we did not perform the experiment during the *O. o. leucorhoa* breeding season.

O. o. oenanthe

There was one plausible model (ΔAICc ≤ 2) of body reserves (body mass above lean body mass as a proportion of body mass) of *O. o. oenanthe* (Model 1, Table 2.1). This model indicated that the effect of supplemental food on body reserves varied between the different stages of the annual cycle and also varied by stage-specific day. Body reserves were higher in fed than control *O. o. oenanthe* at the wintering grounds in PNOD and at the end of the breeding season on Fair Isle, during the pre-migratory phase from July to early September (Table 2.2, Fig. 2.3a, 2.3e). There was, however, no effect of supplemental food on body reserves of *O. o. oenanthe* during the breeding period on Fair Isle (April–June) (Table 2.2, Fig. 2.3c).

Table 2.1. Linear models fit to body reserves of *O. o. oenanthe* and *O. o. leucorhoa* wheatears across the annual cycle. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model i and the best model and $wAICc_i$ is the Akaike weight. Plausible models are considered to be those with $\Delta AICci \leq 2$. Interactions are indicated by x and include all lower order fixed term effects.

Model ID	Dependent variable	Subspecies	Fixed effects	df	$\Delta AICc_i$	$wAICc_i$
1	Body reserves	*O. o. oenanthe*	trt x stage, day	8	0	1
2			trt x stage	7	20.3	< 0.001
3			trt, stage	5	136.5	< 0.001
4			trt	3	151.2	< 0.001
5			stage, day	5	258.3	< 0.001
6			none	2	279.4	< 0.001
7			stage	4	280.3	< 0.001
8	Body reserves	*O. o. leucorhoa*	trt x stage, day	8	0	0.975
9			trt , stage	7	7.9	0.018
10			trt x stage	5	10.2	0.006
11			stage, day	3	14.3	< 0.001
12			stage	2	59.6	< 0.001
13			trt	5	60.3	< 0.001
14			none	4	61.9	< 0.001

Body reserves: % of body mass above lean body mass.
Fixed effects. trt: treatment (fed or control), stage: wintering (PNOD: both *oenanthe* and *leucorhoa*), spring stopover (Fair Isle: *leucorhoa* only), breeding (Fair Isle: *oenanthe* only), start of autumn migration (Fair Isle: *oenanthe*; Qeqertarsuaq: *leucorhoa*), autumn stopver (Fair Isle: *leucorhoa* only), day: stage-specific day, none: intercept-only model.

Table 2.2. Model-averaged parameter estimates (estimates of fixed effects included in models explaining body reserves, with $\Delta AICc_i \leq 2$ with contributions to average weighted by $wAICc_i$ of model *i*), unconditional standard errors and 95% confidence intervals (Burnham & Anderson, 2002). Interactions are indicated by x.

Dependent variable	Subspecies	Fixed effect	Estimate	SE	95% CI	
					Lower	Upper
Body reserves	*O. o. oenanthe*	trt	8.19	4.93	-1.49	17.86
		$stage_{breeding}$	6.72	3.69	-0.51	13.96
		$stage_{Autumn}$	8.23	3.68	1.02	15.44
		trt x $stage_{breeding}$	-6.99	5.14	-17.06	3.07
		trt x $stage_{Autumn}$	13.37	5.08	3.42	23.33
		day	0.06	0.02	0.03	0.09
Body reserves	*O. o. leucorhoa*	trt	30.34	6.39	17.83	42.87
		$stage_{Autumn}$	14.18	4.89	4.60	23.76
		$stage_{AutumnStop}$	15.00	4.93	5.33	24.67
		trt x $stage_{Autumn}$	-19.47	7.92	-34.99	-3.94
		trt x $stage_{AutumnStop}$	-4.13	7.47	-18.76	10.51
		day	-0.20	0.06	-0.32	-0.08

Body reserves: % of body mass above lean body mass.
Fixed effects. trt: treatment (fed vs. control), $stage_{breeding}$: breeding (May and June on Fair Isle) vs. wintering (PNOD) (*oenanthe* only), $stage_{SpringStop}$: spring stopover (Fair Isle) vs. wintering (PNOD) (*leucorhoa* only), $stage_{Autumn}$: start of autumn migration (Fair Isle: *oenanthe*; Qeqertarsuaq: *leucorhoa*) vs. wintering (PNOD), $stage_{AutumnStop}$: autumn stopover (Fair Isle) vs. wintering (PNOD), day: stage-specific day.

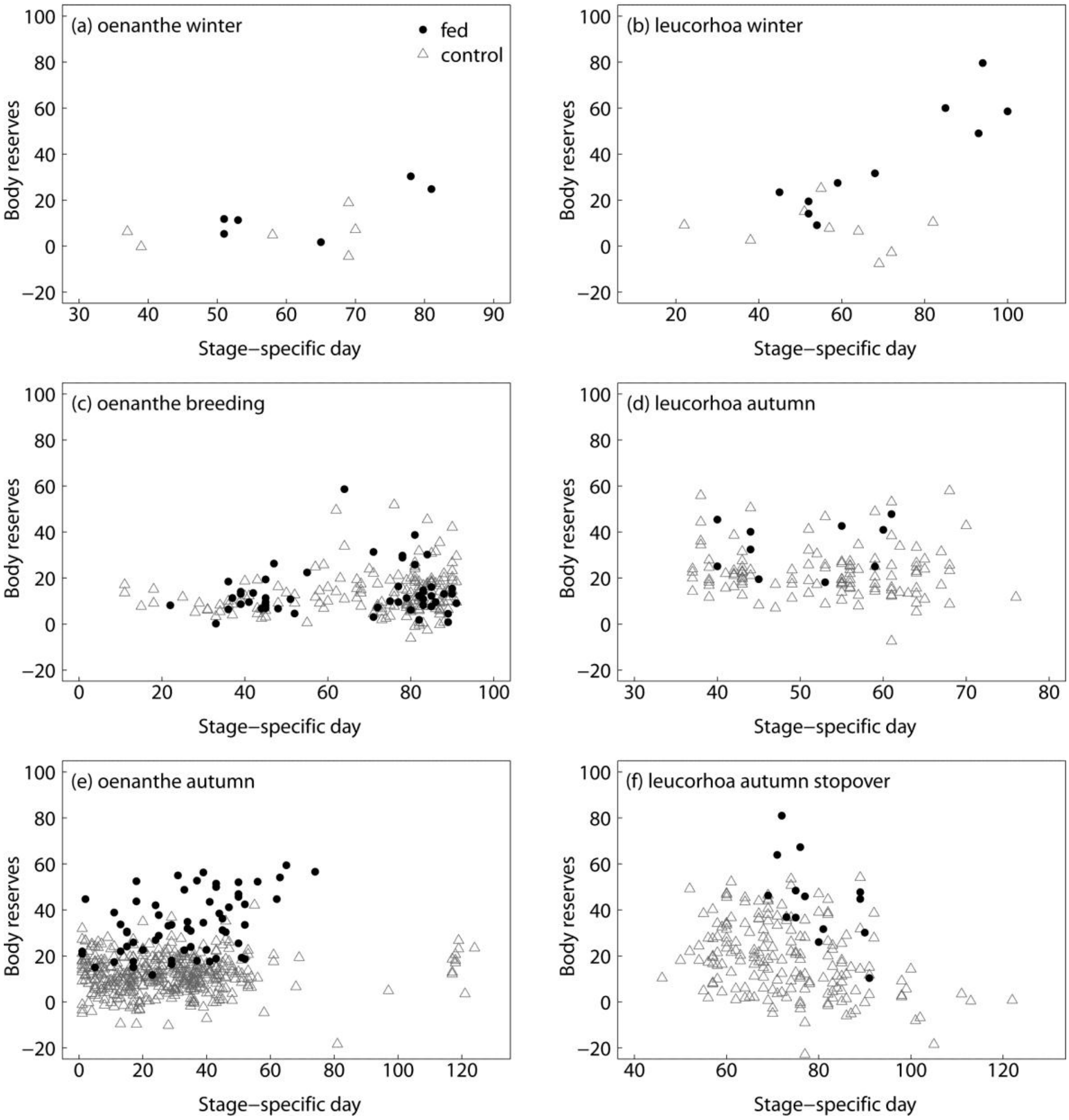


Fig. 2.4. Body reserves (% of lean body mass above lean body mass) of food-supplemented and control northern wheatears at different stages of the annual cycle. (a) *O. o. oenanthe* during late winter at PNOD, (b) *O. o. leucorhoa* during late winter at PNOD, (c) *O. o. oenanthe* breeding on Fair Isle, (d) *O. o. leucorhoa* in the autumn at Qeqertarsuaq, (e) *O. o. oenanthe* in the autumn on Fair Isle and (f) *O. o. leucorhoa* during stopover on Fair Isle.

O. o. leucorhoa

There was one plausible model of body reserves of *O. o. leucorhoa* (Model 8, Table 2.1). This model indicated that the effect of supplemental food on body reserves varied between the different stages of the annual cycle and also varied by stage-specific day. Fed *O. o. leucorhoa* had higher body reserves than control *O. o. leucorhoa* at all stages of the annual cycle that were measured (Table 2.2, Fig. 2.3b, d, f). The effect of food-supplementation on body reserves was greatest during fuelling for spring migration at PNOD (Table 2.2, Fig. 2.3b). Control *O. o. leucorhoa* at Qeqertarsuaq also had lower body reserves than control birds recorded in autumn stopover on Fair Isle, but higher body reserves than control birds recorded at PNOD at the beginning of spring migration. Large body reserves were attained by fed *O. o. leucorhoa* leaving PNOD at the beginning of spring migration and by those stopping over on Fair Isle in the autumn. Body reserves of fed *O. o. leucorhoa* were lower among birds preparing to leave Qeqertarsuaq at the end of the breeding season.

Effects of stage, subspecies and date on fuel deposition rate

There was one plausible model of fuel deposition rate (Table 2.3, Model 15; see Table S2.1 for the full set of candidate models). Fuel deposition rate was higher in *O. o. leucorhoa* than *O. o. oenanthe* (Table 2.4, Fig. 2.4a, c). Fuel deposition rate of *O. o. leucorhoa* during pre-migratory fuelling was lower in the autumn at Qeqertarsuaq than at the start of spring at PNOD (Table 2.4, Fig. 2.4a, b). Fuel deposition rate was similar between autumn migration on Fair Isle and the start of spring migration at PNOD (Table 2.4, Fig. 2.4a, c). The positive parameter estimate for stage-specific day indicated that wheatears fuelling later during a particular stage did so at a faster rate than wheatears fuelling earlier, although this was observed only in *O. o. leucorhoa* at PNOD in spring and, to a lesser extent, *O. o. oenanthe* at Fair Isle in the autumn (Table 2.4, Fig. 2.4a, c).

Table 2.3. Plausible models ($\Delta AICc_i \leq 2$) fit to daily fuel deposition rates (FDR) (generalised least squares models), departure fuel loads (linear models) and departure dates (linear models) of *O. o. oenanthe* and *O. o. leucorhoa* across the annual cycle. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model *i* and the best model and $wAICc_i$ is the Akaike weight. Interactions are indicated by x and include all lower order fixed term effects. Full candidate model sets are presented in Tables S1–S3.

Model ID	Dependent variable	Fixed effects	Random effects	df	$\Delta AICc_i$	$wAICc_i$
15	Daily FDR	stage, subsp, day	SD (subsp)	7	0	1.000
23	DFL	subsp x stage, day	-	6	0	0.456
24		subsp x stage, stage x day	-	7	2.0	0.165
41	Departure date (*O. o. oenanthe* on Fair Isle only)	age, HD	-	4	0	0.751

Daily FDR: Fuel deposition rate (% of body mass above lean body mass gained or lost per 24 h). DFL: Last recorded fuel load (% of body mass above lean body mass) before departure. Departure date: last recorded date on Fair Isle at start of autumn migration (*O. o. oenanthe* only).
Fixed effects. subsp: *O. o. oenanthe* vs. *O. o. leucorhoa*, stage (Daily FDR): spring departure from winter grounds vs. autumn departure from breeding grounds, stage (DFL): start of spring migration at PNOD, start of autumn migration at Qeqertarsuaq, autumn migration at Fair Isle (start and stopover), day: stage-specific day, where 1 = day that first bird departed during that stage, age: adult or juvenile, HD: hatch date (juveniles) or hatch date of last brood in that year (adults).
Random effects. SD (subsp): Standard deviation of effect of subspecies on daily FDR, to account for the large difference in variation between the two subspecies.

Table 2.4. Model-averaged parameter estimates (estimates of fixed effects included in models with $\Delta AICc_i \leq 2$ with contributions to average weighted by $wAICc_i$ of model *i*), unconditional standard errors and 95% confidence intervals (Burnham & Anderson, 2002) for daily fuel deposition rates (FDR), departure fuel loads (DFL) and departure dates across the annual cycle. Interactions are indicated by x.

Dependent variable	Fixed effect	Estimate	SE	95% CI	
				Lower	Upper
Daily FDR	$stage_{autumn.qeqe}$	-5.890	2.620	-11.030	-0.741
	$stage_{autumn.fair}$	0.464	1.070	-1.638	2.567
	$subsp_{oen}$	-6.370	1.580	-9.471	-3.277
	day	0.047	0.025	-0.002	0.095
DFL	$subsp_{oen}$ x $stage_{autumn.fair}$	23.296	9.879	3.932	42.659
	day	0.891	0.154	0.591	1.192
	$stage_{autumn.fair}$ x day	0.375	0.589	-0.781	1.530
Departure date (*O. o. oenanthe* on Fair Isle only)	age_{juv}	-10.680	3.155	-16.864	-4.496
	HD	0.573	0.165	0.250	0.896

Daily FDR: Fuel deposition rate (% of body mass above lean body mass gained or lost per 24 h). DFL: Last recorded fuel load (% of body mass above lean body mass) before departure. Departure date: last recorded date on Fair Isle at start of autumn migration (*O. o. oenanthe* only).

Fixed effects. $stage_i$: location-specific stage of migration relative to start of spring migration at PNOD ($stage_{autumn.qeqe}$: start of autumn migration at Qeqertarsuaq, $stage_{autumn.fair}$: autumn migration at Fair Isle (start and stopover)), day (daily FDR): stage-specific day, $subsp_{oen}$: *O. o. oenanthe* vs. *O. o. leucorhoa*, day (DFL): stage-specific day, where 1 = day that first bird departed during that stage, age_{juv}: juveniles vs. adults, HD: hatch date (juveniles) or hatch date of last brood in that year (adults).

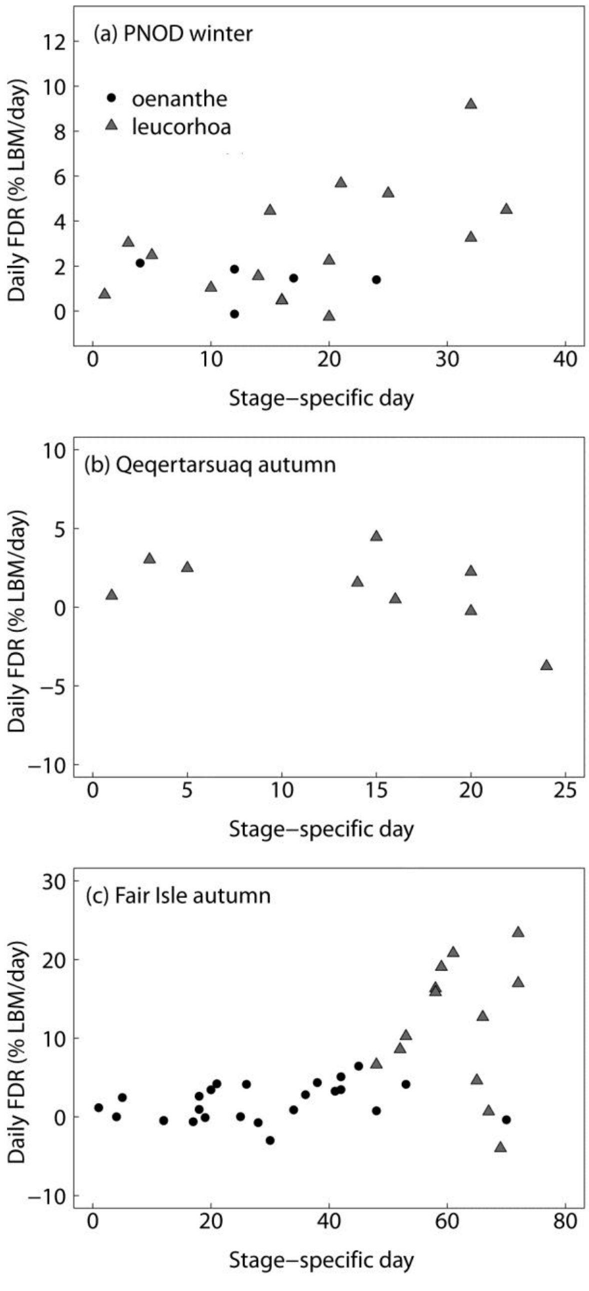


Fig. 2.5. Daily fuel deposition rates (% of lean body mass accumulated per 24 h) of food-supplemented northern wheatears during migratory fuelling at (a) PNOD (winter), (b) Qeqertarsuaq (autumn) and (c) Fair Isle (autumn).

Effects of stage, subspecies and date on departure fuel loads

Two models of departure fuel load were identified as plausible by AIC model selection from the candidate set of 19 models (Models 23–24, Table 2.3; see Table S2.2 for the full set of candidate models). The subspecies x stage interaction term was included in both plausible models because departure fuel loads of *O. o. oenanthe* were significantly higher in the autumn than at the start of spring migration, while departure fuel loads were marginally higher in spring than autumn for *O. o. leucorhoa* (Table 2.4, Fig. 2.5). Departure fuel loads of *O. o. leucorhoa* were also higher than *O. o. oenanthe* in the spring, with no sub-specific difference in the autumn (Fig. 2.5). Stage-specific day was included in the top model, indicating that departure fuel loads increased with date, during both spring and autumn migration (Table 2.4, Fig. 2.5). The interaction term stage x stage-specific day was also included in the second-best model, but the standard error for this effect was larger than the effect size, and the confidence intervals greatly overlapped zero, precluding meaningful interpretation (Table 2.4).

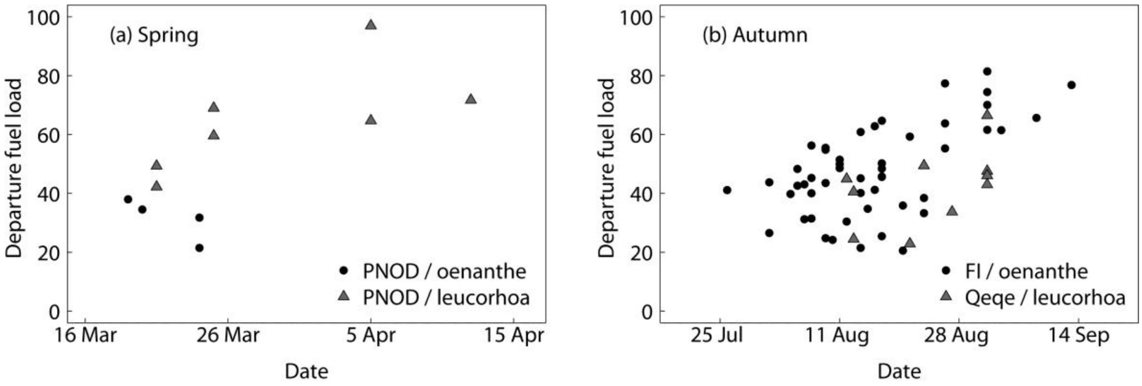


Fig. 2.6. Departure fuel loads (% of lean body mass above lean body mass) of food-supplemented northern wheatears leaving (a) a wintering site (PNOD) and (b) breeding sites (*O. o. leucorhoa*: Qeqertarsuaq, *O. o. oenanthe*: Fair Isle).

There was only one plausible model of departure date of *O. o. oenanthe* (Model 41, Table 2.3). Juveniles departed significantly earlier than adults (Table 2.4). Departure date was positively correlated with hatch date, confirming that late-breeding wheatears depart breeding grounds later than earlier breeding wheatears (Table 2.4). The slope of the effect of hatch date on departure date was significantly less than 1, indicating that birds with later hatch dates depart on migration sooner after fledging (for juveniles) or breeding (for adults) than birds with earlier hatch dates (Table 2.4).

Flight range estimates

Flight ranges were only estimated for food-supplemented wheatears. This was because we were able to measure body masses of food-supplemented wheatears attending feeding stations until very close to the time of departure (assumed to have occurred during the night following the last recorded visit of individual birds), thus allowing us to estimate departure fuel loads. It was not possible to monitor weights of control wheatears until departure. The mean estimated flight range of four *O. o. oenanthe* departing on spring migration from PNOD was 1,346 km (range 913–1,514 km). The mean body reserves were probably just sufficient to cross the Sahara (c. 1,200 km). The smallest body reserves were not sufficient to cross the Sahara without a tail wind, which occur rarely in spring in northwest Africa (predominant wind direction in March/April is from NNW, source: http://windfinder.com). The mean estimated flight range of seven *O. o. leucorhoa* departing PNOD is 2,325 km (range 1,655–3,186 km), sufficient to reach the northern coast of Africa. The lowest range of 1,655 km is enough to cross the Sahara without refuelling, while the birds with the highest body reserves could reach Iberia. The estimated flight ranges of three *O. o. leucorhoa* stopping over on Fair Isle in spring were 830, 2,786 and 3,783 km. The lightest bird could have reached Iceland, while the two heavier birds could have reached the western coast of Greenland and Baffin Island (Canada), respectively.

The mean estimated flight range of ten *O. o. leucorhoa* departing Qeqertarsuaq in autumn was 1,628 km (range 969–2,395 km). None of these birds could fly further than Iceland with these body reserves without wind assistance, while the lightest body reserves were enough to reach the southern coast of Greenland, but not Iceland. The mean estimated flight range of 49 *O. o. oenanthe* departing Fair Isle in the autumn was

1,807 km (range 879 – 2,800 km), enough to reach Morocco. Further refuelling would then be required to make the crossing of the Sahara to the wintering grounds. The lightest body reserves would enable a flight only as far as S England, while the largest body reserves would be enough to reach the northern edge of the Sahara with reserves remaining, but not to cross it. Thirteen *O. o. leucorhoa* departing Fair Isle in the autumn were estimated to have a mean flight range of 2,310 km (range 1,577–3,037 km). The lightest body reserves are enough to reach Iberia, the mean enough to reach Morocco, while the heaviest body reserves could power a flight to the Sahara, but would probably not be enough to cross it.

DISCUSSION

In this study, we show how climate-driven changes in arthropod availability are likely to affect body mass regulation of two subspecies of a long-distance migratory songbird, the northern wheatear. Our findings that fed wheatears had greater body reserves than control wheatears during spring and autumn pre-migratory periods and autumn stopover provides evidence that food is currently limiting migratory fuelling of wheatears across the annual cycle. Changes in food availability caused by climate change are therefore likely to affect the rate and extent of fuel accumulation of wheatears preparing for migration, both in spring and autumn.

Food availability and body reserves across the annual cycle

There were very large differences between the body reserves of fed and control *O. o. oenanthe*, both in the autumn on Fair Isle and *O. o. leucorhoa* at PNOD. Birds leaving the breeding or wintering grounds with larger body reserves will be able to fly further without needing to stop to replenish fuel reserves. This could speed up the whole migratory journey by reducing the time required for refuelling at stopover sites (Alerstam and Lindström 1990). Control wheatears appeared to accumulate only modest fuel stores, consistent with a strategy of short flights with frequent stopover for refuelling, as has previously been observed in *O. o. oenanthe* under natural foraging conditions (Delingat et al. 2006). An increase in departure fuel loads of wheatears with supplemental feeding has been shown previously for birds leaving Iceland and Scotland (Delingat et al. 2008). The present study shows additionally that an increase in food availability increases fuel loads of wheatears at the onset of migration from sub-Saharan Africa. Our results suggest, however, that increased food availability has little impact on fuel deposition of *O. o. leucorhoa* departing Greenland. The food-supplementation experiments on *O. o. leucorhoa* were conducted at the beginning of their autumn migration in western Greenland and it is possible that wheatears only fuel enough to reach southern or eastern Greenland, where more extensive fuelling occurs for the Atlantic crossing. Alternatively, wheatears in western Greenland may be less food-limited than those on Fair Isle or PNOD, such that non-supplemented western Greenland birds were able to source just as much food as supplementary fed birds.

In contrast to the results during periods of fuelling for migration, there was no effect of food supplementation on body masses of *O. o. oenanthe* during the main breeding period (April–June), suggesting that body mass regulation of breeding wheatears is not currently limited by food availability. These results are consistent with our finding that food supplementation has little effect on success rates of first broods of *O. o. oenanthe* on Fair Isle (Chapter 3). Changes in food availability during the breeding season, at least when first broods are reared, are therefore unlikely to have significant impacts on the body condition of breeding adult wheatears on Fair Isle. We did, however, find that chicks of food-supplemented parents were larger in one out of two years (Chapter 3). This finding, together with the results in the present study, suggests that breeding wheatears may be more likely to allocate extra food resources into breeding attempts rather than their own body mass.

The extent to which increased food availability results in earlier arrival at the destination was found to depend on the relationship between food availability, departure date and speed of migration. Results of previous studies show no consistent pattern, with favourable ecological conditions in sub-Saharan Africa reported to result in both advances (Saino et al., 2004) and delays (Tøttrup et al. 2008) of spring passage of migrants through North Africa. Delayed passage across the Sahara has been attributed to delayed departure from wintering grounds (Tøttrup et al. 2008). This could represent a phenotypic response by birds taking advantage of improved food availability to fuel more extensively than in poorer years. By carrying a larger fuel load, migratory birds can speed up the duration of migration by reducing the number of stopovers. A recent study tracking individual wood thrushes (*Hylocichla mustelina*) with light-level geolocators showed that improved body condition resulted in earlier autumn departure but that this did not result in earlier arrival in the tropical wintering sites because of substantial variation in stopover duration (Stutchbury et al. 2011). Several pairs of fed *O. o. oenanthe* raised second broods (Chapter 3), resulting in delayed post-breeding departure. The data on breeding and departure dates of fed birds on Fair Isle indicated, however, that birds compensated for late breeding to some extent by departing sooner after the final breeding attempt. This would be likely to involve faster moult (Morton and Morton 1990), while daily rates of fuel deposition were greater in later-departing birds. Departure fuel loads increased with date in fed *O. o. oenanthe* in the autumn on

Fair Isle and in fed *O. o. leucorhoa* in the winter at PNOD. Direct comparisons between departure fuel loads of fed and control wheatears are not possible as the weights of control wheatears at departure are not known. The lack of correlation between date and body reserves during pre-migratory fuelling periods of control *O. o. oenanthe* in the autumn or control *O. o. leucorhoa* in the winter suggests, however, that late-departing control wheatears did not fuel any more extensively than control wheatears departing earlier. This contrast between fed and control wheatears suggests a possible constraint on the optimal fuelling of late wheatears under current natural conditions, which could be exacerbated if climate change causes late-breeding-season food availability to decline below current levels. Temperature manipulations of upland turf support the prediction of a shorter peak of soil arthropod emergence under warmed conditions, resulting in lower abundance late in the breeding season (Chapter 5). Remote monitoring of wheatear presence/absence (e.g. using radio tracking) would enable the departure timing of food-supplemented and control wheatears to be compared. It is possible that food-supplemented wheatears are able to reach a preferred departure fuel load faster, and depart breeding grounds earlier.

In American redstarts (*Setophaga ruticilla*), spring departure date from Jamaica is related to body mass, which in turn is influenced by winter rainfall (Studds and Marra 2011). The mechanism linking rainfall to body mass appears to be change in food availability, as departure date was negatively correlated with arthropod biomass in the winter habitat. Fuelling rates of northern waterthrushes (*Seiurus noveboracensis*) also vary with winter habitat quality, associated with delayed departure of birds in lower quality habitats (Smith et al. 2010). American redstarts and black-tailed godwits (*Limosa limosa*) that wintered in high quality habitats arrived back at the breeding grounds earlier (Gill et al. 2001, Reudink et al. 2009a), while rainfall in the wintering grounds also affects arrival times of several trans-Saharan migratory bird species (Gordo et al. 2005). Early arrival is associated with higher reproductive success in American redstarts (Marra et al. 1998) and many other species (Lack 1968; Lozano, Perreault & Lemon 1996; Perrins 1970), including northern wheatears (Currie et al. 2000).

Is food availability constraining fuelling in the autumn?

Survival of migratory birds may be positively related to body reserves carried during migration (Newton 2008). Evidence from our Fair Isle study site suggests that changes in food availability may have their greatest effect on migratory fuel loads during the autumn pre-migratory fuelling period, when food abundance begins to decline under natural (i.e. non-supplemented) conditions. Unfortunately, we were unable to monitor fuel deposition rates or departure fuel loads of control wheatears, as these measurements were obtained via food-supplementation. Fuel deposition rate of fed *O. o. oenanthe* showed a slight increase with date in the autumn on Fair Isle, suggesting that there is increasing pressure to fuel at faster rates in birds departing later. We found that birds breeding late on Fair Isle leave sooner after fledging than earlier-breeding birds. This is consistent with a study of stonechats (*Saxicola torquata*), in which moult initiation, moult speed and start of migratory restlessness were negatively correlated with hatching date of juveniles kept in controlled aviary conditions (Helm et al. 2005). We also found that departure fuel loads of fed birds were positively correlated with date in the autumn. Higher departure fuel loads of late-leaving birds compared to earlier-leaving birds are known to occur in other species of migrating passerine (Fransson 1998, Dänhardt and Lindström 2001). One possible explanation is that birds migrating late in the autumn attempt to build up large fuel reserves, in anticipation of declining food abundance *en route*. Birds leaving earlier might be able to carry smaller loads and stopover more frequently and/or for longer periods while food abundance remains relatively high (e.g. Delingat et al. 2006). The lack of correlation between body reserves of control wheatears and date during the autumn pre-migratory period on Fair Isle suggests that food may be limiting the fuelling rates of later birds and hence constraining their ability to compensate for later departure with higher departure fuel loads.

Fuel loads and flight distance

Departure fuel loads of food-supplemented *O. o. leucorhoa* in the autumn at Qeqertarsuaq did not reach the levels of *O. o. leucorhoa* departing PNOD or stopping over on Fair Isle. The autumn migration of *O. o. leucorhoa* involves crossing the north Atlantic from Greenland, to Iceland and north-west Europe (Williamson 1958, 1961), or possibly even non-stop to north-west Africa (Thorup et al. 2006). We therefore expected *O. o. leucorhoa* at Qeqertarsuaq to reach departure fuel loads approximately 50–100 % above lean body mass, as they did in an earlier study (Ottosson et al. 1990). Contrary to this expectation, none of the fed *O. o. leucorhoa* in this study departed Qeqertarsuaq with sufficient body reserves to reach north-west Europe. Six out of 10 did, however, accumulate enough reserves to make a crossing to Iceland. The remaining four would have required refuelling elsewhere in Greenland to successfully cross the Atlantic. The body reserves of control *O. o. leucorhoa* in this study were much higher in birds stopping over on Fair Isle in spring than at other stages of the annual cycle. Food-supplemented birds attained greater body reserves, but there was still variation between different stages of the annual cycle. In broad agreement with our findings, Delingat et al. (2008) reported that departure fuel loads of *O. o. leucorhoa* were significantly higher when departing from Fair Isle towards Iceland/Greenland in spring than when departing from Iceland towards north-west Europe in autumn. Endogenous control mechanisms that respond to photoperiod and geomagnetism are likely to underpin the variation in fuelling extent with time and location that we observed in the fed birds (Berthold 1996). Among *O. o. leucorhoa,* these endogenous controls seem to limit maximum levels of fuel deposition so that the large body reserves required for a trans-Atlantic or trans-Saharan crossing are reached only just before the crossing is to be made. Boström et al. (2010), using magnetic fields to simulate displacement of wheatears preparing for autumn migration demonstrated that birds increase their body reserves in anticipation of crossing a substantial barrier. The energetic costs of flight increase with size of body reserves (Pennycuick 1975, Lindström and Alerstam 1992), so it might therefore be optimal for wheatears to carry moderate fuel reserves and make more frequent stops, even when food availability is high, only building up large body reserves when substantial barriers are to be crossed (Delingat et al. 2006, 2008). Carrying large body reserves may also increase predation risk due to reduced aerial agility (Witter 1994, Lind et al. 1999), although wheatears will sometimes hide or remain motionless to avoid predators rather than fleeing (Schmaljohann and Dierschke 2005).

Conclusions

Our results indicate that changes in food availability affect body mass regulation of a long-distance migratory songbird to different extents across the annual cycle. Migratory fuelling, in both the spring and the autumn, were the stages of the annual cycle in which food manipulation in this study had the greatest measurable effect. Climate change therefore has the potential to affect migratory fuelling of northern wheatears via the effects of altered temperature and rainfall on arthropod abundance and phenology. Migration has been identified as the stage of the annual cycle of migrant songbirds in which the great majority of mortality occurs (Sillett and Holmes 2002). The ability to accumulate enough fuel to reach subsequent destinations on a migratory route and to avoid starvation in unfavourable weather conditions *en route* are both likely to affect survival of migrating birds, and to depend to a large extent on food availability. Furthermore, fuel loads of migrating birds affect departure decisions, as well as determining the frequency at which birds need to stop to refuel, thereby affecting the speed of migration. Migration timing and speed can affect acquisition of favourable territories and synchronisation of breeding attempts with food availability. The consequences of changes to migratory fuelling induced by climatic changes in food availability may therefore have significant effects on fitness and survival of migratory songbirds. Our results also indicate that birds facing contrasting migratory journeys respond differently to changes in food availability. Migration strategy therefore needs to be taken into account when extrapolating results on climate change impacts between species and subspecies. Predictions of climate change impacts on migratory birds will be significantly improved by data on the impacts of altered food availability on migration survival and migration speed.

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REFERENCES

Alerstam, T., and Å. Lindström. 1990. Optimal bird migration: the relative importance of time, energy and safety. Pages 331-351 *in* E. Gwinner, editor. Bird Migration: The Physiology and Ecophysiology. Springer, Berlin.

Bairlein, F. 1994. Manual of field methods. European-African Songbird Migration Network, Wilhelmshaven.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8:1–16.

Bayly, N. 2006. Optimality in avian migratory fuelling behaviour: a study of a trans-Saharan migrant. Animal Behaviour 71:173-182.

Berthold, P. 1996. Control of bird migration. Chapman & Hall, London.

Berthold, P., and S. B. Terrill. 1991. Recent advances in studies of bird migration. Annual Review of Ecology and Systematics 22:357-378.

Boström, J. E., T. Fransson, I. Henshaw, S. Jakobsson, C. Kullberg, and S. Åkesson. 2010. Autumn migratory fuelling: a response to simulated magnetic displacements in juvenile wheatears, *Oenanthe oenanthe*. Behavioral Ecology and Sociobiology 64:1725-1732.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81-83.

Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296-298.

Both, C., and M. E. Visser. 2005. The effect of climate change on the correlation between avian life-history traits. Global Change Biology 11:1606-1613.

Brown, D. R., and T. W. Sherry. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. Oecologia 149:22-32.

Bruderer, B., and A. Boldt. 2008. Flight characteristics of birds. Ibis 143:178-204.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach. Springer-Verlag, New York.

Conder, P. 1989. The Wheatear. Christopher Helm, London.

Cramp, S. (Ed.). 1988. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Volume V: Tyrant flycatchers to thrushes. Oxford University Press, Oxford.

Currie, D., D. B. A. Thompson, and T. Burke. 2000. Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. Ibis 142:389-398.

Dawson, A., S. A. Hinsley, P. N. Ferns, R. H. Bonser, and L. Eccleston. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proceedings of the Royal Society B: Biological Sciences 267:2093-2098.

Delingat, J., F. Bairlein, and A. Hedenström. 2008. Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in northern wheatears (*Oenanthe oenanthe*). Behavioral Ecology and Sociobiology 62:1069-1078.

Delingat, J., V. Dierschke, H. Schmaljohann, B. Mendel, and F. Bairlein. 2006. Daily stopovers as optimal migration strategy in a long-distance migrating passerine: the northern wheatear *Oenanthe oenanthe*. Ardea 94:593–605.

Dell, D., T. H. Sparks, and R. L. H. Dennis. 2005. Climate change and the effect of increasing spring temperatures on emergence dates of the butterfly *Apatura iris* (Lepidoptera: Nymphalidae). European Journal of Entomology 102:161–167.

Dierschke, V., J. Delingat, and H. Schmaljohann. 2003. Time allocation in migrating Northern Wheatears (*Oenanthe oenanthe*) during stopover: is refuelling limited by food availability or metabolically? Journal of Ornithology 144:33–44.

Dierschke, V., and J. Delingat. 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behavioral Ecology and Sociobiology 50:535-545.

Dänhardt, J., and Å. Lindström. 2001. Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Animal Behaviour 62:235-243.

Ellegren, H. 1993. Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. Ornis Scandinavica 24:220-228.

Fransson, T. 1998. A feeding experiment on migratory fuelling in whitethroats, *Sylvia communis*. Animal Behaviour 55:153-162.

Gill, J. A., K. Norris, P. M. Potts, T. G. Gunnarsson, P. W. Atkinson, and W. J. Sutherland. 2001. The buffer effect and large-scale population regulation in migratory birds. Nature 412:436-438.

Gordo, O., L. Brotons, X. Ferrer, and P. Comas. 2005. Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? Global Change Biology 11:12–21.

Goymann, W., F. Spina, A. Ferri, and L. Fusani. 2010. Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. Biology Letters 6:478-481.

Helm, B., E. Gwinner, and L. Trost. 2005. Flexible seasonal timing and migratory behavior: results from stonechat breeding programs. Annals of the New York Academy of Sciences 1046:216-227.

Hulme, M., R. Doherty, T. Ngara, M. New, and D. Lister. 2001. African climate change: 1900-2100. Climate Research 17:145–168.

Jenni-Eiermann, S., and L. Jenni. 1996. Metabolic differences between the postbreeding, moulting and migratory periods in feeding and fasting passerine birds. Functional Ecology 10:62-72.

Jones, T., and W. Cresswell. 2010. The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? Journal of Animal Ecology 79:98-108.

Kaiser, A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. Journal of Field Ornithology 64:246-255.

Lack, D. 1968. Bird migration and natural selection. Oikos 19:1-9.

Lind, J., T. Fransson, S. Jakobsson, and C. Kullberg. 1999. Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. Behavioral Ecology and Sociobiology 46:65-70.

Linden, M., and A. P. Møller. 1989. Cost of reproduction and covariation of life history traits in birds. Trends in Ecology & Evolution 4:367-371.

Lindström, Å., and T. Alerstam. 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. The American Naturalist 140:477-491.

Lozano, G. A., S. Perreault, and R. F. Lemon. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. Journal of Avian Biology 27:164-170.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884-1886.

Miles, J. E., J. S. Bale, and I. D. Hodkinson. 1997. Effects of temperature elevation on the population dynamics of the upland heather psyllid *Strophingia ericae* (Curtis) (Homoptera: Psylloidea). Global Change Biology 3:291–297.

Morton, G. A., and M. L. Morton. 1990. Dynamics of postnuptial molt in free-living mountain white-crowned sparrows. Condor 92:813-828.

Newton, I. 2008. The Migration Ecology of Birds. Academic Press, London.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society B: Biological Sciences 271:59-64.

Ottosson, U., B. Y. R. Sandberg, and J. Pettersson. 1990. Orientation cage and release experiments in Scandinavia and Greenland: the importance of visual cues. Ethology 70:57-70.

Panov, E. N. 2005. Wheatears of Palearctic: Ecology, Behaviour and Evolution of the Genus *Oenanthe*. Page 439. Pensoft, Sofia-Moscow.

Pärt, T. 2001a. The effects of territory quality on age-dependent reproductive performance in the northern wheatear (*Oenanthe oenanthe*). Animal Behaviour 62:379-388.

Pärt, T. 2001b. Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. Proceedings of the Royal Society B: Biological Sciences 268:2267-2271.

Pearce-Higgins, J. W., P. Dennis, M. J. Whittingham, and D. W. Yalden. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. Global Change Biology 16:12-23.

Pennycuick, C. J. 1975. Mechanics of flight. Pages 1-75 *in* D. S. Farner, J. King, and K. C. Parkes, editors. Avian Biology, Vol. 5. Academic Press, New York.

Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242-255.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and the R Development Core Team. 2011. nlme: Linear and Nonlinear Mixed Effects Models.

Post, E., C. Pedersen, C. C. Wilmers, and M. C. Forchhammer. 2008. Phenological sequences reveal aggregate life history response to climatic warming. Ecology 89:363-370.

R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reudink, M. W., P. P. Marra, T. K. Kyser, P. T. Boag, K. M. Langin, and L. M. Ratcliffe. 2009a. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proceedings of the Royal Society B: Biological Sciences 276:1619-1626.

Reudink, M. W., C. E. Studds, P. P. Marra, T. Kurt Kyser, and L. M. Ratcliffe. 2009b. Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American redstart *Setophaga ruticilla*. Journal of Avian Biology 40:34-41.

Saino, N., T. Szep, M. Romano, D. Rubolini, F. Spina, and A. P. Moller. 2004. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. Ecology Letters 7:21-25.

Saino, N., and R. Ambrosini. 2008. Climatic connectivity between Africa and Europe may serve as a basis for phenotypic adjustment of migration schedules of trans-Saharan migratory birds. Global Change Biology 14:250–263.

Sapir, N., I. Tsurim, B. Gal, and Z. Abramsky. 2004. The effect of water availability on fuel deposition of two staging Sylvia warblers. Journal of Avian Biology 35:25–32.

Schaub, M., L. Jenni, and F. Bairlein. 2008. Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. Behavioral Ecology 19:657-666.

Schmaljohann, H., P. J. J. Becker, H. Karaardic, F. Liechti, B. Naef-Daenzer, and C. Grande. 2011. Nocturnal exploratory flights, departure time, and direction in a migratory songbird. Journal of Ornithology 152:439-452.

Schmaljohann, H., and V. Dierschke. 2005. Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*. Journal of Animal Ecology 74:131-138.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296-308.

Smith, J. A. M., L. R. Reitsma, and P. P. Marra. 2010. Moisture as a determinant of habitat quality for a nonbreeding Neotropical migratory songbird. Ecology 91:2874-2882.

Snow, D. W. 1953. The migration of the Greenland wheatear. Ibis 95:376-378.

Stenseth, N. C., and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: nonlinearity and match–mismatch to the environment. Proceedings of the National Academy of Sciences 99:13379-13381.

Strathdee, A. T., J. S. Bale, W. C. Block, S. J. Coulson, I. D. Hodkinson, and N. R. Webb. 1993. Effects of temperature elevation on a field population of *Acyrthosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen. Oecologia 96:457–465.

Studds, C. E., and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86:2380-2385.

Studds, C. E., and P. P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Climate Research 35:115-122.

Studds, C. E., and P. P. Marra. 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. Proceedings of the Royal Society B: Biological Sciences:rspb.2011.0332.

Stutchbury, B. J. M., E. A. Gow, T. Done, M. Macpherson, J. W. Fox, and V. Afanasyev. 2011. Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. Proceedings of the Royal Society B: Biological Sciences 278:131-137.

Svensson, L. 1992. Identification Guide to European Passerines, 4th edition. British Trust for Ornithology, Norfolk.

Thomas, R. J. 1997. Functions of daily singing routines in birds. DPhil thesis, University of Sussex.

Thorup, K., T. E. Ortvad, and J. Ø. Rabøl. 2006. Do Nearctic northern wheatears (*Oenanthe oenanthe leucorhoa*) migrate nonstop to Africa? The Condor 108:446–451.

Tøttrup, A. P., K. Thorup, K. Rainio, R. Yosef, E. Lehikoinen, and C. Rahbek. 2008. Avian migrants adjust migration in response to environmental conditions en route. Biology Letters 4:685-688.

Williamson, K. 1958. Bergmann's rule and obligatory overseas migration. British Birds 51:209-232.

Williamson, K. 1961. The concept of "cyclonic approach". Bird Migration 1:235-240.

Witter, M. 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. Animal Behaviour 48:201-222.

Wood, S. N. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. Journal of the Royal Statistical Society (B) 70:495-518.

SUPPORTING INFORMATION (FIG. S2.1, TABLES S1–S3)

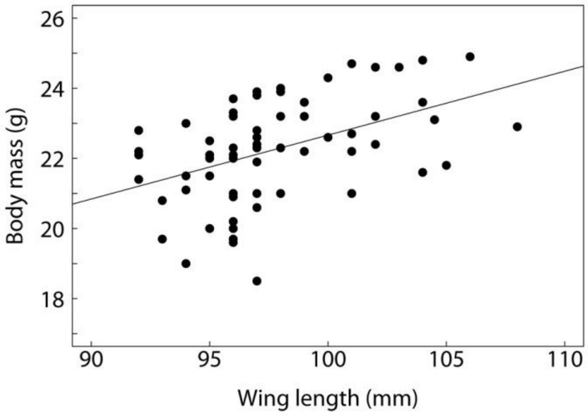

Fig. S1. Subset of lean wheatears (n = 65) selected from birds with fat and muscle scores < 2, and falling within the 50% quantile. We used the regression of body mass on wing length indicated by the line of best fit to calculate lean body mass of all individuals in our analyses (lean body mass = 0.182 x wing length (mm) + 4.445).

Table S2.1. Models fit to daily fuel deposition rates of *O. o. oenanthe* and *O. o. leucorhoa* across the annual cycle. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model *i* and the best model and $wAICc_i$ is the Akaike weight. Plausible models are considered to be those with $\Delta AICc_i \leq 2$. Interactions are indicated by x and include all lower order fixed term effects.

Model ID	Dependent variable	Fixed effects	Random effects	df	$\Delta AICc_i$	$wAICc_i$
15	Daily FDR	stage, subsp, day	SD (subsp)	7	0	1.0
16		stage, subsp	SD (subsp)	5	16.6	<0.001
17		subsp x day, stage	SD (subsp)	7	24.8	<0.001
18		stage x day, subsp	SD (subsp)	8	28.3	<0.001
19		stage, day	SD (subsp)	5	32.4	<0.001
20		subsp	SD (subsp)	3	39.4	<0.001
21		stage	SD (subsp)	4	45.2	<0.001
22		none	SD (subsp)	2	51.0	<0.001

Daily FDR: Fuel deposition rate (% of body mass above lean body mass gained or lost per 24 h).
Fixed effects. stage: location-specific stage of migration (start of spring migration at PNOD, start of autumn migration at Qeqertarsuaq, autumn migration at Fair Isle (start and stopover)), day: stage-specific day, none: intercept-only model.
Random effects. SD (subsp): Standard deviation of effect of subspecies on daily FDR.

Table S2.2. Models fit to departure fuel loads (DFL) of food-supplemented *O. o. oenanthe* and *O. o. leucorhoa* across the annual cycle. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model *i* and the best model and $wAICc_i$ is the Akaike weight. Plausible models are considered to be those with $\Delta AICc_i \leq 2$. Interactions are indicated by x and include all lower order fixed term effects.

Model ID	Dependent variable	Fixed effects	df	$\Delta AICc_i$	$wAICc_i$
23	DFL	subsp x stage, day	6	0	0.456
24		subsp x stage, stage x day	7	2.0	0.165
25		subsp x stage, subsp x day	7	2.4	0.140
26		subsp, stage x day	6	4.4	0.049
27		subsp x stage, subsp x day, stage x day	8	4.6	0.046
28		subsp, stage, day	5	4.6	0.046
29		stage x day	5	4.7	0.043
30		subsp x day, stage x day	7	5.9	0.024
31		subsp x day, stage	6	7	0.014
32		stage, day	4	7.1	0.013
33		subsp, day	4	10.3	0.003
34		subsp x day	5	12.7	<0.001
35		day	3	17.3	<0.001
36		subsp x stage	5	26.9	<0.001
37		none	2	34.7	<0.001
38		stage	3	35.6	<0.001
39		subsp	3	35.7	<0.001
40		subsp, stage	4	37.3	<0.001

DFL: Last recorded fuel load (% of body mass above lean body mass) before departure.
Fixed effects. subsp: *O. o. oenanthe* vs. *O. o. leucorhoa*, stage: spring departure from winter grounds vs. autumn departure from breeding grounds, day: stage-specific day, where 1 = day that first bird departed during that stage.

Table S2.3. Models fit to departure dates of food-supplemented *O. o. oenanthe* at the end of the breeding season on Fair Isle. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model *i* and the best model and $wAICc_i$ is the Akaike weight. Plausible models are considered to be those with $\Delta AICc_i \leq 2$. Interactions are indicated by x and include all lower order fixed term effects.

Model ID	Dependent variable	Fixed effects	df	$\Delta AICc_i$	$wAICc_i$
41	departure date	age, HD	4	0	0.751
42		age x HD	5	2.4	0.230
43		HD	3	8.5	0.011
44		age	3	9	0.008
45		none	2	14.8	< 0.001

Departure date: last date recorded attending feeding station.
Fixed effects. age: adult or juvenile; HD: hatch date (juveniles) or hatch date of last brood in that year (adults); none: intercept-only model.

CHAPTER 3. The impact of increased food availability on reproduction in a long-distance migratory bird: a climate change simulation experiment

ABSTRACT

Climate variation is expected to influence the breeding productivity of insectivorous birds by affecting the abundance and phenology of their food supply. Food availability may constrain the reproductive output of birds by limiting the number of offspring fledged in each nesting attempt, or by limiting the number of nesting attempts. To investigate phenotypic flexibility in breeding parameters induced by changes in food availability, we conducted experimental food supplementation (with mealworms, *Tenebrio molitor*) over 3 years to test the hypothesis that increased food availability would increase the breeding productivity of northern wheatears (*Oenanthe oenanthe*); an insectivorous long-distance migrant bird. The number of offspring fledged over the season was higher for food-supplemented birds than for control birds. This was due to an increase in the number of breeding attempts for supplemented birds that started breeding early in the season, rather than an increase in clutch size, hatching success or fledging rates per nest. This increase was greater for males than females; males could attempt to rear simultaneous broods with multiple females as well as attempting second broods, whereas females only increased their breeding effort via second broods. Food supplementation advanced hatching date, which increased the time available to attempt a second brood. Supplemented birds also produced bigger nestlings in one out of two years. Multiple brooding is currently rare in the study population, but this experiment demonstrates the potential for climate-driven changes in food availability to affect wheatear breeding productivity, primarily via the birds’ phenotypic flexibility in the number of breeding attempts.

INTRODUCTION

Climate change may influence animal population size through its effect on food availability. For example, climate-driven variation in temperature and rainfall is likely to have strong effects on populations of migrant birds by changing the abundance and phenology of their invertebrate food supply (Bale et al. 2002, Dell et al. 2005, Both et al. 2006, Pearce-Higgins et al. 2010). This, in turn, may affect the ability of insectivorous birds to obtain sufficient energy reserves for reproduction or to provide adequate food for their young (Both et al. 2006). Food availability may therefore constrain the reproductive output of migrant birds by limiting the number or quality of offspring fledged in individual nesting attempts, or by limiting the number of nesting attempts during each breeding season (Nagy and Holmes 2005, Illera and Díaz 2006).

Long-distance migratory birds might be expected to be among the taxa most severely affected by climate change, because the strength and direction of modifications to climatic variables may vary between the different locations utilised across the annual cycle, and because of mismatches between the various cues controlling the timing of migration. Thus, migratory birds are exposed to the sum of all climate-related impacts at each location. Indeed, numerous studies have described associations between climate variables and aspects of the annual cycles of migratory birds, including: migration phenology (Gordo and Sanz 2006; Studds and Marra 2011) and speed of migration (Ahola et al. 2004), breeding phenology (Torti and Dunn 2005, Whittingham et al. 2007, Musters et al. 2010), clutch size (Laaksonen et al. 2006, Wilson and Martin 2010), egg size (Jàrvinen 1994), offspring survival (McMahon and Burton 2005), overall nesting success (Rajchard et al. 2006), number of offspring (Winkel and Hudde

1997), territory occupancy (Beale et al. 2006) and winter body condition (Studds and Marra 2007).

Despite these numerous documented instances of correlations between climate variables and the biology of species, populations and individuals, there remain major gaps in our knowledge of the causal mechanisms that underlie such effects (Møller et al. 2004, 2010). To understand and evaluate the mechanisms linking climate change and ecological change, an experimental approach is advocated as it avoids the problem of confounding factors inherent to many correlational studies (Hughes 2000, Møller et al. 2004, Helmuth et al. 2005). Climate change has often been suggested to affect migratory birds via effects on their food supply (White 2008, Both et al. 2009). Few studies have addressed experimentally the impacts of changes in food availability on breeding productivity of long-distance migrant songbirds, many of which are declining (Hagan and Johnston 1992, Buchanan et al. 2006, Heldbjerg and Fox 2008, Thaxter et al. 2010). The few studies that have investigated the effect of changing food availability across entire breeding seasons have focused on Nearctic-Neotropical migrant passerines. In one such study, black-throated blue warblers (*Dendroica caerulescens*) had more breeding attempts per season when food availability was experimentally increased (Nagy and Holmes 2005). Food reductions, however, had little impact on reproductive output of red-eyed vireos (*Vireo olivaceus*) (Marshall et al. 2002).

In temperate and arctic climates, invertebrate abundance is strongly seasonal and birds must therefore time their breeding so that the periods of greatest energetic demand (e.g. egg laying and chick rearing) coincide with this peak in food availability (Martin 1987). Climate change affects phenology of many invertebrates and it appears that declines of many insectivorous migrant birds breeding in Europe may be due to an inability to adjust their migration and / or breeding phenology to match that of their invertebrate prey (Visser et al. 1998, Both et al. 2006, Møller et al. 2008).

In the present study, we experimentally manipulated food availability (simulating a key biological effect of predicted changes in temperature and rainfall) to evaluate the potential role of climate-driven changes in food supply on the breeding productivity of a model species of long-distance migrant. Our central aim was to test whether reproductive success is limited by food availability, and if so, which aspects of reproductive performance and timing are most sensitive to changes in food availability. Our experimental design was not intended to mirror directly the changes in food availability expected under any particular climate change scenario. Rather, we used simplistic food-addition across the breeding season, to explore the amount of (and limits to) phenotypic plasticity in relation to increases in food supply.

We chose the northern wheatear (*Oenanthe oenanthe*) as the study species for its extreme long-distance migrations, its tractability for field experiments, and because a series of detailed recent studies have paved the way for the present work (Pärt 2001a, 2001b, Arlt et al. 2008). Northern wheatears breed in north temperate and arctic regions, and in common with most other long-distance migrant passerine birds, are mainly insectivorous (Cramp 1988, Conder 1989, Panov 2005). Their reproductive success is expected to depend largely on the coincidence of breeding with the peak emergences of their highly seasonal invertebrate prey, as has been shown in other species (Pearce-Higgins and Yalden 2004). The mean annual air temperature within the breeding distribution of the northern wheatear is predicted to increase by 1–4°C by 2100, with the expected amount of warming depending on location (e.g. greater warming is predicted at higher latitudes) and on the greenhouse gas emissions scenario considered (IPCC 2007, Murphy et al. 2009). Experimental warming in line with these predictions within the current range of the northern wheatear (northern UK; Miles et al. 1997) and its predicted future range (the Arctic island of Svalbard; Strathdee et al. 1993) range, led to increases in insect abundance. Such temperature rises may increase insects' developmental rates directly (through physiological effects) or indirectly (by augmenting growth of the plants on which they feed), which may in turn increase the number of generations per year of multivoltine insects (Bale et al. 2002, Altermatt 2010).

Declines in northern wheatear populations have occurred in western and central Europe, perhaps due to agricultural intensification of former habitat (Kneis 1982, Clement 1997, Burfield and Van Bommel 2004). The northern wheatear's breeding range has, however, expanded relatively recently into eastern Canada, possibly as a result of increases in summer temperatures. Similar temperature rises have occurred across the tundra of northern Scandinavia and arctic Russia (Clement 1997).

For all of these reasons, we anticipated that northern wheatears may be highly sensitive to climate-driven changes in food availability, and we therefore aimed to determine the effect of food availability on this species breeding productivity. To achieve this, we used food-supplementation to simulate experimentally the effects of climate-driven changes in invertebrate abundance. We tested the two-part hypothesis that (1) food supplemented northern wheatears would fledge more young per breeding season than unsupplemented control birds and that higher seasonal fledging rates of supplemented birds would be underpinned by (2) earlier clutch initiation, larger clutch sizes, larger eggs, greater hatching success, greater chick size, more fledglings per brood and higher rates of multiple brooding.

MATERIALS AND METHODS

Study location and species

The study was conducted on Fair Isle (59°32'N, 1°39'W), an island of ca. 1,000 ha, lying midway between mainland Shetland and Orkney, north-east of the Scottish mainland, UK (Fig. 3.1). The southern half of the island consisted mainly of improved grassland, grazed by sheep. The northern half of the island was also grazed by sheep and contained a largely unimproved mixture of heather moorland (dominated by *Calluna vulgaris*) and *Festuca, Agrostis*, *Nardus* and maritime grassland communities (Nolan et al. 1994). Breeding northern wheatears were monitored in the north of the island in 2008 and 2010; and in both the north and south of the island in 2009 (Fig. 3.1).

Breeding northern wheatears arrive back on Fair Isle from their sub-Saharan African wintering grounds between the beginning of April and mid-May. Nests are located in holes in the ground (e.g. old burrows of rabbits (*Oryctolagus cuniculus*) or other rodents), under rocks or in dry stone walls. Egg-laying of first clutches on Fair Isle begins in early May and continues into June. Clutch size of northern wheatears ranges from 4 to 8 eggs (Moreno 1989), with a trend towards larger clutches at higher latitudes (Panov 2005). Mean clutch size of northern wheatears breeding at similar latitudes to Fair Isle in nearby southern Scandinavia is typically 6.0-6.4 eggs (Cramp 1988, Moreno 1989). Incubation is performed almost exclusively by the female, and lasts for between 10 and 18 days from the day on which the last egg is laid until the eggs hatch (Moreno

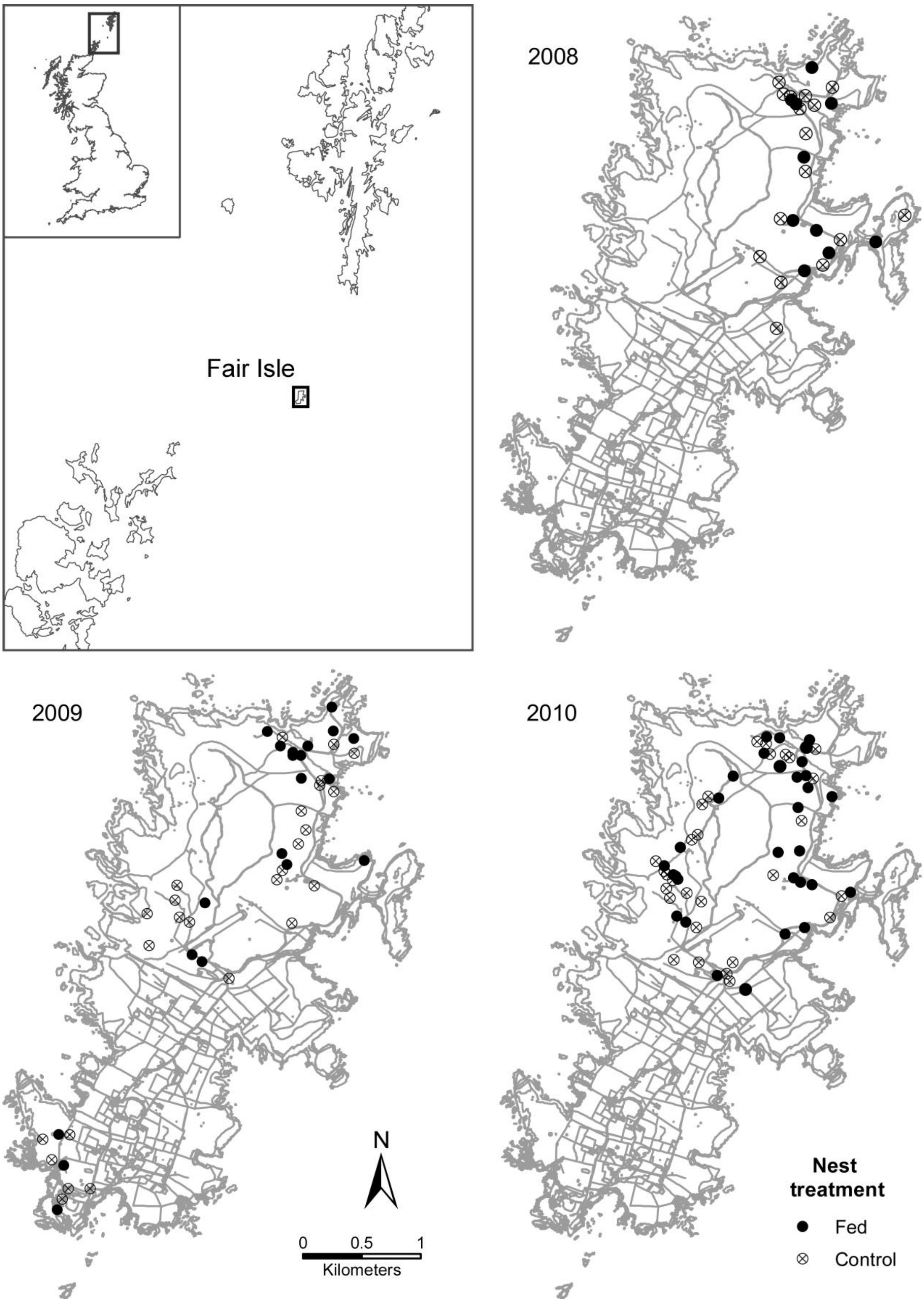

Fig. 3.1. Location of Fair Isle in relation to Great Britain and maps of Fair Isle showing the locations of nests within fed (supplemented with mealworms), and control (no supplemental food) territories in 2008, 2009 and 2010.

1989). Chicks fledge after approximately 15 days. The parents continue to feed their fledged offspring until they become independent, about two weeks after fledging.

Adult northern wheatears were captured in their breeding territories with spring traps (www.moudry.cz, model SB30) baited with mealworms. Plumage features (after Svensson 1992) were used to sex and age captured birds as fledged in the previous year (young), before the previous year (old) or fledged before the current year (unknown if young or old). All breeding males, but only a minority of breeding females, could be aged precisely as young or old. All captured birds were measured (maximum wing chord to 1 mm), weighed on an electronic balance (to 0.1 g), and fitted with a numbered metal ring and a unique combination of plastic colour rings to enable individual identification in the field. Nestlings were ringed when at least 5 days old, usually at 7 days old (or older if they were discovered later).

Feeding experiment

Prey availability for breeding northern wheatears was experimentally increased by providing mealworms (*Tenebrio molitor* larvae) in plastic bowls placed directly on the ground, next to rocks which wheatears frequently made use of as look-out posts (Conder 1989).

During 2008-2010, feeders were put out from the time of territory establishment in late April/early May, and filled with at least 30 g of mealworms (mean ± SD = 37.8 ± 2.7 g, n = 20 mealworm samples). These feeders were refilled on least five of every seven days, until the departure on autumn migration of all of the breeding birds and their offspring that were using the feeders (northern wheatears depart Fair Isle during August and early September). Feeders with higher depletion rates were filled with greater numbers of mealworms. Sample sizes of supplementary fed (treatment) and unfed (control) wheatear pairs were: 2008 – 15 fed, 14 control; 2009 – 23 fed, 22 control; 2010 – 27 fed, 27 control.

The study areas (Fig. 3.1) were chosen for their relatively high densities of breeding northern wheatears. As there are age-related differences in arrival date and breeding success of northern wheatears (Currie et al. 2000, Arlt and Pärt 2007), a standard route through the study site was walked almost daily from mid-April until the end of May, and newly established breeding pairs were selected alternately as fed and control (i.e. unfed) pairs. A pair was selected if behavioural signs of pair establishment were observed (e.g. a male and female chasing away other wheatears but not each other, investigating potential nest sites, Conder 1989). In this way, fed and control pairs were stratified both spatially and with respect to arrival date. This procedure also meant that supplementary feeding only began after territory establishment, thus avoiding the potentially confounding situation of the highest quality individuals establishing territories around feeders, to the exclusion of lower quality individuals.

Each food-supplemented territory was provided with one feeder, located as near to the centre of the territory as possible, to minimise the possibility of wheatears from neighbouring control territories raiding the feeders. Direct observation and small video cameras (Sony Handycam, model DCR-SR32) were used to confirm the identities of the wheatears using the feeders. At least three recording sessions, of at least 1 hour each, were viewed per feeder, but viewing sessions were extended to 4 hours if neither or only one of a pair had attended the feeder during the initial period. During this video monitoring, none of the adult wheatears from control pairs were ever recorded taking mealworms from any of the feeders in any year. Raids on feeders by wheatears from outside the sample population were occasionally recorded, but these were almost always after breeding had finished. Wheatears from supplementary fed pairs were sometimes recorded taking mealworms from other feeders outside their own territory.

To prevent European starlings (*Sturnus vulgaris*) from using the feeders, metal wire mesh cages were placed over the feeding bowls. These cages permitted wheatears to enter through a small hole cut at the bottom of the wire mesh (lined with strong insulating tape to prevent injury) or via a hinged weighted walkway that swung shut when starlings (approximately three to four times heavier than wheatears) attempted to enter, swinging back open again when the starling stepped off the platform. Approximately 1 month was allowed between positioning feeders and deploying cages (about the time that starling raids on feeders intensified as they began feeding chicks) to maximise the likelihood of wheatears continuing to use them. In each year, however, some wheatear pairs (5 in 2008, 6 in 2009 and 2 in 2010) that had at first been attending feeders stopped using them once the cages were placed over them. Such pairs were excluded from some analyses (see Data Analysis section below).

Reproductive parameters

Nests were found as early as possible by observing the parents going to and from nest holes (see Fig. 3.1 for locations). On finding each nest, its status was recorded as (i) being built, (ii) containing eggs or (iii) containing chicks. Nest contents were subsequently checked every other day. Any dead chicks or un-hatched eggs left in the nest at this stage were counted. The full set of reproductive parameters that were measured from egg laying to fledging are described in Table 3.1.

Table 3.1. Reproductive parameters recorded for breeding wheatears in the present study.

Parameter	Description
Identity of parents	The social parentage of each brood was observed by recording the colour ring combinations of the birds involved in incubation and provisioning.
Laying date	The day on which the first egg of a clutch was laid (Day 1 = 1st May). Only estimated for clutches of known size. Estimated by back-dating from date last egg laid or hatching date minus average incubation duration for clutches in this study (12.46 days), assuming one egg was laid per day (Conder, 1989).
Clutch size	The total number of eggs in the completed clutch. Nest contents were not directly visible as the nests were always built in burrows or in rock piles, and so the eggs were counted by touch. These counts proved to be 100% accurate when eggs were taken out of the nest for measuring in 2010 (the only year in which egg size measurements were taken, see below). Clutches were considered to be complete once no new eggs were found on successive visits and the eggs were warm (and therefore being incubated).
Egg volume	In 2010, maximum length and maximum width of the eggs of all accessible clutches were measured (to 0.1 mm) using plastic callipers. Egg volume was then calculated following Hoyt (1979).
Incubation duration	The number of days between the last egg being laid (which is the first day of regular incubation of the clutch) and the first egg hatching.
Hatching date	The day that the first egg or eggs hatched. If all the chicks had already hatched when the nest was found, hatching date was estimated based on development of the chicks, using data from chicks of known age in the study population.

Table 3.1, continued

Hatching success	The number of chicks that hatched, calculated from the clutch size, minus the number of unhatched eggs found in the nest.
Chick size	Chick maximum wing chord (to 1 mm) and body mass (to 0.1 g) were measured at between 5 and 8 days old (usually at 7 days) in 2009 and 2010, at the same time as being fitted with a uniquely numbered metal ring.
Fledgling number	The number of chicks surviving to leave the nest. Fledglings were either counted or calculated by subtracting the number of dead chicks found in the nest cavity after fledging (once fledglings were observed and/or parents were giving intense warning calls from 15 days after the hatching date) from the number of live chicks that were present in the nest at 5-8 days old (Arlt *et al.*, 2008). Although this method does not account for predation of nestlings between ringing and fledging, partial nest predation of wheatears is very rare (less than 1% of successful nests in a detailed study in Sweden (Arlt *et al.*, 2008)), and so should not have a major effect on the results.
Nest survival	After locating active nests, they were checked every 2 or 3 days and recorded as active, failed (no chicks fledged) or successful (if at least one chick was fledged). Successful breeding attempts were defined as nests where fledglings were observed and/or parents gave intense warning calls from 15 days after the hatching date (Arlt *et al.*, 2008).
Breeding attempts	For pairs with successful first broods, the presence or absence of a second breeding attempt was recorded. A second breeding attempt was recorded if at least 1 egg was laid. A separate analysis was carried out, individual males and individual females, since additional broods might be attempted by members of the original pair subsequently pairing with other partners for a second breeding attempt.

Data analysis

The analysis focuses on the effects of food supplementation on each of the parameters of reproductive success outlined above and summarised in Table 3.1. In addition to the potential effect of food supplementation, year, adult age, adult body size and other individual characteristics may all contribute to explaining reproductive success. Furthermore, aspects of breeding parameters early on in a breeding attempt (e.g. breeding date, clutch size) may also influence later measures of breeding success (e.g. chick size, number of juveniles). To investigate these effects, we fitted a series of models using the statistical software R (version 2.10.1, R Development Core Team 2009). Where appropriate (see below), we used general linear models, linear mixed models (fitted by maximum likelihood) and generalised linear mixed models (fitted by the Laplace approximation). Mixed models were fitted using the lme4 package (Bates and Maechler 2009) within R while other models were fitted using the basic R installation. Datasets were reduced so that there were no missing data for any of the independent variables in the full models, to enable direct comparisons between models. Intercept only models (null models) were included within each set of candidate models.

Some males were present in multiple years, or had multiple broods within a year, so male identity (ID) was included where appropriate as a random effect in mixed models. Female ID was used as the random effect instead of male ID in models of reproductive parameters in which female characteristics are likely to be more important than male characteristics (e.g. models of egg volume, hatching success). Male and female ID were never included together, as female ID was entirely nested within male ID. Unringed breeding individuals were included within some analyses, being given unique IDs based on their breeding territories. The number of unringed individuals was relatively high in 2008 (10 males and 7 females out of 22 pairs), becoming less numerous in 2009 and 2010 (5 males and 7 females out of 40 pairs in 2009; 5 males and 5 females out of 48 pairs in 2010). Thus there may have been some pseudoreplication of unringed breeders between years, although only about 50 % of unringed adult birds are expected to return the following year (Chapter 4), suggesting that such pseudoreplication is not likely to have a great impact on the model outputs. Fed pairs that stopped using feeders when cages were deployed were included in analyses of clutch size and egg volume, as they were still being fed during those stages of the breeding cycle. For all other analyses, these pairs were excluded from the dataset.

The performance of competing candidate models was compared using Akaike's Information Criterion, corrected for small sample size (AICc; Burnham and Anderson 2002). Smaller values of AICc indicate better statistical fits. Two statistics were obtained for each model: ΔAIC_i (the difference in AICc between model i and the best model) and $wAIC_i$ (Akaike weight), which indicates the likelihood that each model is the best approximation relative to all the other models in the model set. The models were ranked by ΔAIC_i and the most plausible models were defined as those with $\Delta AIC_i \leq 2$.

Details of specific analyses

Fledging success

(a) Chicks fledged per nesting attempt

Only first clutches were considered in the analyses of the number of chicks fledged per nesting attempt. Clutches that failed due to predation or disturbance by rabbits and re-laid clutches were excluded. Only the earliest clutch of each polygynous male was included, as the females laying the later of these clutches may have previously failed a nesting attempt and moved territory. Generalised linear mixed models (Poisson error family, log link function) were used, with male ID as the random effect. Fixed effects were: treatment, hatching date, year and the interactions treatment x hatching date and treatment x year.

(b) Fledging success per breeding season

The total number of chicks fledged across the whole breeding season was obtained for each parent; male and female parents were analysed separately. Individuals with failed broods were included in the analysis because feeding treatment may influence decisions about re-laying after failed nesting attempts. The analysis was carried out for individual parents instead of pairs, as new pairs could form after failed nesting attempts and males could have simultaneous broods with multiple females. Generalised linear mixed models (Poisson error family, log link function) were used, with female ID as the random effect for the female analysis and with male ID as the random effect for the male analysis. Fixed effects were: treatment, hatching date of first brood (earliest first brood for males with simultaneous broods) and year. For both male and female analyses, treatment x hatching date and treatment x year interactions were included in the full models.

(c*) Fledging success per egg*

Only first broods were considered in the analyses of fledging success per egg. Generalised linear mixed models (binomial error family because eggs either fledged (1) or not (0)) were fitted, with male ID as the random effect. Treatment, year, hatching date and treatment x hatching date were included as fixed effects. Models including treatment x year are not considered as the routine failed to converge.

Hatching dates

We used hatching dates as our main measure of the timing of breeding, as more data were available for hatching dates than for laying dates. We restricted the analysis of hatching dates to data from 2009 and 2010, as in 2008 there were insufficient data on early broods. Only the earliest clutches for each male were included in these analyses (second clutches, re-laid first clutches and clutches with additional females with later initiation dates were excluded). Linear mixed models fitted by maximum likelihood were used to analyse differences in hatching date; the full models included treatment, male age, year, treatment x year and treatment x male age as fixed factors, as well as male ID as a random effect.

Clutch size

There was no pseudoreplication arising from the same individual females appearing in the dataset more than once; thus we used general linear models (Poisson error family, log link function). The full model included treatment, year, female wing length, laying date and all first order interactions involving treatment.

Egg volume

We only measured egg volume in 2010. A linear mixed model was used, with female ID as a random effect and with treatment and female wing length as fixed effects.

Incubation duration

We only used data from 2009 and 2010 to analyse variation in incubation duration, as insufficient data with precise laying and hatching dates were available from 2008. The analysis was of first broods only and there was no pseudoreplication from breeding females appearing more than once. Thus, we used linear models; the full model included treatment, clutch size, female wing length (as an indicator of female size), laying date and all first order interaction terms.

Hatching success

We restricted the analysis of hatching success to first broods (i.e. excluding re-laid clutches and second broods). Clutches with total hatching failure (all predated nests, nests disturbed by rabbits and infertile clutches) were included in these analyses, as food availability may affect female investment in egg production and/or affect the time available to parents for nest defence. Generalised linear mixed models (binomial error family with a logit link function) were used to investigate the effect of the food supplementation treatment on the probability of each egg hatching within each nest. The starting model included treatment, laying date and the treatment x laying date interaction as fixed effects and female ID as a random effect.

Chick size

We only measured chick maximum wing chord in 2009 and 2010. Only first broods were used in the analysis and 382 chicks from first broods were measured. Only 7- and 8-day-old chicks (n = 266 and 70 chicks, respectively) were included in the analyses because for other ages there was no contrast in feeding treatment in the dataset (they were either all fed or all control). Linear mixed models were used, with male ID as the random effect. Fixed effects in the full model were treatment, number of chicks in nest at time of measurement and year, plus the interactions of treatment x number of chicks and treatment x year.

Nest survival

We estimated daily nest survival rates using the Mayfield technique (Mayfield 1975). For each nest visited more than once, the number of days that the nest was active and the number of days failed (either 1 if the nest failed or 0 if it was active) were recorded. Generalised linear mixed models (binomial error family, logit link function) were then fitted, with male ID as the random effect. Treatment, date found, year and the treatment x year interaction were included as fixed effects in the full model.

Breeding attempts

The low frequency of multiple brooding did not allow us to fit models with individual ID as random effects. To avoid pseudoreplication, one data point was randomly selected per individual. General linear models (binomial error family because individuals either had multiple broods in a year (1) or did not (0), with logit link function) were then fitted to the data. Separate analyses were carried out for breeding males and breeding females. For males, treatment, hatching date, age and the interactions of treatment x hatching date and treatment x age were included in the full model. For females, the full model included treatment, hatching date and the treatment x hatching date interaction. Female age was not included in the models as less than half of the females could be aged as young or old.

RESULTS

We found 143 northern wheatear nests during 2008–2010 (Table S3.1, Supplementary Information). 128 of these were first clutches, three were re-lays after first clutch failure, eight were simultaneous clutches (additional clutches fathered by a male concurrently provisioning another nest) and four were second clutches (a clutch following a successful first clutch). The most direct measure of reproductive success is the number of fledglings produced, and so these results are described first. The other reproductive parameters are then examined to investigate in more detail the mechanisms by which the experimental increase in food availability may influence reproductive output.

Fledging success

Chicks fledged per breeding season

More young were fledged during the breeding season by fed males (mean ± SE = 6.32 ± 0.48 fledglings male^{-1}) than by control males (4.76 ± 0.27 fledglings male^{-1}). For breeding males, the only plausible model included the treatment x hatching date interaction and year. The Akaike weight of 0.746 indicated that this model was a three times better approximation than all other considered models combined (Table 3.2, Model 1). This showed that fed males tended to father more fledglings over the course of a season the earlier that they started breeding in a given season, while for control males, no such relationship existed (Fig. 3.2). There was also annual variation in the number of juveniles fledged per season per male. The number of fledglings per male was higher in 2010 than in 2009 and higher in 2009 than in 2008 (Table 3.3).

Table 3.2. Models fit to different reproductive parameters. AICc is the corrected Akaike's Information Criterion, ΔAICci is the difference in AICc between model i and the best model and wAICci is the Akaike weight. The plausible models (ΔAICci ≤ 2) are presented here; see Tables S2 – S14 for the full sets of candidate models. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt, age, trt x age).

Model ID	Reproductive parameter	Fixed effects	Random effects	df	$\Delta AICc_i$	$wAICc_i$
	chicks fledged male^{-1} breeding season^{-1}					
1		trt x HD, yr	male ID	7	0	0.746
	chicks fledged female^{-1} breeding season^{-1}					
2		yr	female ID	4	0	0.242
3		none	female ID	2	0.4	0.198
4		trt	female ID	3	0.5	0.190
5		trt, yr	female ID	5	1.2	0.132
	chicks fledged nesting attempt^{-1}					
6		yr	male ID	4	0	0.333
7		none	male ID	2	1.1	0.188
	egg survival to fledging					
8		none	male ID	2	0	0.351
9		HD	male ID	3	0.6	0.256
	clutch size					
10		none	-	1	0	0.399
11		yr	-	2	1.6	0.176
12		LD	-	2	1.9	0.152
	egg volume					
13		none	female ID	3	0	0.4968
14		FWing	female ID	4	2	0.1856
15		trt	female ID	4	2	0.1833
	incubation duration					
16		clutch	-	3	0	0.350
17		none	-	2	0.4	0.288
	hatching date					
18		trt, yr	male ID	5	0	0.219
19		trt, age, yr	male ID	6	0.2	0.194
20		trt x yr, age	male ID	7	1	0.134
21		trt x yr	male ID	6	1.2	0.122
22		yr	male ID	4	1.2	0.121
23		age, yr	male ID	5	1.5	0.102

Table 3.2, continued

	hatching success					
24		LD	female ID	3	0	0.404
25		none	female ID	2	0.9	0.258
	chick maximum wing chord					
26		trt x chicks, trt x yr, trt x date^{a}, age	male ID	11	0	0.244
27		trt x chicks, trt x yr, date^{a}, age	male ID	10	0.2	0.223
28		trt x chicks, trt x yr, age	male ID	9	0.4	0.196
29		trt x yr, age	male ID	7	2.0	0.090
	nest survival					
30		none	male ID	2	0	0.315
31		trt	male ID	3	0.7	0.225
32		date^{b}	male ID	3	1.6	0.140
33		trt, date^{b}	male ID	4	1.7	0.133
	breeding attempts per male per breeding season					
34		trt, HD	-	3	0	0.208
35		trt, age, HD	-	4	0.2	0.184
36		trt, age	-	3	0.8	0.139
37		trt	-	2	1.8	0.085
38		trt x HD	-	4	1.8	0.084

Fixed effects. trt: treatment (fed or control), age: male age (young (yearling) or old (2+)), yr: year, LD: lay date, FWing: female maximum wing chord, clutch: clutch size, chicks: number of 7- and 8-day-old nestlings, date^{a}: date of measurement (1 = 1st May), date^{b}: date found, HD: hatching date, none: intercept-only model.

Table 3.3. Model-averaged parameter estimates (estimates of fixed effects included in models with ΔAICc$_i \leq 2$ with contributions to average weighted by *w*AICc$_i$ of model), unconditional standard errors and 95% confidence intervals (Burnham and Anderson 2002). Interactions are indicated by x.

Reproductive parameter	Fixed effect	Estimate	SE	95% CI	
				Lower	Upper
chicks fledged per nesting attempt					
	yr2009^{a}	0.229	0.170	-0.103	0.562
	yr2010^{a}	0.350	0.160	0.037	0.663
egg survival to fledging					
	HD	-0.045	0.036	-0.116	0.025
chicks fledged per male per breeding season					
	yr2009^{a}	0.102	0.163	-0.217	0.421
	yr2010^{a}	0.358	0.154	0.057	0.659
	trt x HD	-0.045	0.015	-0.077	-0.014
chicks fledged per female per breeding season					
	yr2009^{a}	0.124	0.429	-0.717	0.965
	yr2010^{a}	0.268	0.417	-0.551	1.086
	trt	0.114	0.316	-0.505	0.734
clutch size					
	yr2010	0.088	0.123	-0.153	0.328
	LD	-0.005	0.011	-0.026	0.016
egg volume					
	FWing	-5.834	18.623	-42.335	30.667
	trt	-18.450	68.110	-151.946	115.046
incubation duration					
	clutch	-0.428	0.247	-0.912	0.056
hatching date					
	trt	-2.314	1.624	-5.498	0.870
	age^{a}	1.992	1.739	-1.416	5.401
	yr2010^{b}	4.210	1.598	1.077	7.343
	trt x yr2010^{b}	-3.213	2.967	-9.028	2.602
hatching success					
	LD	-0.138	0.083	-0.300	0.024
chick maximum wing chord					
	trt x chicks	2.061	1.327	-0.540	4.662
	trt x yr2010^{b}	-10.121	3.315	-16.619	-3.623
	trt x date^{a}	0.325	0.211	-0.089	0.738
	age^{b}	5.439	1.498	2.503	8.374
	date^{a}	0.154	0.010	-0.041	0.349

Table 3.3, continued

nest survival					
	trt	2.071	2.986	-3.781	7.924
	date^{b}	0.075	0.375	-0.659	0.809
breeding attempts per male per breeding season					
	trt	2.296	1.535	-0.712	5.304
	age^{a}	-1.552	1.553	-4.597	1.493
	HD	-0.1336	0.285	-0.691	0.424
	trt x HD	-0.113	0.177	-0.459	0.233

Fixed effects. trt: treatment (fed vs. control), age^{a}: male age (young (yearling) vs. old (2+)), yr2009^{a}: year 2009 vs. year 2008, yr2010^{a}: year 2010 vs. year 2008. yr2010^{b}: year 2010 vs. year 2009, LD: lay date, FWing: female maximum wing chord, clutch: clutch size, chicks: number of nestlings alive in brood at time of measurement, date^{a}: date of measurement (1 = 1st May), age^{b}: age of chicks, date^{b}: date found, HD: hatching date, none: intercept-only model.

More young were fledged by fed females (5.33 ± 0.25 fledglings female^{-1}) than by control females (4.68 ± 0.22 fledglings female^{-1}) (Table 3.3, Fig. 3.2). For breeding females, four out of the ten considered models were plausible predictors of the total number of chicks fledged over the breeding season ($\Delta\text{AICc}_i \leq 2$; Table 3.2, Models 2–5). The best model included year, but this was only 1.2 times better than the model with no fixed effects. Treatment was included in the third best model, and treatment and year in the fourth best. Yearly variation had a larger effect size than treatment (Table 3.3). The trend was for females to fledge more chicks in both 2009 and 2010 compared to 2008, with the most juveniles per female being fledged in 2010.

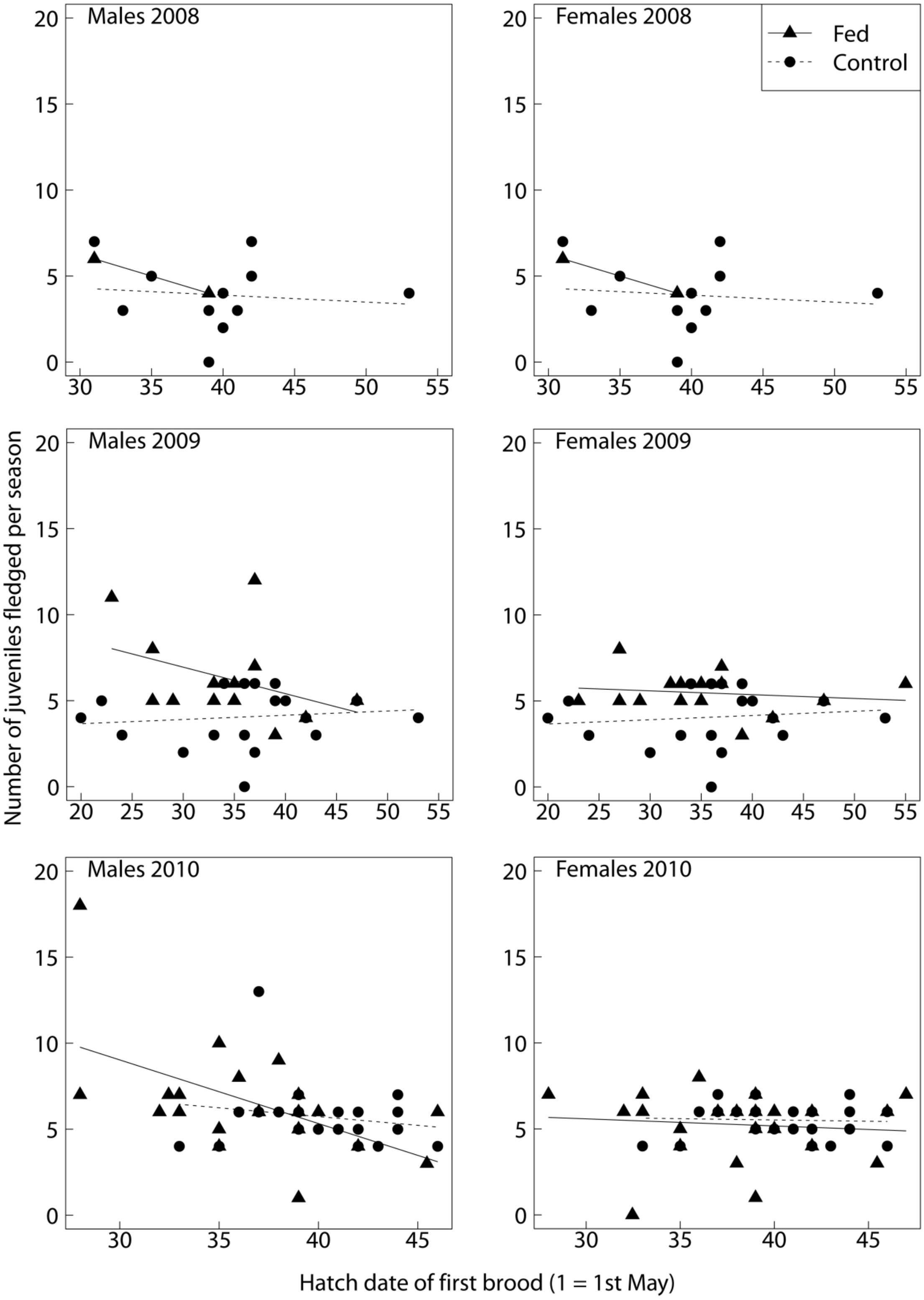

Fig. 3.2. The relationship between hatching date of first broods and number of juveniles fledged across the season for food-supplemented and control male and female wheatears in the three years of the study (2008-2010).

Chicks fledged per nesting attempt

There was no effect of food supplementation on the number of chicks fledged per nesting attempt amongst first broods (Table 3.2). There was, however, annual variation in the number of chicks fledged per nesting attempt; the number of chicks fledging per nest was highest in 2010 and lowest in 2008 (Table 3.3). The best fitting final model included only year as an explanatory factor, while the only other plausible final model ($\Delta \mathrm{AIC}_i \leq 2$) had no fixed effects (Table 3.2, Models 6–7).

Egg survival to fledging

The best model to explain number of chicks fledged per egg amongst first broods included no fixed effects (Table 3.2, Model 8). The only other plausible model included hatching date (Model 9). The survival of eggs to fledging was inversely related to hatching date (Table 3.3).

Clutch size

Mean clutch size was 6.3 eggs (range 4-8). Treatment was not included in any plausible model of clutch size. The best model included no fixed effects (Table 3.2, Model 10) and this model was more than twice as likely as either of the other two plausible models, which included year and laying date, respectively (Table 3.2, Models 11–12). There was a trend for clutch size to decrease with laying date (Table 3.3).

Egg volume

Mean egg volume (± SE) was 2761 ± 14.42 mm^3 (range 2036 – 3229 mm^3). The three plausible models for describing egg volume were the null model, the model containing female wing length and the model containing treatment (Table 3.2, Models 13–15).

Counter-intuitively, egg volume decreased with increasing female wing length (Table 3.3), and egg volume was lower in fed broods. There was little support for an effect of either female wing length or treatment on egg volume. However, the confidence intervals of both effects overlap zero (Table 3.3) and the AICc weights show that the null model is 2.58 and 2.71 times more probable than the female wing length-only model and the treatment-only model, respectively.

Incubation duration

The best model for describing incubation duration included only clutch size as a fixed effect, while the model including no fixed effects was the only other plausible model (Table 3.2, Models 16–17). Incubation duration declined with increasing clutch size (Table 3.3).

Hatching date

Variation between years was included in all six plausible models of hatching date (Table 3.2, Models 18–23), with mean hatch date 4.2 days later in 2010 than 2009 (Table 3.3). Three of the six plausible models indicated that the clutches of younger males hatched later than those of older males (Table 3.2, Models 19, 20 and 23). Mean hatch date of broods of fed birds was 2.3 days earlier than broods of control birds across the two years (Table 3.3, Fig. 3.3). Two of the plausible models included the interaction of treatment x year (Table 3.2, Models 20 and 21). This suggested that the effect of treatment on hatching date was stronger in 2010 than 2009. Broods of fed birds hatched approximately 3 days earlier than did broods of control birds in 2010 (Table 3.3, Fig. 3.3).

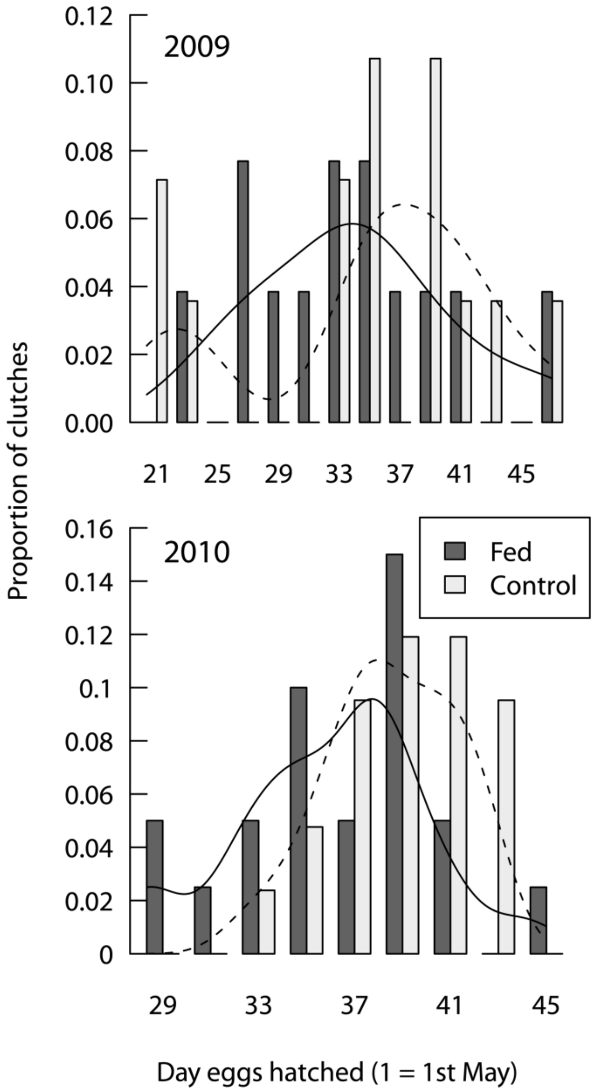

Fig. 3.3. Distribution of dates of hatching of first clutches in 2009 and 2010 according to treatment. Density estimation curves are superimposed to aid interpretation (solid = fed, dashed = control).

Hatching success

4 out of 62 clutches failed to hatch, due to predation and rabbit disturbance. The best model of hatching success included only laying date (Table 3.2, Model 24), with a trend for hatching success to decline with laying date (Table 3.3). The null model was the only other plausible model (Table 3.2, Model 25).

Chick size

Treatment x year was included in all four plausible models of chick size (chick maximum wing chord) (Table 3.2, Models 26–29) and the effect of food supplementation was greater in 2009 than 2010 (Fig. 3.4). Treatment x brood size was included in three of the four plausible models (Models 26–28). Food supplementation had a greater positive effect on chick size in larger broods (Table 3.3). Treatment x date was included in one of the plausible models (Model 26) and date was included in one other plausible model (Model 27). The impact of food supplementation appeared to increase with date, while chick size also appeared to increase with date (Table 3.3).

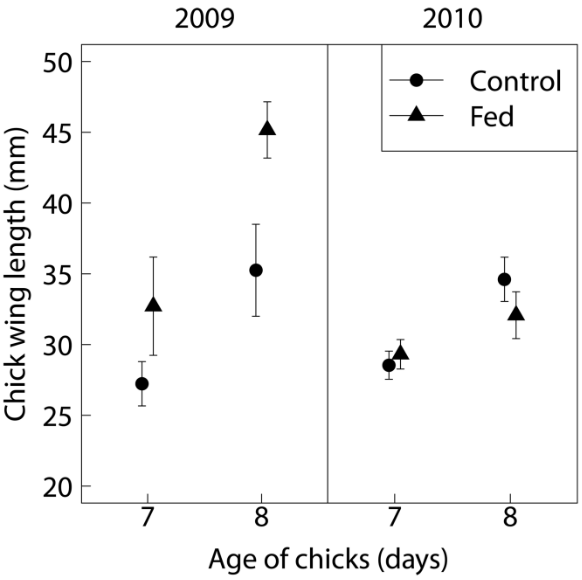

Fig. 3.4. Variation in wing length (mean ± 95 % confidence limits) in relation to age for fed and control chicks in 2009 and 2010.

Nest survival

Out of 43 nests of fed parents, 41 were successful (i.e. ≥ 1 chick fledged) and 60 of 67 nests of control parents were successful. Mayfield daily nest survival rates (mean ± SE) were 99.6 ± 4.0 % for nests of fed parents and 97.4 ± 1.8 % for nests of control parents. The null model was the most likely of the considered models (Table 3.2, Model 30). Treatment was included in two of the four plausible models (Table 3.2, Models 31 and

33), as was finding date (Table 3.2, Models 32 and 33). However, the confidence intervals for the effects of both treatment and finding date indicated little statistical support for either variable (Table 3.3).

Number of breeding attempts

Multiple breeding attempts by individual wheatears were recorded in 2009 and 2010, but not in 2008 (Table 3.4). There were more second broods in 2009 than in 2010 but more simultaneous broods in 2010 than 2009.

Males

Nine out of 41 fed males and one out of 61 control males had multiple broods. Treatment was included in all five plausible models (Table 3.2, Models 34–38). Hatching date was included in three of the plausible models (Table 3.2, Models 34–35 and 38) and male age was included in two of the plausible models (Table 3.2, Models 35–36). The interaction of treatment x hatching date was included in one of the plausible models (Table 3.2, Model 38). Food supplementation had a larger effect than the other independent variables on the probability of multiple brooding (Table 3.3). Multiple brooding by males was more likely if they were old and/or had first broods that hatched early (Table 3.3). The treatment x hatching date interaction indicated that the difference in probability of multiple brooding between fed and control males declined with hatching date (Table 3.3).

Females

Four out of 41 fed females had second broods (these were all consecutive broods with the same male), whereas none of the 61 unfed females had second broods. Fed females were significantly more likely to have multiple broods than control females (Fisher's Exact Test $P = 0.027$). As there were no cases of multiple broods within the control group of females, we did not use linear modelling to test for an effect of food supplementation on multiple brooding by females.

DISCUSSION

Numerous studies have demonstrated that insects (the main food source of small migratory birds) respond to changes in temperature, with effects including altered phenology, distribution and abundance (e.g. Parmesan et al. 1999, Altermatt 2010, Hill et al. 2011). In this study we simulated experimentally the effects of climate-driven changes in food availability on the reproductive performance of a model species of long-distance migratory insectivorous bird. The experimental increase in food availability led to an increase in the annual reproductive output of the northern wheatears breeding on Fair Isle and our detailed measurement of reproductive parameters within this experiment allows us to identify the likely mechanisms by which changes in food availability (such as those driven by climate change) may impact on the reproductive output of migrant birds.

Food supplementation did not appear to influence the success of individual nesting attempts, but was associated with increases in the number of fledglings produced across the whole breeding season (from a mean of 4.4 to 6.3 young fledged per male and from 4.3 to 5.3 per female). The main changes in the reproductive parameters underpinning this increased reproductive output across the season were changes in hatching date, chick size and the number of breeding attempts. Specifically, increased food availability led to an advance in hatching date of first broods by approximately 2.3 days, an increase in the wing length of chicks measured at 7 days of age in 2009 (but not in 2010) (which could either represent a larger fledging size, or more rapid growth towards an unaltered fledging size) and an increase in second and simultaneous breeding attempts.

The increase in the number of breeding attempts primarily involved those individuals that both started breeding early and were food supplemented. This effect was especially pronounced for male wheatears, due to an increase in simultaneous brooding (i.e. two or more nests with different females) in addition to second brooding. In contrast, female wheatears appear unable to maintain two nests simultaneously, and so were limited to second brooding as a means to increase their numbers of breeding attempts. The magnitude of this impact of the supplementary feeding on annual reproductive output varied between years; the smaller effect of the treatment in 2010 being mainly due to the higher success of control nests relative to that in 2009. This suggests that reproduction is more strongly constrained by food availability in some years than in others, presumably due to variation in natural food availability and/or weather conditions. Consistent with our findings, food supplementation led to increases in number of breeding attempts in black-throated blue warblers (Nagy and Holmes 2005) and song sparrows (*Melospiza melodia*) (Arcese and Smith 1988), while experimental and natural reductions in food availability led to fewer nesting attempts in black-throated blue warblers (Rodenhouse and Holmes 1992). In contrast, a food reduction experiment indicated that red-eyed vireos (a single-brooded neo-tropical migrant) delayed laying when food abundance was low, but there was little effect on reproductive success (Marshall et al. 2002), while one recent study found that brood sizes of blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) were reduced by food supplementation (Harrison et al. 2010). The latter two examples indicate that caution is needed in the extent to which the results of food supplementation experiments should be generalised across species.

The earlier date of first clutches (as measured by hatching date) induced by food supplementation may have contributed to an increased reproductive output through two different mechanisms. Firstly, there was a trend for clutch size to be larger in earlier first clutches. Clutch size sets the upper limit on reproductive success of a breeding attempt, so larger early clutches could potentially produce more fledged chicks. We found no evidence, however, that the food supplementation itself increased either clutch size, or the number of chicks fledged from first broods. Secondly, wheatears that initiated their first brood earlier and had access to supplemental food were more likely to have second broods (or, in the case of males, have simultaneous broods) than food-supplemented wheatears that initiated their first brood later, or than non-supplemented control birds. A higher proportion of pairs that initiated a first brood subsequently initiated second broods in 2009 (6.5 %) than in 2010 (1.9 %), which is consistent with the earlier start to breeding in 2009 (the earliest hatch date in 2009 was 8 days earlier than that in 2010). The proportion of males initiating simultaneous broods was, however, higher in 2010 (9.6 %) than 2009 (4.3 %). The time to complete simultaneous broods should be approximately the same as single broods, while completing a second brood will approximately double the duration of the breeding period. The frequency of second brooding is therefore likely to be more dependent than the frequency of simultaneous brooding on a long breeding season.

These results together suggest that an increase in food availability across the breeding season may lead to earlier (and possibly larger) first clutches, followed by additional reproductive attempts. Additional breeding attempts were very rare in early-breeding control pairs, suggesting that the increase in the number of breeding attempts was likely to depend on food availability in combination with early breeding, and not just on early breeding *per se*.

Similar effects of food supplementation on breeding date have been described in other passerine species. Food supplementation of European blackbirds (*Turdus merula*) led to advances in laying date of yearling females but not older females (Desrochers 1992). The fed yearling females had laying dates similar to those of older females (fed or control), while control yearling females had later laying dates. Birds initiating first broods later were less likely than earlier-starting birds to make second breeding attempts, and so breeding productivity for the whole breeding season declined with laying date of the first clutch. Similarly, food supplementation of great tits advanced laying date to a greater degree in yearling females than in older females (Källander 1974). It was suggested that later laying by yearling females under control (unsupplemented) conditions was due to lack of experience and therefore reduced foraging efficiency.

These results are broadly consistent with an earlier observational study of northern wheatears in East Anglia, UK (Tye 1992), where earlier breeding was associated with greater fledging success of first broods and with a higher probability of second brooding (though not with an increase in clutch size). An increase in clutch size with earlier laying is, however, well documented in the literature for a range of species (e.g. Winkler and Allen 1996), including northern wheatears; in a long-term study in Sweden, laying date of wheatears was inversely related to reproductive output, although laying date was not as important as age in explaining reproductive success (Pärt 2001a). Older male wheatears had higher reproductive success than yearling males, probably because older birds arrive on breeding grounds earlier and potentially gain the best territories (Pärt 2001a, 2001b). In the present experimental study, hatching date was important in explaining the extent to which wheatears improved reproductive output with increased food availability (and therefore improved territory quality) via the number of breeding attempts. High quality early-arriving males with supplementary food may be able to expend more energy on defending larger territories and attracting mates, while lower quality late-arriving males may be more constrained in their territory choice, and hence in their ability to attract additional females for simultaneous broods, or to initiate a consecutive breeding attempt.

The low rates of total nest failure in this study are in stark contrast with the studies of wheatears in East Anglia and Sweden. Only about 8 % of first clutches in the current study failed to produce any fledglings, while total failure rates of about 41 %, 30 % and 21 % were recorded in East Anglia (Tye 1992) and two studies in Sweden (Moreno 1989, Arlt et al. 2008), respectively, most of which were due to predation. Such low natural failure rates on Fair Isle make it less likely that an effect of food availability on nest survival rates would be detectable. The low level of nest predation risk on Fair Isle may lead to brood-provisioning adult wheatears spending more time foraging and less time in predator-avoidance behaviour (e.g. vigilance) than in locations with greater predation levels. It is possible that increases in food availability have a greater effect on the reproductive parameters measured on Fair Isle than among wheatears living in areas with greater predation risk, such as Sweden or East Anglia, and this would be an interesting avenue of future research.

In addition to increasing the number of chicks fledging over the season, the experimentally increased food availability in the present study also resulted in increased chick quality (and therefore probably fledgling quality), as measured by chick size. There was variation between years in the magnitude of the impact of food supplementation on chick size, suggesting that food availability is not always limiting to chick growth under current natural (unsupplemented) conditions. In 2009, the chicks of food-supplemented pairs were larger than the chicks of unsupplemented pairs, suggesting that chick growth was being limited by the parents' ability to find food. These results are consistent with those of natural and experimental food reduction, which led to decreased nestling growth rates of black-throated blue warblers (Rodenhouse and Holmes 1992). In contrast, in 2010 there was no difference in the size of wheatear chicks between food-supplemented and control pairs, suggesting that chick growth in this year was not being limited by food availability. It is not known if the observed difference in chick size between treatment groups in 2009 was due to greater female investment in eggs (i.e. egg size) or to a greater delivery of food to the nestlings, or both of these explanations (egg size was not recorded in 2009, but in 2010 there was no effect of food-supplementation on egg volume).

Although food supplementation had measurable effects on hatching date, the number of breeding attempts and chick growth, other parts of the breeding cycle appeared to be unaffected by changing food availability. There was no difference in clutch size or hatchling survival of first broods, while there were only marginal effects on hatching success (due mainly to poor hatching success of two early control nests). These results together explain why food-supplementation also did not increase the number of chicks fledged from first broods. Similarly, food supplementation had no effect on number of fledglings from first broods in black-throated blue warblers (Nagy and Holmes 2005), while clutch size was higher in food-supplemented pairs in only five of 14 reviewed species (comprising non-migratory and short-distance migrant species) (Arcese and Smith 1988).

The present study provides evidence that the number of breeding attempts that can be fitted into each breeding season, and hence the total number of chicks that can be produced, is currently limited both by food availability, and by the date of initiation of the first brood - which is itself limited by food availability. Our food supplementation was uniformly high across the whole breeding season, yet high altitude and high latitude moorland habitats typically have short growing/breeding seasons, with highly peaked food availability for breeding birds such as wheatears (Both 2010). Climate-induced changes in natural food availability at the start and end of the season are therefore predicted to have a particularly strong effect on the number of breeding attempts that can be fitted into the breeding season. This will be the case for those individuals which are able to initiate and complete their first brood early enough to initiate a second brood, which would tend to intensify selection for early breeding. Phenological changes associated with climate change are, indeed, already resulting in earlier spring arrivals and longer durations of stay on the breeding grounds of wheatears and many other species (e.g. Cotton 2003), which would facilitate the ability of birds to fit additional breeding attempts into the breeding season - if food availability allows. The variation between years in the frequency of second broods in our study suggests that other factors (e.g. weather and availability of key prey taxa) as well as overall food availability may affect multiple brooding.

This study has shown that changes in food availability of the northern wheatear affect both breeding phenology following arrival on the breeding grounds, nestling growth and reproductive output. This identifies a likely mechanism by which climate change may affect the reproductive performance of long-distance migratory birds via climate-driven changes in their food supply. Caution is required in extrapolating the results of our 3-year experiment with northern wheatears in Shetland, UK, to other populations, species or even to other years (Both 2010). There may be latitudinal (and / or altitudinal) and between-year variations in the degree of food-limitation of breeding productivity. Equivalent longitudinal studies at northern and southern range margins of the northern wheatear may aid in the prediction of climate change impacts on distributional changes. Furthermore, our experiment isolates the effects of increases in food availability on breeding parameters, but there may also be independent, direct effects of temperature on breeding parameters (e.g. via thermoregulation and incubation behaviours of parent birds) (Stevenson and Bryant 2000, Salvante et al. 2007, Visser et al. 2009).

The effects of climate change on the phenology and overall abundance of invertebrate prey are currently poorly understood and may differ substantially between the short-, medium- and long-term as temperature variations increasingly exceed the range to which indigenous invertebrate taxa are physiologically and genetically adapted. Our experimental manipulations were not designed to mimic specific climate change scenarios. Rather, our experiment measures the degree of behavioural flexibility of a range of different breeding parameters to increases in food availability, revealing the extent to which individual birds can respond instantly to current changes in environmental conditions. If the range of climate (and thus food) variability that the birds' phenotypic plasticity encompasses is exceeded, then there will be selective pressure for evolutionary change. Indeed phenotypic plasticity, combined with genetic variance, contributes to the phenotypic variation on which selection can act, facilitating evolutionary change.

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REFERENCES

Ahola, M., T. Laaksonen, K. Sippola, T. Eeva, K. Rainio, and E. Lehikoinen. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. Global Change Biology 10:1610-1617.

Altermatt, F. 2010. Climatic warming increases voltinism in European butterflies and moths. Proceedings of the Royal Society B: Biological Sciences 277:1281-7.

Arcese, P., and J. N. M. Smith. 1988. Effects of population density and supplemental food on reproduction in song sparrows. Journal of Animal Ecology 57:119-136.

Arlt, D., P. Forslund, T. Jeppsson, and T. Pärt. 2008. Habitat-specific population growth of a farmland bird. PloS ONE 3:e3006.

Arlt, D., and T. Pärt. 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. Ecology 88:792-801.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8:1–16.

Bates, D., and M. Maechler. 2009. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-32.

Beale, C. M., I. J. Burfield, I. M. W. Sim, G. W. Rebecca, J. W. Pearce-Higgins, and M. C. Grant. 2006. Climate change may account for the decline in British ring ouzels *Turdus torquatus*. Journal of Animal Ecology 75:826-35. doi

Both, C. 2010. Food availability, mistiming, and climatic change. Pages 129-147 *in* A. P. Møller, W. Fiedler, and P. Berthold, editors. Effects of Climate Change on Birds. Oxford University Press, Oxford.

Both, C., M. van Asch, R. G. Bijlsma, A. B. van den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? Journal of Animal Ecology 78:73-83.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81-83.

Buchanan, G. M., M. C. Grant, R. A. Sanderson, and J. W. Pearce-Higgins. 2006. The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. Ibis 148:615-628.

Burfield, I. J., and F. P. J. Van Bommel. 2004. Birds in Europe: Population Estimates, Trends and Conservation Status. Page 374. BirdLife International, Cambridge.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach. Springer-Verlag, New York.

Clement, P. 1997. Wheatear *Oenanthe oenanthe*. Pages 530-531 *in* W. J. M. Hagemeijer and M. J. Blair, editors. The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. T & A.D. Poyser, London.

Conder, P. 1989. The Wheatear. Christopher Helm, London.

Cotton, P. A. 2003. Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences 100:12219-12222.

Cramp, S. (Ed.). 1988. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Volume V: Tyrant flycatchers to thrushes. Oxford University Press, Oxford.

Currie, D., D. B. A. Thompson, and T. Burke. 2000. Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. Ibis 142:389-398.

Dell, D., T. H. Sparks, and R. L. H. Dennis. 2005. Climate change and the effect of increasing spring temperatures on emergence dates of the butterfly *Apatura iris* (Lepidoptera: Nymphalidae). European Journal of Entomology 102:161–167.

Desrochers, A. 1992. Age-related differences in reproduction by European blackbirds: restraint or constraint? Ecology 73:1128 - 1131.

Gordo, O., and J. J. Sanz. 2006. Climate change and bird phenology: a long-term study in the Iberian Peninsula. Global Change Biology 12:1993-2004.

Hagan, J. M., and D. W. Johnston (Eds.). 1992. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institute Press, Washington, DC.

Harrison, T. J. E., J. A. Smith, G. R. Martin, D. E. Chamberlain, S. Bearhop, G. N. Robb, and S. J. Reynolds. 2010. Does food supplementation really enhance productivity of breeding birds? Oecologia 164:311-320.

Heldbjerg, H., and T. Fox. 2008. Long-term population declines in Danish trans-Saharan migrant birds. Bird Study 55:267-279.

Helmuth, B., J. G. Kingsolver, and E. Carrington. 2005. Biophysics, physiological ecology, and climate change: does mechanism matter? Physiology 67:177-201.

Hill, J. K., H. M. Griffiths, and C. D. Thomas. 2011. Climate change and evolutionary adaptations at species' range margins. Annual Review of Ecology and Systematics 56:143-159.

Hughes, L. 2000. Biological consequences of global warming: is the signal there already. Trends in Ecology & Evolution 15:56-61.

IPCC. 2007. Summary for policymakers. Page *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate Change 2007: The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge.

Illera, J. C., and M. Díaz. 2006. Reproduction in an endemic bird of a semiarid island: a food-mediated process. Journal of Avian Biology 37:447-456.

Jàrvinen, A. 1994. Global warming and egg size of birds. Ecography 17:108-110.

Kneis, P. 1982. Zur verbreitung und bestandsentwicklung, habitatund und nistplatzwahl sowie reproduktion des steinschmatzers *Oenanthe oenanthe* in der DDR: analyse der beringungsdaten 1964 bis 1978. Berichte aus der Vogelwarte Hiddensee 3:55-81.

Källander, H. 1974. Advancement of laying of great tits by the provision of food. Ibis 116:365-367.

Laaksonen, T., M. Ahola, T. Eeva, R. A. Väisänen, and E. Lehikoinen. 2006. Climate change, migratory connctivity and changes in laying date and clutch size of the pied flycatcher. Oikos 114:277–290.

Marshall, M. R., R. J. Cooper, J. A. DeCecco, J. Strazanac, and L. Butler. 2002. Effects of experimentally reduced prey abundance on the breeding ecology of the red-eyed vireo. Ecological Applications 12:261–280.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics 18:453-487.

Mayfield, H. F. 1975. Suggestions for calculating nest success. The Wilson Bulletin 87:456–466.

McMahon, C. R., and H. R. Burton. 2005. Climate change and seal survival: evidence for environmentally mediated changes in elephant seal, *Mirounga leonina*, pup survival. Proceedings of the Royal Society B: Biological Sciences 272:923-928.

Miles, J. E., J. S. Bale, and I. D. Hodkinson. 1997. Effects of temperature elevation on the population dynamics of the upland heather psyllid *Strophingia ericae* (Curtis) (Homoptera: Psylloidea). Global Change Biology 3:291–297.

Moreno, J. 1989. The breeding biology of the wheatear *Oenanthe oenanthe* in South Sweden during three contrasting years. Journal of Ornithology 130:321-334.

Murphy, J. M., D. M. H. Sexton, G. J. Jenkins, B. B. B. Booth, C. C. Brown, R. T. Clark, M. Collins, G. R. Harris, E. J. Kendon, R. A. Betts, S. J. Brown, K. A. Humphrey, M. P. McCarthy, R. E. McDonald, A. Stephens, C. Wallace, R. Warren, R. Wilby, and R. Wood. 2009. UK Climate Projections Science Report: Climate change projections. Exeter, UK.

Musters, C. J. M., W. J. ter Keurs, and G. R. de Snoo. 2010. Timing of the breeding season of black-tailed godwit *Limosa limosa* and northern lapwing *Vanellus vanellus* in The Netherlands. Ardea 98:195-202.

Møller, A. P., W. Fiedler, and P. Berthold (Eds.). 2004. Advances in Ecological Research: Birds and Climate Change. Elsevier, Amsterdam.

Møller, A. P., W. Fiedler, and P. Berthold (Eds.). 2010. Effects of Climate Change on Birds. Oxford University Press, New York.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences 105:16195-16200.

Nagy, L. R., and R. T. Holmes. 2005. Food limits annual fecundity of a migratory songbird: an experimental study. Ecology 86:675–681.

Nolan, A. J., P. D. Hulme, and D. Wheeler. 1994. The status of *Calluna vulgaris* (L.) Hull on Fair Isle. Botanical Journal of Scotland 47:1-16.

Panov, E. N. 2005. Wheatears of Palearctic: Ecology, Behaviour and Evolution of the Genus *Oenanthe*. Page 439. Pensoft, Sofia-Moscow.

Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, and M. S. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579-583.

Pearce-Higgins, J. W., P. Dennis, M. J. Whittingham, and D. W. Yalden. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. Global Change Biology 16:12-23.

Pearce-Higgins, J. W., and D. W. Yalden. 2004. Habitat selection, diet, arthropod availability and growth of a moorland wader: the ecology of European golden plover *Pluvialis apricaria* chicks. Ibis 146:335–346.

Pärt, T. 2001a. The effects of territory quality on age-dependent reproductive performance in the northern wheatear (*Oenanthe oenanthe*). Animal Behaviour 62:379-388.

Pärt, T. 2001b. Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. Proceedings of the Royal Society B: Biological Sciences 268:2267-2271.

R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rajchard, J., J. Procházka, and P. Kindlmann. 2006. Long-term decline in common swift *Apus apus* annual breeding success may be related to weather conditions. Ornis Fennica 83:66-72.

Rodenhouse, N. L., and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding black-throated blue warblers. Ecology 73:357-372.

Salvante, K. G., R. L. Walzem, and T. D. Williams. 2007. What comes first, the zebra finch or the egg: temperature-dependent reproductive, physiological and behavioural plasticity in egg-laying zebra finches. Journal of Experimental Biology 210:1325-1334.

Stevenson, I. R., and D. M. Bryant. 2000. Climate change and constraints on breeding. Nature 406:366-367.

Strathdee, A. T., J. S. Bale, W. C. Block, S. J. Coulson, I. D. Hodkinson, and N. R. Webb. 1993. Effects of temperature elevation on a field population of *Acyrthosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen. Oecologia 96:457–465.

Studds, C. E., and P. P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Climate Research 35:115-122.

Studds, C. E., and P. P. Marra. 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. Proceedings of the Royal Society B: Biological Sciences:rspb.2011.0332.

Svensson, L. 1992. Identification Guide to European Passerines, 4th edition. British Trust for Ornithology, Norfolk.

Thaxter, C. B., A. C. Joys, R. D. Gregory, S. R. Baillie, and D. G. Noble. 2010. Hypotheses to explain patterns of population change among breeding bird species in England. Biological Conservation 143:2006-2019.

Torti, V. M., and P. O. Dunn. 2005. Variable effects of climate change on six species of North American birds. Oecologia 145:486–495.

Tye, A. 1992. Assessment of territory quality and its effects on breeding success in a migrant passerine, the wheatear *Oenanthe oenanthe*. Ibis 134:273-285.

Visser, M. E., L. J. M. Holleman, and S. P. Caro. 2009. Temperature has a causal effect on avian timing of reproduction. Proceedings of the Royal Society B: Biological Sciences 276:2323-31.

Visser, M. E., A. J. Van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings of the Royal Society B: Biological Sciences 265:1867-1870.

White, T. C. R. 2008. The role of food, weather and climate in limiting the abundance of animals. Biological Reviews 83:227-248.

Whittingham, L. A., P. O. Dunn, and J. T. Lifjeld. 2007. Egg mass influences nestling quality in tree swallows, but there is no differential allocation in relation to laying order or sex. The Condor 109:585–594.

Wilson, S., and K. Martin. 2010. Variable reproductive effort for two ptarmigan species in response to spring weather in a northern alpine ecosystem. Journal of Avian Biology 41:319-326.

Winkel, W., and H. Hudde. 1997. Long-term trends in reproductive traits of tits (*Parus major*, *P. caeruleus*) and pied flycatchers *Ficedula hypoleuca*. Journal of Avian Biology 28:187-190.

Winkler, D. W., and P. E. Allen. 1996. The seasonal decline in tree swallow clutch size: physiological constraint or strategic adjustment? Ecology 77:922-932.

SUPPORTING INFORMATION (TABLES S3.1–S3.14)

Table S3.1. Total number of first, re-lay (clutch following failure of first clutch), second (clutch following successful first clutch, i.e. ≥ 1 chick fledged) and simultaneous (clutch initiated by male with a different female before completion of active first clutch) clutches recorded in each of the three years of this study.

Year	Treatment	Clutch type			
		First	Re-lay	Simultaneous	Second
2008	Fed	9	0	0	0
	Control	21	0	0	0
2009	Fed	19	0	2	3
	Control	27	1	0	0
2010	Fed	25	1	5[a]	1
	Control	27	1	1	0

[a] Two of these clutches were fathered by the same male.

Table S3.2. Model comparisons for number of juveniles fledged per male per season. As including male age reduced the data set from 92 to 76, and it was insignificant in all cases, it was excluded in the final analyses. Random effect is Male ID. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model $_i$ and the best model and $wAICc_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	$\Delta AICc_i$	$wAICc_i$
trt x HD, yr	-37.69	7	90.7	0	0.746
trt x HD, trt x yr	-37.21	9	94.6	3.9	0.106
trt x HD	-42.33	5	95.4	4.7	0.073
trt, HD, yr	-41.61	6	96.2	5.5	0.048
trt, yr	-44.03	5	98.8	8	0.013
trt, HD	-45.93	4	100.3	9.6	0.006
trt	-47.10	3	100.5	9.8	0.006
yr	-47.04	4	102.5	11.8	0.002
HD	-49.21	3	104.7	14	< 0.001
none	-51.18	2	106.5	15.8	< 0.001

Fixed effects: trt: treatment (fed or control), yr: year, HD: hatching date of first brood (earliest brood if male had simultaneous broods), none: intercept-only model.

Table S3.3. Model comparisons for number of juveniles fledged per female per season. Random effect is female ID. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model $_i$ and the best model and $wAICc_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	$\Delta AICc_i$	$wAICc_i$
yr	-34.14	4	76.7	0	0.242
none	-36.49	2	77.1	0.4	0.198
trt	-35.47	3	77.2	0.5	0.190
trt, yr	-33.64	5	77.9	1.2	0.132
HD	-36.49	3	79.2	2.5	0.069
trt, HD	-35.47	4	79.4	2.7	0.064
trt, HD, yr	-33.61	6	80.1	3.4	0.044
trt x HD	-35.03	5	80.7	4	0.033
trt x HD, yr	-33.16	7	81.6	4.9	0.021
trt x HD, trt x yr	-31.83	9	83.7	7	0.007

Fixed effects: trt: treatment (fed or control), yr: year, HD: hatching date of first brood, none: intercept-only model.

Table S3.4. Model comparisons for number of fledglings per first nesting attempt. First broods only, offered excluded, excludes total failures due to predation. Random effect is Male ID. AICc is the corrected Akaike's Information Criterion, ΔAICc$_i$ is the difference in AICc between model $_i$ and the best model and *w*AICc$_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	ΔAICc$_i$	wAICc$_i$
yr	-17.12	4	42.7	0	0.333
none	-19.85	2	43.8	1.1	0.188
yr, HD	-17.02	5	44.7	2.1	0.119
trt, yr	-17.11	5	44.9	2.2	0.109
trt	-19.72	3	45.7	3	0.074
HD	-19.76	3	45.8	3.1	0.070
trt, yr, HD	-17.02	6	47	4.3	0.038
trt, HD	-19.67	4	47.8	5.1	0.026
trt x HD, yr	-16.74	7	48.8	6.1	0.016
trt x yr	-17.00	7	49.3	6.6	0.012
trt x HD	-19.48	5	49.6	7	0.010
trt x yr, HD	-16.90	8	51.5	8.9	0.004
trt x HD, trt x yr	-16.68	9	53.6	10.9	0.001

Fixed effects: trt: treatment (fed or control), yr: year, HD: hatching date, none: intercept-only model.

Table S3.5. Model comparisons for fledging success: the proportion of all chicks per nest that fledged. Random effect is Male ID. AICc is the corrected Akaike's Information Criterion, ΔAICc$_i$ is the difference in AICc between model $_i$ and the best model and *w*AICc$_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	ΔAICc$_i$	wAICc$_i$
none	-47.28	2	98.8	0	0.352
HD	-46.48	3	99.4	0.6	0.257
trt	-47.27	3	101	2.2	0.117
trt, HD	-46.48	4	101.7	2.9	0.081
yr	-46.77	4	102.3	3.5	0.061
trt x HD	-45.64	5	102.4	3.6	0.057
yr, HD	-46.04	5	103.2	4.4	0.038
trt, yr	-46.77	5	104.7	5.9	0.018
trt, yr, HD	-46.02	6	105.7	6.9	0.011
trt x HD, yr	-45.14	7	106.5	7.7	0.008

Fixed effects: trt: treatment (fed or control), yr: year, HD: hatching date, none: intercept-only model.

Table S3.6. Linear model comparisons for clutch size. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model $_i$ and the best model and $wAICc_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	$\Delta AICc_i$	$wAICc_i$
none	-107.77	1	217.6	0	0.399
yr	-107.51	2	219.2	1.6	0.176
LD	-107.66	2	219.5	1.9	0.152
trt	-107.77	2	219.8	2.1	0.137
LD, yr	-107.40	3	221.2	3.6	0.065
LD, FW, yr	-107.37	4	223.5	5.9	0.021
trt, LD, yr	-107.40	4	223.6	5.9	0.020
trt, FW, yr	-107.48	4	223.7	6.1	0.019
trt, LD, FW, yr	-107.37	5	225.9	8.3	0.006
trt x LD, FW, yr	-107.37	6	228.4	10.8	0.002
trt x yr	-107.43	6	228.5	10.9	0.002
trt x LD, trt x yr, FW	-107.35	7	231	13.4	< 0.001

Fixed effects: trt: treatment (fed or control), yr: year, LD: lay date, FWing: female wing length, none: intercept-only model.

Table S3.7. Model comparisons for egg volume. Random effect is female ID. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model $_i$ and the best model and $wAICc_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	$\Delta AICc_i$	$wAICc_i$
none	-1523	3	3052.4	0	0.4978
FWing	-1523	4	3054.4	2	0.186
trt	-1523	4	3054.4	2	0.183
trt, FWing	-1523	5	3056.4	4	0.068
trt x FWing	-1522	6	3056.4	4	0.067

Fixed effects: trt: treatment (fed or control), FWing: female wing length, none: intercept-only model.

Table S3.8. Linear model comparisons for incubation duration in 2009 and 2010. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model $_i$ and the best model and $wAICc_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	$\Delta AICc_i$	$wAICc_i$
clutch	-30.37	3	68.1	0	0.350
none	-31.92	2	68.5	0.4	0.288
clutch, FWing	-30.27	4	70.9	2.8	0.086
FWing	-31.80	3	70.9	2.9	0.084
trt, clutch	-30.34	4	71	2.9	0.080
trt	-31.90	3	71.1	3	0.077
trt, FWing	-31.78	4	73.9	5.8	0.019
trt, clutch, FWing	-30.24	5	74.2	6.1	0.016

Fixed effects: trt: treatment (fed or control), FWing: female wing length, clutch: clutch size, none: intercept-only model.

Table S3.9. Model comparisons for hatching date. Random effect is Male ID. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model $_i$ and the best model and $wAICc_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	$\Delta AICc_i$	$wAICc_i$
trt, yr	-209.3	5	429.5	0	0.219
trt, age, yr	-208.2	6	429.8	0.2	0.194
trt x yr, age	-207.3	7	430.5	1	0.134
trt x yr	-208.7	6	430.7	1.2	0.122
yr	-211.0	4	430.7	1.2	0.121
age, yr	-210.0	5	431.1	1.5	0.102
trt x age, yr	-208.2	7	432.2	2.7	0.057
trt x age, trt x yr	-207.3	8	433.1	3.5	0.037
trt	-214.2	4	437	7.5	0.005
none	-215.6	3	437.5	7.9	0.004
trt, age	-213.6	5	438.2	8.7	0.003
age	-215.0	4	438.7	9.1	0.002

Fixed effects: trt: treatment (fed or control), age: male age (young (yearling) or old (2+)), yr: year, none: intercept-only model.

Table S3.10. Model comparisons for hatching success. Random effect is female ID. The interaction treatment x year could not be included in any model because of convergence problems. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model $_i$ and the best model and $wAICc_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	$\Delta AICc_i$	$wAICc_i$
LD	-49.66	3	105.7	0	0.404
none	-51.21	2	106.6	0.9	0.258
trt, LD	-49.66	4	108	2.3	0.129
trt	-51.14	3	108.7	3	0.091
trt x LD	-49.42	5	109.9	4.2	0.050
LD, yr	-49.58	5	110.2	4.5	0.042
trt, LD, yr	-49.58	6	112.7	7	0.012
trt, yr	-51.13	5	113.3	7.6	0.009
trt x LD, yr	-49.35	7	114.8	9	0.004

Fixed effects: trt: treatment (fed or control), yr: year, LD: lay date, none: intercept-only model.

Table S3.11. Model comparisons for maximum wing chord of 7- and 8-day-old chicks in 2009 and 2010. Random effect is Male ID. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model $_i$ and the best model and $wAICc_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	$\Delta AICc_i$	$wAICc_i$
trt x chicks, trt x date, trt x yr, age	-955.4	11	1933.6	0	0.244
trt x chicks, trt x yr, date, age	-956.6	10	1933.8	0.2	0.223
trt x chicks, trt x yr, age	-957.8	9	1934.1	0.4	0.196
trt x yr, age	-960.6	7	1935.6	2	0.090
trt x yr, chicks, age	-959.8	8	1936	2.4	0.073
trt x yr, chicks, date, age	-958.9	9	1936.3	2.6	0.065
trt x yr, date, age	-960.2	8	1936.9	3.3	0.047
trt x date, trt x yr, chicks, age	-958.5	10	1937.7	4	0.033
trt x date, trt x yr, age	-960.0	9	1938.6	4.9	0.021
trt x chicks, date, yr, age	-962.2	9	1943	9.3	0.002
trt x chicks, trt x date, yr, age	-961.3	10	1943.2	9.6	0.002
trt, chicks, date, yr, age	-964.1	8	1944.7	11.1	< 0.001
trt x chicks, trt x date, age	-963.2	9	1945	11.4	< 0.001
trt x date, chicks, yr, age	-963.9	9	1946.3	12.7	< 0.001
trt x chicks, yr, age	-965.0	8	1946.5	12.9	< 0.001
trt, chicks, yr, age	-966.6	7	1947.5	13.9	< 0.001
trt, yr, date, age	-966.6	7	1947.6	14	< 0.001
trt, yr, age	-967.9	6	1948.1	14.5	< 0.001
trt x chicks, date, age	-965.9	8	1948.2	14.5	< 0.001
trt x date, yr, age	-966.6	8	1949.5	15.9	< 0.001
trt x chicks, age	-968.7	7	1951.7	18	< 0.001
trt x date, chicks, age	-968.4	8	1953.1	19.5	< 0.001
trt, chicks, date, age	-969.8	7	1953.9	20.2	< 0.001
trt, chicks, age	-972.0	6	1956.2	22.5	< 0.001
trt, age	-973.8	5	1957.7	24.1	< 0.001
trt, date, age	-972.8	6	1957.9	24.3	< 0.001
trt x date, age	-972.0	7	1958.3	24.7	< 0.001
chicks, yr, date, age	-977.1	7	1968.4	34.8	< 0.001
yr, date, age	-979.5	6	1971.3	37.7	< 0.001
chicks, date, age	-979.8	6	1971.9	38.2	< 0.001
chicks, yr, age	-979.8	6	1971.9	38.3	< 0.001
yr, age	-981.1	5	1972.5	38.8	< 0.001
chicks, age	-982.2	5	1974.7	41	< 0.001
date, age	-982.6	5	1975.3	41.7	< 0.001
age	-983.8	4	1975.7	42	< 0.001
none	-1008.0	3	2021.2	87.5	< 0.001

Fixed effects: trt: treatment (fed or control), age: male age (young (yearling) or old (2+)), yr: year, chicks: number of 7- and 8-day-old nestlings alive in nest at time of measurement, date: date of measurement (1 = 1st May), none: intercept-only model.

Table S3.12. Model comparisons for first brood nest survival. All models have Male ID as the random factor. Main effects were included for all interactions. AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model $_i$ and the best model and $wAICc_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	$\Delta AICc_i$	$wAICc_i$
none	-26.58	2	57.3	0	0.315
trt	-25.87	3	58	0.7	0.225
date	-26.34	3	58.9	1.6	0.140
trt, date	-25.31	4	59	1.7	0.133
yr	-25.95	4	60.3	3	0.071
yr, date	-25.2	5	61	3.7	0.050
trt, yr	-25.6	5	61.8	4.5	0.033
trt, date, yr	-24.75	6	62.3	5	0.025
trt x yr	-25.42	7	65.9	8.7	0.004
trt x yr, date	-24.43	8	66.3	9	0.004

Fixed effects: trt: treatment (fed or control), yr: year, date: date found, none: intercept-only model.

Table S3.13. Model comparisons for number of breeding attempts per male per season (successful first broods, second broods and simultaneous broods with additional females). AICc is the corrected Akaike's Information Criterion, $\Delta AICc_i$ is the difference in AICc between model $_i$ and the best model and $wAICc_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	$\Delta AICc_i$	$wAICc_i$
trt, HD	-20.92	3	48.2	0	0.208
trt, age, HD	-19.92	4	48.4	0.2	0.184
trt, age	-21.32	3	49	0.8	0.139
trt	-22.90	2	50	1.8	0.085
trt x HD	-20.70	4	50	1.8	0.084
trt x age, HD	-19.68	5	50.3	2.1	0.073
trt x HD, age	-19.82	5	50.6	2.4	0.064
trt x age	-21.18	4	51	2.8	0.052
age, HD	-22.44	3	51.2	3	0.045
HD	-24.02	2	52.2	4	0.028
trt x age, trt x HD	-19.60	6	52.5	4.3	0.024
age	-25.14	2	54.5	6.3	0.009
none	-26.99	1	56	7.8	0.004

Fixed effects: trt: treatment (fed or control), age: male age (young (yearling) or old (2+)), HD: hatching date of first brood, none: intercept-only model.

Table S3.14. Model comparisons for probability of multiple brooding by females in one breeding season. AICc is the corrected Akaike's Information Criterion, ΔAICc$_i$ is the difference in AICc between model $_i$ and the best model and *w*AICc$_i$ is the AICc weight of the model. Interactions are indicated by x and include all lower order terms as well (e.g. trt x age represents trt + age + trt x age).

Fixed effects	Log-likelihood	df	AICc	ΔAICc$_i$	wAICc$_i$
trt, HD	-9.42	3	26	0	0.657
trt x HD	-9.42	4	28.2	2.2	0.222
trt	-13.00	2	30.7	4.7	0.062
HD	-13.14	2	31.1	5	0.053
none	-16.45	1	35.5	9.5	0.006

Fixed effects: trt: treatment (fed or control), HD: hatching date of first brood, none: intercept-only model.

CHAPTER 4. Effects of increased food availability at a breeding site on annual survival of a long-distance migratory bird, the northern wheatear

ABSTRACT

Temperature- and rainfall-driven change in food availability is one likely mechanism by which climate change may affect animal population dynamics and species distributions. We used experimental food supplementation at a breeding site to examine and compare the impact of changing food supply on annual survival of adult migratory birds and their offspring. Climate change presents particular challenges to long-distance migratory birds because they must time their migrations to coincide with food availability at locations hundreds or thousands of kilometres apart. Climate-driven changes in the overall abundance of food or the phenology of peaks in food availability may therefore be critical factors influencing annual survival. In this study we provided supplemental food to northern wheatears (*Oenanthe oenanthe*) breeding on Fair Isle, UK, to simulate a climate-linked increase in food availability. Food-supplemented wheatears exhibited higher rates of annual survival than control wheatears, and the strength of this effect varied with age. Food-supplementation led to c. 1.5 times higher annual survival of juveniles and c. 1.2 times higher survival of adults. Survival of juveniles was related to their own food availability as fledglings but not to whether their parents were food-supplemented or unfed controls. Combined with increased breeding productivity associated with food-supplementation (Chapter 3), our results suggest that a climate-driven increase in food availability, of the magnitude simulated in our experiment, would increase the population growth rate of wheatears on Fair Isle from approximately $\lambda = 0.92$ to $\lambda = 1.14$. Such an effect suggests that the food supplementation would turn Fair Isle from a population sink to a population source, if extended to the whole island.

INTRODUCTION

Climate change is widely expected to cause changes in the abundance and distribution of different animal taxa (Stenseth et al. 2002, Walther et al. 2002, Parmesan 2006). However, we currently have only a limited understanding of the underlying mechanisms by which climate impacts on animal populations. Many animal populations are limited primarily in a “bottom-up” manner by food abundance (White 2008) which is itself influenced by climate variability (Both and Visser 2005, Pearce-Higgins et al. 2010, Altermatt 2010). Temperature- and rainfall-driven changes in food availability are therefore likely mechanisms by which climate change may affect animal population dynamics and species distributions. Indeed, climate variables have been shown to correlate with a wide range of biological processes relevant to foragers and their food supplies, including phenology (Parmesan and Yohe 2003, Saino et al. 2007), development rates (Bale et al. 2002), body condition (Studds and Marra 2007), breeding productivity (Both et al. 2006, Matthysen et al. 2011) and survival (McDonald et al. 2004).

Climate change presents particular challenges to long-distance migratory birds because they must time their migrations to coincide with food availability at locations hundreds or thousands of kilometres apart. Climate-driven changes in the overall abundance of food or the phenology of peaks in food availability may therefore be critical factors influencing annual survival. Population growth rates (positive or negative) represent the sum of breeding productivity, individual survival and rates of immigration and emigration. In this study, we test the impacts of food supply on the survival between breeding seasons of a long-distance migratory bird, using experimental food supplementation at a geographically isolated breeding site, to examine and compare the impact of changing food supply on the annual survival of adult birds and their offspring.

Migratory birds must accumulate large fuel reserves (constituting muscle mass and fat deposits) at the onset of migration, requiring a large energy intake (Blem 1980, Klaassen 1996). Food availability during the breeding season, pre-migratory fuelling period and migration stopovers affects the body condition of migratory birds (Brown and Sherry 2006). This, in turn, is likely to affect survival - both directly via starvation risk, and indirectly via ecological factors such as predation risk. The limited available evidence, based on only one species, suggests that most mortality of adult long-distance migratory birds occurs during migration (Sillett and Holmes 2002). Body condition at the end of the breeding season affects timing of autumn departure (Stutchbury et al. 2011) and possibly also timing of arrival at winter grounds, which in turn affects the acquisition of high quality wintering habitats for territorial species. Body condition at the end of winter also determines arrival times at breeding sites (Gill et al. 2001; Studds and Marra 2005; Marra, Hobson, and Holmes 1998). Food availability may also affect the costs of reproduction to survival of adult birds, due to the increased effort required to provision offspring when food is scarce (Low et al. 2010).

Juvenile birds are more likely to starve during the critical nestling and post-fledging periods, if food availability limits the ability of parents to provide their offspring with adequate food. Heavy mortality of juvenile birds typically occurs during the nestling and early post-fledging stages (Anders et al. 1997), while juvenile mortality rates during the first migration are likely to equal or exceed those suffered by adults, due to inexperience. Post-fledging mortality of juvenile long-distance migratory birds has, however, rarely been studied directly. Predation was the primary cause of mortality of fledgling wood thrush (*Hylocichla mustelina*), a Neotropical migratory bird (Anders et al. 1997). By limiting nutritional status, food availability can indirectly influence predation risk, for example by causing birds to take greater risks in foraging, or by limiting the energetic resources available for the birds to flee predators (Witter 1994, Duncan Rastogi and Zanette 2006). Hence, climate-linked changes in food availability at breeding sites may be expected to have an even greater effect on juvenile survival than on adult survival.

While most mortality of adult migratory songbirds occurs outside of the breeding season (Sillett and Holmes 2002, Mazerolle et al. 2005), events and conditions (e.g. food availability) during the breeding season appear to be linked to annual survival rates, both directly and via carry-over effects into subsequent life cycle stages (Chase et al. 1997, Low et al. 2010). For example, annual survival rates of northern wheatears (*Oenanthe oenanthe*) in Sweden differ between breeding habitats, which vary in their food availability (Arlt et al. 2008). In habitats with tall, dense vegetation, it is more difficult for northern wheatears to locate food, hence parents have to fly longer distances to provision their offspring (Pärt 2001a, 2001b, Low et al. 2010). In such habitats, the risk of nest predation (many females are predated during nest predation events) is also increased (Low et al. 2010). Such correlations between annual survival and habitat quality may be confounded by the quality of individual birds, since higher quality birds may occupy higher quality habitat. However, experimental manipulations of vegetation height confirmed that northern wheatear adult survival – both female and male – during the breeding season, as well as subsequent (post-breeding) survival rates, were lower in habitats with tall field layers (Low et al. 2010). Climate change may therefore affect survival rates of northern wheatears by altering the availability of their invertebrate prey during the breeding season, and hence affecting adult reproductive costs.

In this study we provided supplementary food to breeding northern wheatears (henceforth “wheatears”) to simulate a climate-linked increase in food availability. Northern wheatears are small, insectivorous long-distance migratory songbirds that breed in open habitats across the Mediterranean, temperate and Arctic regions of the northern hemisphere, wintering in sub-Saharan Africa. We hypothesise that food availability during the short breeding season may affect the time and energetic trade-offs of reproductive effort, post-breeding moult and timing of autumn departure, all of which may affect subsequent survival. In addition, we hypothesise that food availability is likely to affect survival rates of juvenile birds in their first weeks post-fledging while gaining foraging experience. From these hypotheses, we predict that food-supplemented adults and juveniles will experience higher annual survival than unfed control birds. We also predict a stronger effect of food supplementation on juveniles relative to adults. Rather than attempting to simulate a specific climate-change scenario, our simulation was of an overall, uniform increase in food availability throughout the breeding and pre-migratory fuelling periods, to measure and compare the strength of food-limitation on the annual survival of adult and juvenile birds.

MATERIALS AND METHODS

Study site

Fair Isle (59°32'N, 1°39'W) is a small island (ca. 1,000 ha) midway between mainland Shetland and Orkney (each ca. 40 km away), north-east of the Scottish mainland, UK.

The island consists mainly of improved and unimproved grassland (*Festuca, Agrostis*, *Nardus* and maritime grassland communities) and heather moorland (dominated by *Calluna vulgaris*), all grazed by sheep (*Ovis aries*) (Nolan et al. 1994).

Experimental design

Food supplementation was carried out throughout the breeding seasons of 2008–2010. As arrival date correlates with breeding success of wheatears (Currie et al. 2000, Arlt and Pärt 2007), a standard route through the study site was walked almost daily from mid-April until the end of May, and newly-established pairs of wheatears were selected alternately as food-supplemented (henceforth ‘fed’) and non-food-supplemented (henceforth ‘control’) pairs. In this way, fed and control pairs were stratified both spatially and with respect to arrival date. This procedure also avoided the potentially confounding situation of the highest quality individuals establishing territories around feeders, to the exclusion of lower quality individuals. Prey availability in fed territories was increased experimentally by providing mealworms (*Tenebrio molitor*) in plastic bowls, placed directly on the ground. Each fed territory was provided with one feeder, located as near as possible to the centre of the territory, to minimise the possibility of wheatears from neighbouring control territories raiding the feeders. Bowls were filled with at least 30 g of mealworms (mean ± SD = 37.8 ± 2.7 g, n = 20 samples) and refilled on at least five of every seven days. Food supplementation was continued until the departure on autumn migration of all fed parent wheatears and their offspring (August–September). The majority of wheatears in the study were marked with individual-specific colour-ring combinations, allowing the identities of wheatears using the feeders to be observed; both directly in the field, and remotely using small video cameras (Sony Handycam DCR-SR32, Sony Corporation, http://sony.co.uk). To confirm the identities of wheatears attending each of our feeders, at least three recording sessions, of at least 1 hour each, were viewed per feeder, but viewing sessions were extended to 4 hours if neither or only one of a pair had attended the feeder during the initial period. None of the adult control wheatears were recorded taking mealworms from any feeder.

After allowing wheatears to become accustomed to using the feeders for approximately 4 weeks, cages were placed over them with holes cut in the mesh large enough for wheatears to pass through but too small for larger birds (e.g. European starlings *Sturnus vulgaris*). In each year, however, some wheatear pairs stopped attending feeders once cages were installed (5 pairs in 2008, 6 pairs in 2009 and 2 pairs in 2010). Individuals of such pairs were regarded as control birds. If only one individual of a pair stopped attending a feeder (3 out of 4 pairs in 2008, 8 out of 18 pairs in 2009 and 18 out of 30 pairs in 2010), both were included in the analysis as fed birds because the food supplementation of the offspring via the fed parent may affect the reproductive costs and subsequent survival of its (unfed) partner.

Fully-grown wheatears were captured either with spring traps (www.moudry.cz, model SB30) baited with mealworms, or in Fair Isle Bird Observatory’s permanent Heligoland traps (large funnel traps). Plumage features were used to sex and age captured birds according to Svensson (1992) as fledged in the current year (juvenile), or before the current year (adult). We did not age adults more precisely (as second year or older) because ageing methodology for adult females is unreliable (Svensson 1992). All captured birds were marked with unique combinations of a numbered metal ring and four plastic colour leg rings to enable individual identification in the field. Nestlings were ringed with a numbered metal ring alone when approximately 7 days old. Colour rings were only fitted once chicks were at least 9 days old, as their tarsi only become slim enough along the full length to fit multiple rings from that age. Young wheatears were therefore re-caught for colour ringing, either in the nest towards the end of the nestling period (where possible), or with spring traps after fledging.

Following Arlt et al. (2008), fledging was determined when juveniles were observed outside the nest chamber or when parents gave intense warning calls > 15 days after the hatch date and the nest chamber was empty. Each nest was searched for dead nestlings after fledging. Nestlings found dead at the nest were excluded from analysis of first year survival; we separately analysed the effects of the food supplementation on fledging rates (Chapter 3). Ringed nestlings not subsequently found dead at the nest were assumed to have fledged.

We searched the whole island for colour-marked birds throughout the 2009–2010 breeding seasons and intensively for 3 weeks in June 2011, using a telescope or a camera with telephoto lens to confirm colour combinations. Opportunistic re-sighting data over the same period were also provided by Fair Isle Bird Observatory staff and other ornithologists. We verified most additional sightings in the field or from photographs. We attempted to recapture for colour ringing and identification any breeding wheatears wearing only a metal ring, as these individuals were likely to have been ringed as nestlings in previous years. Only three such birds were known to have avoided capture over the re-sighting period (2009–2011).

Data analysis

We analysed adult and first year survival rates separately, because the sex of juveniles only becomes known if they survive their first year and return to the study area, yet we wanted to include sex as a variable in adult survival models. Each field season was treated as a single re-sighting "occasion", with each individual being either seen or not seen in each year.

Adult survival

Data from 237 individually marked adult (119 males and 118 females) wheatears were used to estimate the effect of food availability on adult survival. In addition to the experimental treatment conditions (fed or unfed), we considered *a priori* that sex and year may influence annual survival.

Adult birds in this study could shift experimental state (fed or control) between years, precluding the use of standard Cormack-Jolly-Seber mark-recapture models to estimate state-specific survival. We therefore used multi-state mark-recapture models to estimate survival rates of adults (Arnason 1972, 1973, Schwarz et al. 1993, Brownie et al. 1993, Nichols et al. 1994, Nichols and Kendall 1995). We used the package RMark (Laake and Rextad 2011) in the statistical programme R (version 2.13.0, R Development Core Team, 2011) to implement mark-recapture models in the programme MARK (version 6.1, White and Burnham 1999).

In our multi-state models, we used ϕ to denote the probability that an organism in a particular state survived to the next re-sighting occasion (to the next year, in the context of our study; Brownie et al. 1993; Hestbeck et al. 1991; Schwarz et al. 1993).

The transition parameter (ψ) is the probability of switching between the two states, fed and control. This parameter was held constant across groups because the probability of being a fed bird in a given year was random with respect to experimental treatment in the previous year and with respect to individual and environmental variables. The detection parameter (p) of a particular state is the probability that a marked individual alive in that state on a particular re-sighting occasion is encountered on that occasion (i.e. in that year). This detection parameter p is less than 1 when there are gaps in any individual capture history (e.g. a gap occurs when an individual is observed in year t, not in year t+1 and seen again in year t+2, and hence was alive but missed in year t+1).

As a necessary first step of our analysis, we carried out a goodness of fit test on the most general (global) time-dependent model, denoted $\{\phi_{\text{treatment x sex, treatment x year}}, \psi, p_{\text{sex, year}}\}$, where survival probability ϕ was allowed to vary by treatment and sex in an interactive manner (we use x to denote interactions), transition probability ψ was constant across groups and detection probability p was allowed to vary by sex and year. Goodness of fit tests were conducted with the median-$\hat{c}$ procedure (Cooch and White 2011) with 500 samples in MARK. The dispersion parameter $\hat{c}$ of the global model indicated moderate overdispersion in the data ($\hat{c} \pm \text{SE} = 1.987 \pm 0.030$) (Burnham and Anderson 2002). As recommended by Burnham and Anderson (2002), we therefore conducted model selection based on values of the Akaike Information Criterion adjusted for small sample size and the degree of overdispersion (QAICc), to identify models within candidate sets that most parsimoniously explained variation in adult detection probability and survival. We first tested a candidate set of models of p: $\{p_{\text{sex, year}}\}$, $\{p_{\text{sex}}\}$, $\{p_{\text{year}}\}$and $\{p\}$ – which we considered *a priori* as possible predictors of detection probability – using a reasonably complex model for ϕ $\{\phi_{\text{treatment, sex, year}}\}$ and with ψ

constant across groups {ψ} (Table S4.1, Supporting Information). Sex was considered as a factor because of the possibility of females being on the nest, and therefore out of sight (although we attempted to minimise the risk of missing individuals by conducting multiple visits to all areas). Parameter estimates for survival probability ϕ when detection varied across all years indicated highly implausible survival rates of adults in the period 2010–2011 of > 0.95. Detection probability p for 2011 can only be directly estimated by conducting resighting in 2012, and so ϕ for 2010–2011 cannot be adjusted for an estimate of p specific to 2011. As our fieldwork in 2011 focused exclusively on resighting and retrapping individuals, it is likely that all returning colour-ringed individuals were observed in 2011 (or at least very few were missed) but it is less likely that this was the case in the preceding years. We therefore considered only models in which p was allowed to vary in 2009 and 2010 but fixed at 1 for 2011 or at the mean of 2009 and 2010 (Table S4.1, Supporting Information). This resulted in more biologically realistic values for survival (see Results).

Next, we built our global model of adult survival, with a reasonably complex but biologically plausible combination of variables {$\phi_{\text{treatment x sex, treatment x year}}$}, modelling p using the most plausible model structures identified in the previous step (i.e. those with ΔAICc $\leq$2) and with ψ constant across groups. We then built a series of reduced parameter models starting with the global model of adult survival, with ϕ decreasing in complexity until the final fully-constrained model, in which ϕ was constant across groups. In this way, we built a set of ten candidate nested models that we considered to be biologically reasonable potential explanations of variation in adult annual survival.

Model averaging was carried out to derive parameter estimates and confidence intervals, based on the AICc weight (*w*AICc) of each model *i* (Burnham and Anderson 2002). $w\text{AICc}_i$ determines the contribution of each parameter estimate within model *i* to the mean of that parameter across all considered models. Model averaging was carried out with RMark, implemented in MARK.

First year survival

Data for 599 individually-marked juveniles were used to estimate the effect of food availability on first year survival. Of these, 495 were ringed as nestlings (and subsequently fledged; nestlings that died before fledging were excluded) and the remaining 104 were ringed after fledging. Of the 533 juveniles from known nests (i.e. ringed as nestlings or as juveniles that could be assigned to parents based on parent provisioning behaviour), 243 had fed parents and 290 had control parents.

Two separate analyses of first year survival were carried out. In the first analysis, we considered only the 533 juveniles from known nests, to investigate the effect of experimental treatment during the nestling stage on subsequent first year survival of fledged juveniles. “Fed juveniles” were those with fed parents and “control juveniles” were those with control parents.

In the second analysis, we included only the 252 colour ringed juveniles that were captured or observed (having been previously colour-ringed as nestlings) between fledging and autumn departure. In this second analysis, “fed juveniles” (n = 67) were those attending feeding stations themselves and “control juveniles” (n = 185) were those not attending feeding stations, regardless of whether their parents were fed or control.

Of the fed juveniles, 45 were offspring of parents that were fed, 11 were offspring of control parents and 11 could not be assigned to parents (and therefore were of unknown nest treatment). 38 of the control juveniles were offspring of fed parents, 92 were offspring of control parents and 55 could not be assigned to parents. To avoid including transient birds in these samples, only fledglings yet to finish post-juvenile moult at the time of capture were included, as juvenile northern wheatears generally begin migration once their moult has finished (Cramp 1988).

First year survival probability (ϕ) and detection probability (p) were estimated with extensions of Cormack-Jolly-Seber (CJS) models, as outlined by Lebreton et al. (1992), using RMark, implemented in MARK. Factors considered in these models were nest treatment (fed parents or control parents), juvenile treatment (fledged individual was fed or control), presence/absence of colour rings and year.

A complex but biologically plausible global model of first-year survival ϕ was built for each of the two juvenile datasets and tested for goodness of fit with the median-$\hat{c}$ procedure (500 samples), as with the adult global model. These were $\{\phi_{\text{nest treatment x year}}, p_{\text{presence/absence of colour rings, year}}\}$ for juveniles of known nest treatment, where survival probability ϕ was allowed to vary by nest treatment and year interactively, and detection probability p by the presence or absence of colour rings and by year, and $\{\phi_{\text{treatment x year}}, p_{\text{year}}\}$ for colour-ringed juveniles observed after fledging, where survival probability was allowed to vary by treatment and year interactively and detection probability by year. The dispersion parameter $\hat{c}$ of the global model of first year survival for juveniles of known nest treatment was 1.151 ± 0.046. As this dispersion parameter was only marginally above 1, this model suffered from only very moderate overdispersion. The dispersion parameter $\hat{c}$ for the global model for colour-ringed juvenile birds observed after fledging was 0.783 ± 0.088. Therefore, this model suffered from moderate underdispersion (Burnham and Anderson 2002). As recommended by Cooch and White (2011), we set $\hat{c}$ =1 (i.e. made no adjustment to $\hat{c}$) for both candidate sets of models of first year survival.

We used values of AICc to test candidate sets of models of detection probability p with various factors (presence/absence of colour rings, experimental treatment, year and interactions of these factors) for the two analyses of juvenile survival, using a reasonably complex structure of ϕ (nest treatment: $\phi_{\text{nest treatment x year}}$; juvenile treatment: $\phi_{\text{treatment x year}}$). As for the adult analysis, for the analysis of juveniles that were observed or captured post-fledging we considered models in which p was allowed to vary in 2009 and 2010, but in 2011 was fixed at 1 or the mean of 2009 and 2010 (Table S4.2, Supporting Information). We then carried over the plausible models of p (i.e. those with ΔAICc $\leq$2) to the analyses of survival probability ϕ. In these analyses, we tested candidate sets of reduced-parameter models, starting with general models of ϕ – $\{\phi_{\text{nest treatment x year}}\}$ for juveniles of known nest treatment and $\{\phi_{\text{treatment x year}}\}$ for juveniles observed or captured post-fledging – and ending with fully constrained models $\{\phi\}$. Each model of ϕ within these candidate sets was considered with each of the plausible models of p identified in the preliminary step above.

Model averaging of parameter estimates was carried out in the same way as for adult survival.

Population growth rate

We used the model averaged parameter estimates for adult and first year survival (nest treatment data set), combined with data on fledglings produced per breeding season from our related analyses (Chapter 3) to estimate the net effect of supplementary feeding on population growth rates of fed and control wheatears. The population growth rate (λ_t) for each treatment group (fed and control) was estimated with the following equation:

$$\lambda_t = \frac{\left(N_{male,t} \times \phi_{male,t}\right) + \left(N_{fem,t} \times \phi_{fem,t}\right) + \left(N_{male,t} \times N_{juvs\,male^{-1},t} \times \phi_{juvs,t}\right)}{N_{male,t} + N_{fem,t}},$$

where $N_{male,t}$ is the number of colour ringed breeding males in year t ($N_{fem,t}$ for females), $\phi_{male,t}$ is the survival rate estimate of males in year t ($\phi_{fem,t}$ for females), $N_{juvs\ male}{}^{-1}$ is the mean number of fledglings produced per male in year t and $\phi_{juvs,t}$ is the survival rate estimate of fledglings in year t. Upper 95% confidence intervals for the estimates of λ_t were then calculated with the following equation:

$$Upper\ CI = \frac{\left(\left(N_{male} \times \left(\phi_{male} + \left(\mathrm{X} \times SE_{\phi male}\right)\right)\right) + \left(N_{female} \times \left(\phi_{female} + \left(\mathrm{X} \times SE_{\phi female}\right)\right)\right) + \left(N_{male} \times \left(\left(N_{juvs\,male}{}^{-1} + \left(\mathrm{X} \times SE_{N_{juvs\,maleH}{}^{-1}}\right)\right) \times \left(\phi_{juvs} + \left(\mathrm{X} \times SE_{\phi juvs}\right)\right)\right)\right)\right)}{\left(N_{male} + N_{female}\right)}$$

,

where X is a correction factor for multiple upper bounds (0.718), derived from the fourth root of α (because there are 4 separate standard errors in the equation). Lower 95% confidence intervals were calculated with a similar equation:

$$Lower\,CI = \frac{\left(\left(N_{male} \times \left(\phi_{male} - \left(\mathrm{X} \times SE_{\phi male}\right)\right)\right) + \left(N_{female} \times \left(\phi_{female} - \left(\mathrm{X} \times SE_{\phi female}\right)\right)\right) + \left(N_{male} \times \left(\left(N_{juvs\,male}{}^{-1} - \left(\mathrm{X} \times SE_{N_{juvs\,maleH}{}^{-1}}\right)\right) \times \left(\phi_{juvs} - \left(\mathrm{X} \times SE_{\phi juvs}\right)\right)\right)\right)\right)}{\left(N_{male} + N_{female}\right)}$$

RESULTS

Adult survival

Model selection to determine the best structure for detection probability p resulted in five out of the eight candidate models being identified as plausible (ΔQAICc ≤ 2) $\{p_{\text{sex}}\}$ (fixed at 1 and fixed at 0.901, the mean of 2009 and 2010), $\{p\}$ (fixed at 1 and fixed at 0.901) and $\{p_{\text{sex, year}}\}$ (2011 fixed at 1) (Table S4.1 and Fig S1a, Supporting Information). These included effects of sex and year, as well as a model of equal detection probability across groups. All five plausible models of p were then carried over to the candidate list of survival models.

Table 4.1. Multistate models of annual adult survival (ϕ) ranked by ΔQAICc. Subscripts of ϕ denote variables used in the model for survival: no subscript = constant across groups and time, trt = experimental treatment (fed or control), sex and year.

	Model			No. parameters	ΔQAICc	*w*AICc	Deviance
(1)	ϕ_{trt}	ψ	$p_{\text{sex [2011 = 1]}}$	5	0.0	0.101	86.0
(2)	ϕ	ψ	$p_{\text{sex [2011 = 1]}}$	4	1.0	0.062	89.1
(3)	ϕ_{trt}	ψ	$p_{\text{[2011 = 1]}}$	4	1.3	0.053	89.4
(4)	$\phi_{\text{trt x year}}$	ψ	$p_{\text{sex [2011 = 0.901]}}$	9	1.5	0.047	79.2
(5)	$\phi_{\text{trt x year}}$	ψ	$p_{\text{sex [2011 = 1]}}$	9	1.5	0.047	79.2
(6)	$\phi_{\text{trt, sex}}$	ψ	$p_{\text{sex [2011 = 1]}}$	6	2.0	0.037	86.0
(7)	ϕ_{trt}	ψ	$p_{\text{sex, year [2011 = 1]}}$	6	2.1	0.036	86.0
(8)	ϕ_{trt}	ψ	$p_{\text{sex [2011 = 0.901]}}$	5	2.2	0.034	88.2
(9)	$\phi_{\text{trt, year}}$	ψ	$p_{\text{sex [2011 = 1]}}$	7	2.2	0.034	84.1
(10)	ϕ	ψ	$p_{\text{[2011 = 1]}}$	3	2.4	0.031	92.5
(11)	$\phi_{\text{trt x year}}$	ψ	$p_{\text{[2011 = 0.901]}}$	8	2.4	0.030	82.2
(12)	$\phi_{\text{trt x year}}$	ψ	$p_{\text{[2011 = 1]}}$	8	2.4	0.030	82.2
(13)	$\phi_{\text{trt, year}}$	ψ	$p_{\text{sex [2011 = 0.901]}}$	7	2.8	0.025	84.7
(14)	ϕ_{year}	ψ	$p_{\text{sex [2011 = 0.901]}}$	6	2.9	0.024	86.8
(15)	ϕ_{year}	ψ	$p_{\text{sex [2011 = 1]}}$	6	2.9	0.024	86.8
(16)	ϕ	ψ	$p_{\text{sex [2011 = 0.901]}}$	4	2.9	0.024	91.0

Table 4.1, continued

(17)	ϕ_{sex}	ψ	$p_{\text{sex [2011 = 1]}}$	5	3.0	0.023	89.0
(18)	ϕ	ψ	$p_{\text{sex, year [2011 = 1]}}$	5	3.0	0.022	89.1
(19)	$\phi_{\text{trt, sex}}$	ψ	$p_{\text{[2011 = 1]}}$	5	3.1	0.022	89.1
(20)	$\phi_{\text{trt, year}}$	ψ	$p_{\text{[2011 = 1]}}$	6	3.2	0.021	87.1
(21)	$\phi_{\text{trt x year}}$	ψ	$p_{\text{sex, year [2011 = 1]}}$	10	3.2	0.020	78.7
(22)	ϕ_{trt}	ψ	$p_{\text{[2011 = 0.901]}}$	4	3.6	0.016	91.7
(23)	$\phi_{\text{trt, year}}$	ψ	$p_{\text{[2011 = 0.901]}}$	6	3.8	0.015	87.7
(24)	ϕ_{year}	ψ	$p_{\text{[2011 = 0.901]}}$	5	3.9	0.014	89.9
(25)	ϕ_{year}	ψ	$p_{\text{[2011 = 1]}}$	5	3.9	0.014	89.9
(26)	$\phi_{\text{trt, year}}$	ψ	$p_{\text{sex, year [2011 = 1]}}$	8	4.0	0.014	83.7
(27)	$\phi_{\text{trt x sex}}$	ψ	$p_{\text{sex [2011 = 1]}}$	7	4.0	0.013	85.9
(28)	$\phi_{\text{trt, sex}}$	ψ	$p_{\text{sex, year [2011 = 1]}}$	7	4.1	0.013	85.9
(29)	$\phi_{\text{trt, sex}}$	ψ	$p_{\text{sex [2011 = 0.901]}}$	6	4.2	0.012	88.1
(30)	ϕ_{sex}	ψ	$p_{\text{[2011 = 1]}}$	4	4.2	0.012	92.3
(31)	ϕ	ψ	$p_{\text{[2011 = 0.901]}}$	3	4.5	0.011	94.6
(32)	ϕ_{year}	ψ	$p_{\text{sex, year [2011 = 1]}}$	7	4.6	0.010	86.5
(33)	$\phi_{\text{sex, year}}$	ψ	$p_{\text{sex [2011 = 0.901]}}$	7	4.9	0.009	86.7
(34)	$\phi_{\text{sex, year}}$	ψ	$p_{\text{sex [2011 = 1]}}$	7	4.9	0.009	86.8
(35)	ϕ_{sex}	ψ	$p_{\text{sex [2011 = 0.901]}}$	5	4.9	0.009	91.0
(36)	ϕ_{sex}	ψ	$p_{\text{sex, year [2011 = 1]}}$	6	5.0	0.008	89.0
(37)	$\phi_{\text{trt x sex}}$	ψ	$p_{\text{[2011 = 1]}}$	6	5.1	0.008	89.1
(38)	$\phi_{\text{trt x sex, trt x year}}$	ψ	$p_{\text{sex [2011 = 0.901]}}$	11	5.3	0.007	78.6
(39)	$\phi_{\text{trt, sex}}$	ψ	$p_{\text{[2011 = 0.901]}}$	5	5.4	0.007	91.4
(40)	$\phi_{\text{trt x sex, trt x year}}$	ψ	$p_{\text{sex [2011 = 1]}}$	11	5.5	0.006	78.9
(41)	ϕ_{sex}	ψ	$p_{\text{[2011 = 0.901]}}$	6	5.7	0.006	89.7
(42)	$\phi_{\text{sex, year}}$	ψ	$p_{\text{[2011 = 1]}}$	6	5.8	0.006	89.8
(43)	$\phi_{\text{trt x sex, trt x year}}$	ψ	$p_{\text{[2011 = 0.901]}}$	10	5.9	0.005	81.5
(44)	$\phi_{\text{trt x sex}}$	ψ	$p_{\text{sex, year [2011 = 1]}}$	8	6.1	0.005	85.9
(45)	ϕ_{sex}	ψ	$p_{\text{[2011 = 0.901]}}$	4	6.2	0.005	94.3
(46)	$\phi_{\text{trt x sex}}$	ψ	$p_{\text{sex [2011 = 0.901]}}$	7	6.2	0.004	88.1
(47)	$\phi_{\text{trt x sex, trt x year}}$	ψ	$p_{\text{[2011 = 1]}}$	10	6.3	0.004	81.8
(48)	$\phi_{\text{sex, year}}$	ψ	$p_{\text{sex, year [2011 = 1]}}$	8	6.6	0.004	86.4
(49)	$\phi_{\text{trt x sex, trt x year}}$	ψ	$p_{\text{sex, year [2011 = 1]}}$	12	7.2	0.003	78.4
(50)	$\phi_{\text{trt x sex}}$	ψ	$p_{\text{[2011 = 0.901]}}$	6	7.4	0.002	91.4

Detection probability for 2011 was fixed at different levels, as denoted within brackets following the *p* model notation: 1, [2011 = 1] and the mean of *p* in 2009 and 2010, 0.901 [2011 = 0.901].

Table 4.2. Model-averaged estimates of annual survival probability (ϕ) (year t to year t + 1) of adult wheatears by sex, year and experimental treatment. Contributions to estimates from each model are weighted by wAICc.

		Treatment[1]	
		Fed	Control
Sex	Year t	ϕ (95% CI)	ϕ (95% CI)
Male	2008	0.577 (0.311–0.805)	0.474 (0.324–0.628)
	2009	0.520 (0.263–0.767)	0.456 (0.316–0.603)
	2010	0.661 (0.354–0.874)	0.505 (0.348–0.661)
Female	2008	0.567 (0.302–0.798)	0.467 (0.318–0.623)
	2009	0.510 (0.253–0.761)	0.449 (0.310–0.597)
	2010	0.652 (0.345–0.870)	0.498 (0.339–0.658)

[1] Experimental treatment of individuals during year t (fed = supplementary fed, control = no supplementary feeding).

Six models of adult survival were identified as plausible (ΔQAICc ≤ 2, Table 4.1, Models 1–6). Treatment was included in five of the six plausible models (Models 1 and 3–6), year was included in two plausible models (interactively with treatment) (Models 4–5) and sex was included in one plausible model (Model 6). One of the plausible models assumed constant survival across groups (Models 2). Model-averaged parameter estimates (Table 4.2) indicated that survival was highest in the period 2010–2011. Estimated annual survival was approximately 1.2 times higher for fed adults than control adults across both sexes and all years (range 1.14–1.31) (Fig. 4.1). The effect of treatment was greatest in 2010, with adult survival estimates approximately 1.31 times higher for fed birds than for control birds from 2010 to 2011. The reasonably wide confidence intervals suggest, however, that these results need to be treated with some degree of caution.

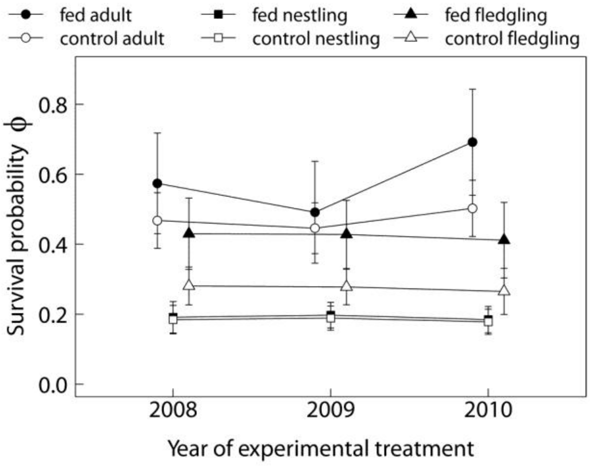

Fig. 4.1. Model-averaged survival estimates (± 1 SE) in the three years of this study of adults, yearlings in the nest treatment subset and yearlings in the fledgling treatment subset. Adult survival estimates are averaged across models without sex effects to aid clarity, as sex was of only minor importance in QAICc ranking (Table 4.1).

First year survival

For the analysis of the effect of coming from a food-supplemented nest on first-year survival, two structures of detection probability *p* were supported by the data $\{p_{\text{presence/absence of colour rings}}\}$ and $\{p_{\text{presence/absence of colour rings, year}}\}$ (Table S4.2 and Fig S1b, Supporting Information). These indicated that detection probability was, as expected, higher for colour-ringed birds (because their identity could be confirmed without requiring recapture). These two structures of *p* were then used in the candidate set of models of first-year survival in the analysis of nest treatment.

For the analysis of the effect of supplementary feeding of fledged juveniles on first-year survival, three out of four considered structures of *p* were supported; two of which indicated that detection probability was constant across groups (one with *p* for 2011 fixed at 1 and one with *p* for 2011 fixed at the mean of 2009 and 2010) and one with detection probability varying by year (with *p* for 2011 fixed at the mean of 2009 and 2010) (Table S4.2, Fig. S1c, Supporting Information). These structures of *p* were used in the candidate set of models of juvenile survival in the analysis of juvenile treatment.

There were two plausible models of first year survival of juveniles of known nest treatment (Table 4.3, Models 51–52). Firstly, a model with constant survival across groups and detection probability higher for colour-ringed birds than those which were metal ringed only. Secondly, a model with survival varying by experimental treatment, with detection probability again higher for colour ringed birds. Model-averaging indicated that there was very little difference in first year survival between juveniles from fed nests and juveniles from control nests (Table 4.4, Fig. 4.1).

Table 4.3. Models of first year survival (ϕ) of wheatears determined to have fledged successfully, ranked by ΔAICc. Subscripts denote factors used in the survival and detection probability (p) models: no subscript = constant across groups and time, nest treatment (nest_trt; fed parents or control parents), juvenile treatment (trt; fed or control), year and presence/absence of colour rings (col).

	Model		No. parameters	ΔAICc	*w*AICc	Deviance
Juveniles of known nest treatment[1]						
(51)	ϕ	p_{col}	4	0	0.479	29.2
(52)	$\phi_{\text{nest\_trt}}$	p_{col}	5	1.7	0.203	28.9
(53)	ϕ_{year}	p_{col}	6	3.2	0.099	28.3
(54)	ϕ	$p_{\text{col, year}}$	6	3.7	0.077	28.8
(55)	$\phi_{\text{nest\_trt, year}}$	p_{col}	7	4.9	0.041	28.0
(56)	ϕ_{year}	$p_{\text{col, year}}$	8	5.1	0.038	26.1
(57)	ϕ_{trt}	$p_{\text{col, year}}$	7	5.4	0.032	28.5
(58)	$\phi_{\text{nest\_trt, year}}$	$p_{\text{col, year}}$	9	6.8	0.016	25.8
(59)	$\phi_{\text{nest\_trt x year}}$	p_{col}	9	7.6	0.011	26.5
(60)	$\phi_{\text{nest\_trt x year}}$	$p_{\text{col, year}}$	11	9.4	0.004	24.2
All juveniles[2]						
(61)	ϕ_{trt}	$p_{\text{[2011 = 0.675]}}$	4	0.0	0.390	11.5
(62)	ϕ_{trt}	$p_{\text{year [2011 = 0.675]}}$	5	1.9	0.153	11.3
(63)	ϕ_{trt}	$p_{\text{[2011 = 1]}}$	4	2.3	0.122	13.9
(64)	ϕ	$p_{\text{[2011 = 0.675]}}$	3	3.0	0.088	16.6
(65)	$\phi_{\text{trt, year}}$	$p_{\text{[2011 = 1]}}$	6	3.9	0.056	11.3
(66)	$\phi_{\text{trt, year}}$	$p_{\text{[2011 = 0.675]}}$	6	3.9	0.055	11.3
(67)	ϕ	$p_{\text{[2011 = 1]}}$	3	4.7	0.037	18.3
(68)	ϕ	$p_{\text{year [2011 = 0.675]}}$	4	4.9	0.034	16.4
(69)	$\phi_{\text{trt, year}}$	$p_{\text{year [2011 = 0.675]}}$	7	5.9	0.021	11.2
(70)	ϕ_{year}	$p_{\text{[2011 = 0.675]}}$	5	7.1	0.011	16.5
(71)	ϕ_{year}	$p_{\text{[2011 = 10]}}$	5	7.1	0.011	16.5
(72)	$\phi_{\text{trt x year}}$	$p_{\text{[2011 = 0.675]}}$	8	7.9	0.007	11.1
(73)	$\phi_{\text{trt x year}}$	$p_{\text{[2011 = 1]}}$	8	7.9	0.007	11.1
(74)	ϕ_{year}	$p_{\text{year [2011 = 0.675]}}$	6	9.0	0.004	16.3
(75)	$\phi_{\text{trt x year}}$	$p_{\text{year [2011 = 0.675]}}$	9	9.9	0.003	10.9

[1] Subset of juveniles with known experimental nest treatment (parents fed or control) because parent ID could be confidently determined. Includes juveniles with metal rings (with/without colour rings), that were assumed to have fledged or observed/captured after fledging.

[2] All colour-ringed juveniles that were observed/captured after fledging, including those of unknown nest treatment.

Detection probability of the data set of all colour-ringed juveniles for 2011 was fixed at different levels, as denoted within brackets following the *p* model notation: 1, [2011 = 1] and the mean of *p* in 2009 and 2010, 0.675 [2011 = 0.675].

Table 4.4. Model-averaged estimates of first year survival (ϕ) probability (hatching year to the following year) of juvenile wheatears by year and juvenile experimental treatment. Contributions to estimates from each model are weighted by *w*AICc.

	Treatment	
Hatching year	Fed	Control
	ϕ (95% CI)	ϕ (95% CI)
Juveniles of known nest treatment[1]		
2008	0.191 (0.118–0.294)	0.184 (0.117–0.277)
2009	0.197 (0.135–0.279)	0.189 (0.130–0.266)
2010	0.185 (0.122–0.270)	0.178 (0.118–0.260)
All juveniles[2]		
2008	0.430 (0.250–0.630)	0.281 (0.187–0.397)
2009	0.428 (0.255–0.620)	0.278 (0.190–0.388)
2010	0.412 (0.226–0.626)	0.265 (0.157–0.412)

[1] Subset of juveniles with known experimental nest treatment (parents fed or control) because parent ID could be confidently determined. Includes juveniles with metal rings (with/without colour rings), that were assumed to have fledged or observed/captured after fledging.

[2] All colour-ringed juveniles that were observed/captured after fledging, including those of unknown nest treatment.

We then analysed models of first year survival with the data set containing only juveniles that were observed (having been colour-ringed in the nest) or captured and colour-ringed between fledging and autumn departure. Two plausible models were identified, both including treatment only, one with detection probability constant across years (with p for 2011 fixed at the mean of 2009 and 2010) and one with detection probability varying by year (with p in 2011 fixed at the mean of 2009 and 2010) (Table 4.3, Models 61–62). Model weights showed that these models were more than four times as well supported by the data than the nested models, which did not incorporate a treatment effect (Models 64 and 68, $w_{61+62}/w_{64+68} = 0.390 + 0.153/0.088 + 0.034 = 4.45$; Table 4.3). Model-averaged estimates indicated that individuals receiving supplementary feeding as fledged juveniles were approximately 1.5 times more likely to survive their first year than control juveniles (Table 4.4, Fig 4.1).

Comparing the results for juveniles of known nest treatment with those of juveniles observed only after fledging, estimates of first year survival rates were approximately twice as high for juveniles observed after fledging than juveniles ringed in the nest and assumed to have fledged, indicating that a substantial percentage of first year mortality occurs in the first few days after fledging (Table 4.4). Furthermore, the effect of supplementation seemed to be greater once juveniles had left the nest than during the nestling stage (Table 4.4, Fig 4.1).

Population growth rate

The estimated population growth rate λ of fed wheatears was close to or greater than 1 (where 1 = no change in population size between years) in all years of this study, while for control wheatears it was lower than 1 in two out of three years (mean and [95% confidence intervals] for λ = 0.98 [0.76, 1.22] for fed birds in 2008, 0.81 [0.67, 0.97] for control birds in 2008, 1.20 [0.96, 1.46] for fed birds in 2009, 0.85 [0.72, 0.98] for control birds in 2009, 1.24 [1.01, 1.48] for fed birds in 2010 and 1.10 [0.93, 1.28] for control birds in 2010).

DISCUSSION

The abundance of terrestrial arthropods in North temperate and Arctic regions is predicted to alter under climate change scenarios of increased temperature and altered rainfall (Strathdee et al. 1993, Miles et al. 1997, Pearce-Higgins et al. 2010, Chapter 5). While abundance of sap-sucking insects (Hemiptera) increases with climate warming

(Strathdee et al. 1993, Miles et al. 1997), other arthropod taxa decline in abundance (Pearce-Higgins et al. 2010), or advance their phenology such that abundances are lower during late summer (Chapter 5). The overall availability of arthropod prey of northern long-distance migrant songbirds is therefore predicted to change, which could have consequences for their survival rates. Our results showed that for one such species, the northern wheatear, survival rates of adult and juvenile birds are sensitive to changes in food availability at a breeding location in northern Scotland. Combining the results of this study with parallel findings on breeding productivity (Chapter 3) suggests that at our study site, increased food availability may result in a population increase, although this may be moderated by density-dependent effects on recruitment (which we did not measure).

Observed return rates to a particular location are the product of survival of individuals that return to that location (i.e. ruling out both mortality and emigration) and the probability that they are then observed (Lebreton et al. 1992). The estimated detection probabilities in this study were high (> 0.90 for adults and > 0.67 for yearlings) and thus we are confident that they allow us to estimate accurately the numbers of birds surviving and returning. The apparent adult survival rates are highly likely to reflect actual adult survival rates because breeding site fidelity in northern wheatears is very strong (Cramp 1988, Conder 1989, Panov 2005). We cannot, however, rule out the possibility that the variation we observed in apparent first year survival was driven by natal dispersal decisions related to post-fledging food availability. In common with many other bird species (Greenwood and Harvey 1982), first year northern wheatears disperse further from their natal sites than adults disperse from previous nest sites (Fulton 2010). Circumstantial evidence however, supports the argument that the difference in first year return rates we observed are due to real survival differences, rather than differences in natal dispersal between fed and unfed individuals. Fair Isle is a small, isolated island, the nearest neighbours of which are another small, isolated island to the SW (North Ronaldsay, Orkney) and a larger island to the NE (mainland Shetland), each approximately 40 km away. Both of these sites are presumably the most likely destinations of young wheatears surviving the winter that do not return to Fair Isle to breed. At a mainland site in Sweden (at a similar latitude to Fair Isle), median natal dispersal distance is approximately 1.3 km (dispersal distances within the 10/90% quantile = 0.47/3.39 km), within a search area extending to 6 km from natal sites (Arlt et al. 2008). As on Fair Isle, North Ronaldsay has a bird observatory running a regular bird census programme during the summer, while both North Ronaldsay and Shetland (e.g. the Sumburgh Head bird reserve at the southern tip of the Shetland Mainland, which is the nearest point to Fair Isle) attract many amateur ornithologists each year. The chances of observation of colour-ringed wheatears breeding at either location are therefore high. The only such record during the three years of this study was of an adult male breeding on North Ronaldsay in 2011 that had been a fed nestling on Fair Isle in 2010. At the same time, we have received reports of nine wheatears that had been colour-ringed on Fair Isle and recorded on passage elsewhere in the UK (including one on North Ronaldsay) in the same period (personal communications from various observers, usually with photographic evidence), only one of which was not subsequently seen on Fair Isle. We therefore believe that the levels of natal or breeding dispersal from Fair Isle are likely to be very low and that dispersal decisions are not the cause of the food availability-linked variation in apparent first year survival.

Adult survival rate estimates were higher for fed than control birds in all years. While the width of the confidence intervals of these estimates require caution to be applied in their interpretation, it is nonetheless compelling that for both males and females, survival rate estimates for fed birds were higher than for control birds in all years (0.51–0.66 for fed birds and 0.45–0.51 for control birds). The survival estimates for control and fed adults were approximately within the range reported for adult northern wheatears under natural conditions in Sweden, at a similar latitude to the current study (0.41–0.62, Arlt et al. 2008; 0.42–0.50, Low et al. 2010). Food supplementation in our study may have compensated for periods of low natural food availability, thereby reducing nutritional stress, reducing the work load of feeding dependent offspring, and ensuring plentiful food during moult and fuelling for migration. All of these benefits would be likely to lead to higher survival of adults due to lower reproductive costs (Low et al. 2010), improved quality of newly-moulted feathers (Norris et al. 2004b) and improved body condition at the onset of migration (Fransson 1998; Chapter 2).

Our results suggested that fed juveniles (i.e. those that used feeding stations as opposed to those fledging from fed nests) were more likely to survive their first year than control juveniles (i.e. those observed after fledging but which did not use feeding stations). In contrast, there was no support for the hypothesis that survival rates of juveniles were enhanced by higher food availability to parents provisioning dependent offspring (nestlings and juveniles during the first 2 weeks after fledging). Consistent with these results, we found that fledging success of first broods was no different between fed and control pairs (Chapter 3). This suggests that under current natural foraging conditions on Fair Isle, brood size and the fledging rate of first broods are not limited by food availability. An alternative explanation is that food availability does limit growth and survival of chicks, but that parents do not increase feeding rates even when food availability increases. We did find that, in 2009, chicks of fed parents were significantly larger than chicks of control parents (Chapter 3). The current study, however, failed to find convincing evidence that this led to higher survival rates of those chicks from fed broods. In contrast, there was a marked effect of juvenile treatment on first year survival rate estimates: survival estimates for juveniles using feeders ranged from 0.41 to 0.43, while for juveniles not using feeders (but observed after fledging), estimates ranged from 0.27 to 0.28. Evidence that fed birds had better body condition than control birds post-breeding comes from an analysis of body mass of wheatears of the same study population (Chapter 2). Food availability between fledging of first broods and departure on autumn migration could be limiting the body condition of wheatears under current natural foraging conditions. Late-season food limitation is likely to affect juvenile birds to a greater extent than adult birds, because adults have greater foraging experience and knowledge of local foraging resources than juveniles, gained in previous seasons. Changes in late-breeding-season food availability due to climate change (or other factors such as land use change) could therefore affect body condition of juvenile wheatears. Experimental warming by 2ºC of upland turf samples from wheatear habitat in mid-Wales suggests that climate warming will lead to a reduction of late-breeding-season food availability due to a shortening of the arthropod emergence peak (Chapter 5). This could affect the quality of post-juvenile moult, starvation risk on Fair Isle, predator avoidance behaviour (due to the need for increased risk taking under conditions of nutritional stress) and the rate and extent of fat and muscle accumulation for autumn migration. Feather quality is likely to influence survival via its effects on thermoregulation and flight performance (Nilssen and

Svensson 1996, Dawson et al. 2000). Variation in post-breeding food availability could affect quality of flight feathers only in adults, because juveniles retain their juvenile flight feathers until the end of the subsequent breeding season. Foraging conditions could affect the quality of adult and juvenile body feathers moulted post-breeding, however, with subsequent effects on thermoregulation. The substantially higher rates of first year survival of juveniles that had already survived the immediate post-fledging period, compared to those monitored from the nestling stage, reveal that much first year mortality occurs around the time of fledging on Fair Isle, before departure on autumn migration. Birds departing Fair Isle with greater fat and muscle stores may have an improved likelihood of surviving migration to the wintering grounds, due to an increased resistance to starvation during periods of poor weather, or at stopover sites of poor foraging conditions. To gain a better understanding of how much mortality occurs at the breeding location or in non-breeding areas (migration or wintering sites) would require intensive re-sighting or remote tracking of birds until departure.

Habitat-specific differences in population growth rates of wheatears have previously been shown to be determined by differences in adult survival more than reproductive success (Arlt et al. 2008). Foraging conditions determined by vegetation height underpin these differences in habitat-specific population growth (Arlt et al. 2008, Low et al. 2010). In our studies on wheatears, we have shown that an increase in food availability leads to increased fledgling production (Chapter 3) and that more of these fledglings then survive to recruit to the local population (current study). We also found that increased food availability had a positive impact on adult survival rates. The combination of these factors provided an estimate of a 1.2 times higher annual population growth rate in our fed birds than our control birds. This estimate is likely to be conservative within the context of our experiment, because the cages that we used to prevent more voracious species (starlings) stealing food also stopped some target wheatears, causing them to be excluded from the food-supplemented treatment group (and treated as controls) even though they had received a limited amount of supplementary food early in the breeding season. If the food supplementation was extended to all wheatear territories on Fair Isle, our results suggest that the island would turn from a population sink to a population source. Environmental conditions in the non-breeding season of migratory birds are undoubtedly important determinants of population sizes (Marra et al. 1998, Sillett and Holmes 2002, Norris et al. 2004a). The results of this study suggest that climate-linked changes in breeding season food availability can affect survival. The direction of change in food availability will determine whether this could exacerbate or buffer lowered survival in the sub-Saharan wintering areas, where climate change could lead to lower food availability.

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REFERENCES

Altermatt, F. 2010. Climatic warming increases voltinism in European butterflies and moths. Proceedings of the Royal Society B: Biological Sciences 277:1281-7.

Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. T. Iii. 1997. Juvenile survival in a population of Neotropical migrant birds. Conservation Biology 11:698-707.

Arlt, D., P. Forslund, T. Jeppsson, and T. Pärt. 2008. Habitat-specific population growth of a farmland bird. PloS ONE 3:e3006.

Arlt, D., and T. Pärt. 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. Ecology 88:792-801.

Arnason, A. N. 1972. Parameter estimates from mark-recapture experiments on two populations subject to migration and death. Researches on Population Ecology 13:97-113.

Arnason, A. N. 1973. The estimation of population size, migration rates, and survival in a stratified population. Researches on Population Ecology 15:1-8.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8:1–16.

Blem, C. R. 1980. The energetics of migration. Pages 175-224 *in* S. A. Gauthreaux, Jr, editor. Animal Migration, Orientation and Navigation. Academic Press, London.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81-83.

Both, C., and M. E. Visser. 2005. The effect of climate change on the correlation between avian life-history traits. Global Change Biology 11:1606-1613.

Brown, D. R., and T. W. Sherry. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. Oecologia 149:22-32.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173-1187.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach. Springer-Verlag, New York.

Chase, M. K., N. Nur, and G. R. Geupel. 1997. Survival, productivity, and abundance in a Wilson’s Warbler population. The Auk 114:354-366.

Conder, P. 1989. The Wheatear. Christopher Helm, London.

Cooch, E. G., and G. C. White. 2011. Program MARK: A Gentle Introduction, 9th edition. Available online at: http://www.phidot.org/software/mark/docs/book/

Cramp, S. (Ed.). 1988. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Volume V: Tyrant flycatchers to thrushes. Oxford University Press, Oxford.

Currie, D., D. B. A. Thompson, and T. Burke. 2000. Patterns of territory settlement and consequences for breeding success in the Northern Wheatear *Oenanthe oenanthe*. Ibis 142:389-398.

Dawson, A., S. A. Hinsley, P. N. Ferns, R. H. Bonser, and L. Eccleston. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proceedings of the Royal Society B: Biological Sciences 267:2093-2098.

Duncan Rastogi, A., and L. Zanette. 2006. Food availability affects diurnal nest predation and adult antipredator behaviour in song sparrows, *Melospiza melodia*. Animal Behaviour 72:933-940.

Fransson, T. 1998. A feeding experiment on migratory fuelling in whitethroats, *Sylvia communis*. Animal Behaviour 55:153-162.

Fulton, D. 2010. The breeding population of northern wheatears at Clee Hill, Shropshire, 1998-2009. British Birds 103:223-228.

Gill, J.A., K. Norris, P.M. Potts, T.G. Gunnarsson, P.W. Atkinson, and W.J. Sutherland. 2001. The buffer effect and large-scale population regulation in migratory birds. Nature 412:436-438.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1-21.

Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada Geese. Ecology 72:523-533.

Klaassen, M. 1996. Metabolic constraints on long-distance migration in birds. Journal of Experimental Biology 199:57-64.

Laake, J., and E. Rextad. 2011. RMark - an alternative to building linear models in MARK. Page C1-C108 *in* E. G. Cooch and G. C. White, editors. Program Mark: A Gentle Introduction, 9th edition. Available online at: http://www.phidot.org/software/mark/docs/book/

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67-118.

Low, M., D. Arlt, S. Eggers, and T. Pärt. 2010. Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. Journal of Animal Ecology 79:214–224.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884-1886.

Matthysen, E., F. Adriaensen, and A. A. Dhondt. 2011. Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus*, *Parus major*). Global Change Biology 17:1-16.

Mazerolle, D. F., K. W. Dufour, K. A. Hobson, and H. E. Den Haan. 2005. Effects of large-scale climatic fluctuations on survival and production of young in a Neotropical migrant songbird, the yellow warbler *Dendroica petechia*. Journal of Avian Biology 36:155-163.

McDonald, P. G., P. D. Olsen, and A. Cockburn. 2004. Weather dictates reproductive success and survival in the Australian brown falcon *Falco berigora*. Journal of Animal Ecology 73:683-692.

Miles, J. E., J. S. Bale, and I. D. Hodkinson. 1997. Effects of temperature elevation on the population dynamics of the upland heather psyllid *Strophingia ericae* (Curtis) (Homoptera: Psylloidea). Global Change Biology 3:291–297.

Nichols, J. D., J. E. Hines, K. H. Pollock, R. L. Hinz, and W. A. Link. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. Ecology 75:2052-2065.

Nichols, J. D., and W. L. Kendall. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. Journal of Applied Statistics 22:835-846.

Nilssen, J. A., and E. Svensson. 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. Proceedings of the Royal Society B: Biological Sciences 263:711-714.

Nolan, A. J., P. D. Hulme, and D. Wheeler. 1994. The status of *Calluna vulgaris* (L.) Hull on Fair Isle. Botanical Journal of Scotland 47:1-16.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004a. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society B: Biological Sciences 271:59-64.

Norris, D. R., P. P. Marra, R. Montgomerie, T. K. Kyser, and L. M. Ratcliffe. 2004b. Reproductive effort, molting latitude, and feather color in a migratory songbird. Science 306:2249-2250.

Panov, E. N. 2005. Wheatears of Palearctic: Ecology, Behaviour and Evolution of the Genus *Oenanthe*. Pensoft, Sofia-Moscow.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology and Systematics 37:637-669.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Pearce-Higgins, J. W., P. Dennis, M. J. Whittingham, and D. W. Yalden. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. Global Change Biology 16:12–23.

Pärt, T. 2001a. Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. Proceedings of the Royal Society B: Biological Sciences 268:2267-2271.

Pärt, T. 2001b. The effects of territory quality on age-dependent reproductive performance in the northern wheatear (*Oenanthe oenanthe*). Animal Behaviour 62:379-388.

R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Saino, N., D. Rubolini, N. Jonzén, T. Ergon, A. Montemaggiori, N. C. Stenseth, and F. Spina. 2007. Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. Climate Research 35:123-134.

Schwarz, C. J., J. F. Schweigert, and A. N. Arnason. 1993. Estimating migration rates using tag-recovery data. Biometrics 49:177-193.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296-308.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292-1296.

Strathdee, A. T., J. S. Bale, W. C. Block, S. J. Coulson, I. D. Hodkinson, and N. R. Webb. 1993. Effects of temperature elevation on a field population of *Acyrthosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen. Oecologia 96:457–465.

Studds, C.E., and P.P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86:2380-2385.

Studds, C. E., and P. P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Climate Research 35:115-122.

Stutchbury, B. J. M., E. A. Gow, T. Done, M. Macpherson, J. W. Fox, and V. Afanasyev. 2011. Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. Proceedings of the Royal Society B: Biological Sciences 278:131-137.

Svensson, L. 1992. Identification Guide to European Passerines, 4th edition. British Trust for Ornithology, Norfolk.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120-138.

White, T. C. R. 2008. The role of food, weather and climate in limiting the abundance of animals. Biological Reviews 83:227-248.

Witter, M. 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. Animal Behaviour 48:201-222.

Supporting Information

Table S4.1. ΔQAICc ranking of multi-state models of detection probability (p) of adult wheatears. The same covariate structure for survival (ϕ) is used for all candidate models, while the transition parameter (ψ) is fixed at 1 for all models. Subscripts denote factors allowed to vary for the ϕ and p parameters (trt (treatment), sex and year). No subscript = constant across groups and time.

Model				No. parameters	ΔQAICc	*w*AICc	Deviance
(S1)	$\phi_{\text{trt, sex, year}}$	ψ	$p_{\text{sex [2011 = 1]}}$	8	0.0	0.239	84.0
(S2)	$\phi_{\text{trt, sex, year}}$	ψ	$p_{\text{sex [2011 = 0.901]}}$	8	0.5	0.181	84.5
(S3)	$\phi_{\text{trt, sex, year}}$	ψ	$p_{\text{[2011 = 1]}}$	7	0.8	0.157	86.9
(S4)	$\phi_{\text{trt, sex, year}}$	ψ	$p_{\text{[2011 = 0.901]}}$	7	1.4	0.121	87.4
(S5)	$\phi_{\text{trt, sex, year}}$	ψ	$p_{\text{sex, year [2011 = 1]}}$	9	1.8	0.097	83.7
(S6)	$\phi_{\text{trt, sex, year}}$	ψ	$p_{\text{year [2011 = 1]}}$	8	2.3	0.075	86.3
(S7)	$\phi_{\text{trt, sex, year}}$	ψ	$p_{\text{sex, year [2011 = 0.901]}}$	9	2.4	0.073	84.2
(S8)	$\phi_{\text{trt, sex, year}}$	ψ	$p_{\text{year [2011 = 0.901]}}$	8	2.8	0.057	86.8

Detection probability of the data set of all colour-ringed juveniles for 2011 was fixed at different levels, as denoted within brackets following the p model notation: 1, [2011 = 1] and the mean of p in 2009 and 2010, 0.675 [2011 = 0.675].

Table S4.2. ΔAICc ranking of models of detection probability (*p*) of yearling wheatears. The same covariate structure for survival ϕ is used for all candidate models. Subscripts denote factors allowed to vary for the ϕ and *p* parameters: nest treatment (nest_trt), juvenile treatment (trt), presence/absence of colour rings (col), year and no subscript = constant across groups and time.

Model			No. parameters	ΔAICc	*w*AICc	Deviance
Juveniles of known nest treatment[1]						
(S9)	$\phi_{\text{nest\_trt x year}}$	p_{col}	9	0	0.692	26.5
(S10)	$\phi_{\text{nest\_trt x year}}$	$p_{\text{col, year}}$	11	1.9	0.271	24.2
(S11)	$\phi_{\text{nest\_trt x year}}$	p	8	6.1	0.032	34.7
(S12)	$\phi_{\text{nest\_trt x year}}$	p_{year}	10	9.6	0.006	34.1
All juveniles[2]						
(S13)	$\phi_{\text{trt, year}}$	$p_{\,[2011 = 1]}$	6	0.0	0.371	11.3
(S14)	$\phi_{\text{trt, year}}$	$p_{\,[2011 = 0.675]}$	6	0.1	0.360	11.3
(S15)	$\phi_{\text{trt, year}}$	$p_{\text{year}\,[2011 = 0.675]}$	7	2.0	0.137	11.2
(S16)	$\phi_{\text{trt, year}}$	$p_{\text{year}\,[2011 = 1]}$	7	2.1	0.132	11.2

[1] Subset of juveniles with known experimental nest treatment (parents fed or control) because parent ID could be confidently determined.

[2] All ringed juveniles, including those of unknown nest treatment.

Detection probability of the data set of all colour-ringed juveniles for 2011 was fixed at different levels, as denoted within brackets following the *p* model notation: 1, [2011 = 1] and the mean of *p* in 2009 and 2010, 0.675 [2011 = 0.675].

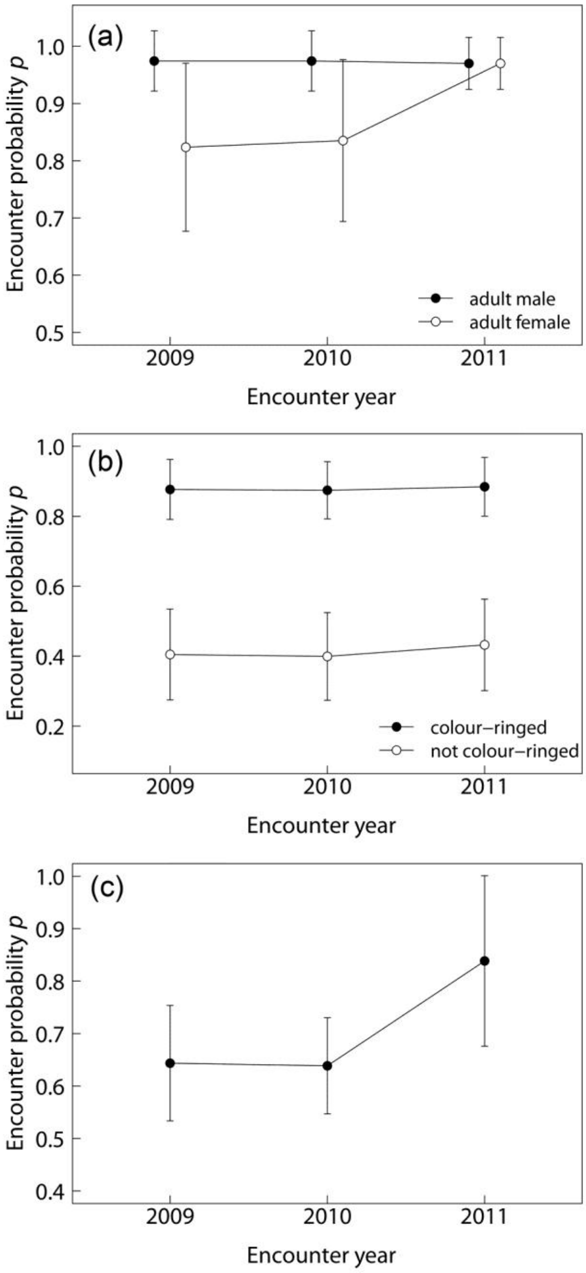

Fig. S1. Model-averaged encounter probabilities (± 1 SE) in the three years of this study of (a) adult males and adult females (note that in 2011, resighting probabilities were fixed at 1 or the mean of 2009 and 2010 in different models), (b) yearlings in the nest treatment subset that were either colour-ringed or not colour-ringed (i.e. metal ringed only) and (c) yearlings in the fledgling treatment subset (note that in 2011, resighting probabilities were fixed at 1 or the mean of 2009 and 2010 in different models).

CHAPTER 5. Manipulations of soil water content and temperature alter the availability of arthropod prey to an upland migrant bird, the northern wheatear (*Oenanthe oenanthe*)

ABSTRACT

An important mechanism by which climate change affects animals is likely to be through changes in the abundance and phenology of their food supply, yet the effects of climate on food availability are generally poorly understood. Here we determine the effects of experimental manipulations of temperature and soil moisture on the emergence of arthropod prey of insectivorous birds, from turf samples obtained from upland grassland and kept in individual containers. Manipulations of both temperature and soil water content affected arthropod phenology and abundance, as well as the size of arthropods that emerged. Warming by 2°C in combination with elevated soil moisture caused a higher peak of abundance among the non-Sciaridae arthropod taxa. Warming by 2°C caused a shorter peak of abundance of these univoltine taxa at lower levels of soil moisture. There was, however, no difference in total abundance of these taxa between temperature or soil moisture treatments. Abundance of the only multivoltine insects in our samples, the Sciaridae, was greatly increased by warming in combination with increasing soil moisture. Mean body length of arthropods emerging from warmed turf was greater than those from unheated turf at the beginning of the season, and smaller at the end. Extreme low soil water content reduced arthropod emergence. Arthropods are expected to be smaller at the end of hot summers, whilst abundance of individual taxa will depend on life-history. The phenology of the arthropods emerging from grassland turf samples in the present study suggests that the window of high food availability to upland grassland birds such as the northern wheatear will be shorter and earlier during warmer and drier summers, which are predicted to become more frequent in Wales over the next century.

INTRODUCTION

Understanding how climate affects the abundance and phenology of animal food availability is important for predicting ecological responses to climate change (Helmuth et al. 2005). For organisms living in seasonal environments, synchronisation of energetically expensive stages of the life cycle with periods of high food availability is essential to maximise fitness (Perrins 1970). For example, migratory songbirds living in temperate regions typically have a diet dominated by arthropods, which have a pronounced peak in abundance during the spring and summer (Van Noordwijk et al. 1995, Visser et al. 2006). By altering the abundance and phenology of their arthropod prey, climate change can have impacts on the survival and breeding success of migratory songbirds (Both et al. 2006; Mazerolle et al. 2005; Norris et al. 2004, Chapters 2, 3 and 4).

There is compelling evidence that some migratory songbirds have undergone phenological changes over recent decades that are associated with climate-driven changes in food availability; for example by advancing the timing of migration and egg-laying, so that chick-rearing still coincides with peaks in food abundance that are occurring progressively earlier during the breeding season (Dunn and Winkler 1999, Jenni and Kéry 2003, Cotton 2003, Crick 2004, Tryjanowski et al. 2005, Visser and Both 2005). The ability of birds to track changes in food abundance is expected to have a major effect on breeding performance and survival, and hence on population sizes and distributions (Møller et al. 2008). For example, declines of some European populations of pied flycatcher, *Ficedula hypoleuca,* appear to be due to an inability to adjust arrival dates sufficiently to match the advancing phenology of their arthropod food resources, brought about by recent climate change (Both and Visser 2001).

Food manipulation experiments (simulating climate-driven changes in food availability) have demonstrated directly the effect that changing food abundance at breeding areas can have on breeding productivity of migratory birds (Nagy and Holmes 2005; Rodenhouse and Holmes 1992; Chapter 3). Food supplementation led to increases in the number of breeding attempts in black-throated blue warblers, *Dendroica caerulescens,* (Nagy and Holmes 2005) and northern wheatears, *Oenanthe oenanthe,* (Chapter 3). Food supplementation also had a positive impact on first year survival of northern wheatears (Chapter 4). Experimental food reductions led to fewer nesting attempts in black-throated blue warblers (Rodenhouse and Holmes 1992), but had no impact on breeding productivity of red-eyed vireos, *Vireo olivaceus* (Marshall et al. 2002).

Although these studies indicate that the timing and abundance of food availability has a major effect on the population dynamics of migratory birds, the details of how future climate change will actually affect food availability for birds in any particular habitat remain largely unknown. Climate change is known to affect population sizes (Bale et al. 2002), distribution (Musolin 2007) and phenology (Buse and Good 1996, Musolin 2007) of individual arthropod taxa. However, the responses of insect life-histories to climate change are both complex and varied, depending on an individual species' life-history and ecology (Briones et al. 1997). Marked changes in species distribution – of taxa including Odonata, Orthoptera and Lepidoptera – in response to unusually hot summers, provide useful information about the potential effects of climate change (Cannon 1998), but there has yet to be an overall test of the hypotheses that climate change will affect both (i) the productivity and (ii) the phenology of entire insect communities in any habitat. This is a critical question in the context of understanding the mechanisms underlying the effects of climate on the breeding and migration strategies of insectivorous birds. It is, for example, not known whether climate change is causing an overall increase or decrease in upland arthropod biomass, or how the peaks in total arthropod availability may be advanced or delayed by climate changes. The present study addresses this gap in current knowledge of the changes taking place in upland ecosystems, by testing the effects of projected climate change on a whole community of grassland arthropods and provides insights into the trophic mechanisms which may underlie currently observed widespread changes in bird behaviour, phenology and populations.

Both changing temperature and changing rainfall patterns can impact arthropod abundance and phenology (Bale et al. 2002). Soil moisture content may be more important than average temperatures, for example because many arthropod larvae (particularly Tipulidae) are sensitive to desiccation (Coulson et al. 1976, Briones et al. 1997). Soil moisture is related to both precipitation (the amount of water falling onto the soil) and temperature (affecting evaporation of water from the soil). Climate change is predicted to lead to warmer, dryer summers in the UK uplands (Holden et al. 2007), which has been shown to cause significant declines in abundance of tipulids, a key prey category for many upland breeding birds (Pearce-Higgins et al. 2010, Carroll et al. 2011). Experimental increases of upland peatland moisture levels led to increases in abundance of tipulids, a keystone taxon of peatland ecosystems (Carroll et al. 2011). Temperature also affects arthropod development rates, diapause and emergence (Butterfield, 1976; Bale et al. 2002). Although an increase in temperature may cause earlier arthropod emergence (Masters et al. 1998, Gordo and Sanz 2006), these early emergents may have a lower adult weight and fecundity (Butterfield 1976). This may in turn affect both their reproductive success and their value as food for migratory birds.

The majority of upland birds in the UK forage on arthropods. This arguably makes them particularly sensitive to climate change (Pearce-Higgins 2010) because arthropods are themselves known to be sensitive to climate change (Bale et al. 2002, Pearce-Higgins et al. 2010, Bale and Hayward 2010). Furthermore, years of land-use changes, including recent agricultural intensification, have had major impacts on the suitability of many areas of the uplands as bird habitat (Buchanan et al. 2006, Amar et al. 2011).

Adults and larvae of Diptera represent a large proportion of the diets of upland birds (Buchanan et al. 2006). Higher temperatures should allow faster development times, which for multivoltine species (i.e. species with more than one generation per year) such as many Diptera, may allow additional generations per year. It is predicted that higher ambient temperatures will allow many multivoltine species to expand their geographical ranges to higher latitudes and altitudes (Bale et al. 2002). Indeed, this has already been observed in a number of UK butterfly species (Pollard et al. 1995).

In this study we test the potential net effect of climate change on phenology and abundance of the community of arthropods emerging from upland grassland swards, by experimentally manipulating temperature and soil moisture content. We focused on likely prey of the northern wheatear, a widespread Afro-Palearctic migrant songbird, that in the UK inhabits mainly upland moorland and grassland habitats (Cramp 1988, Conder 1989). This bird species was chosen as a case-study because we have previously shown how changes in food abundance affect the survival, body mass regulation and breeding productivity of northern wheatear (Chapters 2–4). In the present study, we used experimental manipulations of temperature and soil water content to enable us to predict the effects of future climate change on the arthropod prey of northern wheatears, thus examining the mechanism linking projected changes in temperature and rainfall in wheatear breeding habitats, with our results on the effects of changing food availability on demographic change in wheatear populations. We tested the hypotheses that (1) a 2 ºC increase in temperature (within the range of projected warming by 2100; IPCC 2007, Murphy et al. 2009) would lead to advanced emergence phenology and greater arthropod abundance, and (2) extreme (high or low) soil moisture content would have a negative impact on arthropod abundance in upland grassland sward. As most upland grassland and moorland migratory birds forage primarily on arthropods (especially insects), these results are applicable across upland migratory bird communities, including taxa of conservation concern such as ring ouzels (*Turdus torquatus*), skylarks (*Alauda arvensis*) and golden plovers (*Pluvialis apricaria*).

MATERIALS AND METHODS

Sampling site, turf collection and maintenance

We extracted 72 samples of turf, measuring approx. 40 cm long x 25 cm wide x 10 cm deep, from an upland, semi-natural, grassland site at Coed-y-Wern farm, Pwllgloyw, in the Brecon Beacons National Park, mid-Wales, UK (51°59'N, 3°25'W). Mean turf weight (± SE) was c. 6.48 ± 0.05 kg (range 5.6–7.3 kg). The turf collection site comprised short-grazed grassland sward and scattered rocks and so represented typical northern wheatear breeding habitat in the British uplands (Cramp 1988). Indeed, territory-holding northern wheatears had been observed at the site in the years preceding our turf removal (R.J. Thomas, pers. obs.). The underlying soil was a mixture of red sandstone and clay typical of the Brecon Beacons National Park and the field was grazed by ponies (*Equus ferus caballus*), sheep (*Ovis aries*) and rabbits (*Oryctolagus cuniculus*). The plant composition of the turf was typical of short-grazed upland grassland, dominated by common bent (*Agrostis capillaris*) with sheep's fescue (*Festuca ovina*), springy turf moss (*Rhytidiadelphus squarrosus*), glittering wood moss (*Hylocomium splendens*) and occasional ribwort plantain (*Plantago lanceolata*), common dog violet (*Viola riviniana*), bird's foot trefoil (*Lotus corniculatus*) and creeping thistle (*Cirsium arvense*).

The turf samples were collected on 25th March 2011. The date of sample collection was chosen in order for the experiment to begin at the time when wheatears were beginning to arrive and breed in the Welsh uplands, and in fact coincided with the first sighting of wheatears on the southern coasts of England and Wales in late March 2011. The experiment was carried out across 19 weeks, from late March to late July 2011, in order to encompass the arrival and breeding season of northern wheatears until independence of first-brood fledglings in June–July (Cramp 1988). Importantly, the experimental period included the later stages of the breeding season in June–July, when wheatears would be expected to initiate second broods if sufficient food resources were available to them (Chapter 3).

Each turf sample was placed in a separate plastic seed propagator tray with a transparent plastic lid and closable ventilation holes (obtained from B&Q ltd). The turf samples, in their propagators, were kept under covered outdoor shelters (an unused aviary) with wire mesh walls (gauge size ca. 2 cm) and a Perspex roof, to maintain them at approximately outdoor temperatures and light levels, including diurnal and seasonal fluctuations, whilst keeping the samples sheltered from rainwater and direct sunlight.

The vegetation in each of the turf samples was cut weekly with scissors to a height of 10 cm, to simulate natural grazing conditions that would occur in an upland setting. When the turf samples were collected, the vegetation on the samples had been grazed to a shorter length (c. 3–4 cm) over the preceding winter; however this was shorter than the height that wheatear habitat would typically be grazed to during the summer (pers. obs), and so the vegetation of the sampled turfs was allowed to grow to 10 cm before cutting began.

Experimental design

Each turf sample was randomly assigned to one of six treatment groups (Table 5.1), in a 3 x 2 factorial experiment (with n = 12 turf samples in each treatment) with three soil moisture treatments (raised, control, lowered) and two temperature treatments (ambient and warmed).

Table 5.1. The six combinations of soil moisture and temperature treatment, in a 3 x 2 factorial design. Increased soil moisture turfs were watered weekly to raise soil water content above 12%. Turfs with minimal change in soil moisture were kept as close to their starting soil water content levels as possible (within 9–12% soil water content). Turfs with decreased soil water content were kept below 9% soil water content. The temperature of ambient temperature turfs was allowed to fluctuate with outside conditions. Warmed turfs had their temperature raised approximately 2 °C above the ambient turfs.

group	moisture treatment	temperature treatment	n
A1	increased	ambient	12
A2	increased	warmed	12
B1	minimal change	ambient	12
B2	minimal change	warmed	12
C1	decreased	ambient	12
C2	decreased	warmed	12

Soil moisture treatments

We used a soil moisture probe (Lutron PMS-714) to measure volumetric soil water content to 0.1%. Readings were taken every 2 to 3 days, by inserting the probe horizontally into the centre of each turf sample, from 4 cm below the soil surface. This standard procedure allowed for the most repeatable measurements and direct comparison between samples**,** as water content may vary between the edges and the centre of each turf. The mean (± SE) initial volumetric soil water content of samples removed from the sampling site was 9.9 ± 0.1% (range 7.7–11.9%). During week 13, 12 water content readings taken in the field at the sampling site ranged from 9–12%.

Turf groups A1 and A2 (increased soil moisture treatments) were watered weekly for the first four weeks of the experiment in order to raise the volumetric soil water content above 12% (the upper range recorded in the turf samples just after removal from the field). Each sample was watered with up to 300 ml of water, but with less if saturation of the soil was reached (i.e. water began draining from the bottom of the turf into the bottom of the seed tray). Samples were not watered at all if water was already pooled in the bottom of the tray, as these samples were considered to be already saturated. After the 4 weeks of initial watering, soil water content was maintained at an elevated level for each treatment, by watering those samples which had dried by 1% volumetric water content or more. During watering, water was added to the turf in 50 ml increments, whilst monitoring with the soil moisture probe, until the target water content was attained.

Groups B1 and B2 were kept as close to their initial (week 1) soil water content as possible. Any condensation that formed on the inside surface of the propagator lid was poured back onto the soil to minimise water loss. Samples were monitored with the soil moisture probe and watered when having lost 1% or more volumetric water content from their target level (as above in A1 and A2).

Groups C1 and C2 were initially dried through the repeated removal of condensation from the inside surface of the propagator lids using a towel. This was carried out three times weekly for the first four weeks. Volumetric water content was monitored and after the initial drying period, samples were watered whenever they had lost 1% volumetric water content (as in the above treatments).

Particularly warm spells of weather caused faster drying than the 1% per 2 to 3 days that we aimed for, before moisture levels were restored by watering. In addition, peaks of higher than expected soil water content occurred when soil water content continued to rise after watering – as water diffused/percolated through the compacted clay soil – or after heavy rainfall that entered the shelter. The desired water contents were restored in these cases by wiping away condensation from the inside surfaces of the lids. Despite these practical difficulties, the required differences between treatment groups in mean soil water content were apparent across the study period (Fig. 5.1).

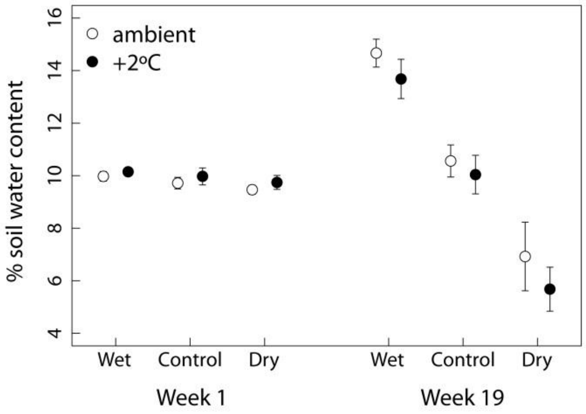

Fig. 5.1. Mean soil water content (± 1 SE) at three soil moisture treatments (wet (elevated soil moisture), control (within pre-manipulation range: 9–12%) and dry) and two warming treatments (ambient and + 2 ºC) in week 1 and week 19.

Two samples in the dry heated treatment (C2) were colonised by ants. The structure of the ant's nests, within the soil, made water content measurement with the soil moisture probe impossible. These samples were therefore removed from all analyses.

Temperature treatments

Groups A1, B1 and C1 (temperature controls) were left at ambient temperature. Groups A2, B2 and C2 (elevated temperature treatment) were placed on thermostatically controlled heat mats (Bio Green, Bischoffen-Oberweidbach, Germany) to elevate soil temperatures to 2 ºC above ambient. Temperatures of turf samples were monitored using mercury thermometers placed inside the propagator, on top of the soil, three times weekly throughout the experiment, and the heat mat thermostats adjusted accordingly if necessary. On some occasions, temperature differences were recorded between those samples near the edge of the shelter and those in the middle. These edge effects depended upon the weather, but since they never exceeded 1 ºC, and because the six treatment groups were evenly distributed with regard to these edge effects, they were considered not to have interfered with differences between temperature treatments.

Monitoring arthropods

Oecos drystick yellow fly papers (Oecos, Kimpton, UK) –henceforth referred to as "sticky traps" – were placed inside each propagator for 1 week in every 2 weeks throughout the experiment. This discontinuous sampling was chosen to allow the life cycles of arthropods emerging from the turf to continue as much as possible during non-trapping weeks, rather than trapping all arthropods as soon as they emerged. We identified arthropods caught on sticky traps to family level, and measured their body length to 0.5 mm.

Arthropod sampling at the field site

During week 13 (on 2 June 2011), twelve pitfall traps and eight sticky traps were set at the site from which the experimental turf samples were taken. The traps were collected one week later. Sticky traps were placed on the surface of the vegetation and covered with a propagator lid to simulate experimental conditions. Pitfall traps were set at ground level and covered with a raised lid to prevent flooding.

Data analysis

For analysis, we carefully selected which arthropod families to include, according to their relevance to the diet of northern wheatears, whether they had soil-based life cycle stages (eggs / larvae / over-wintering adults) and whether they were adequately sampled by sticky-trapping. For one or more of these reasons, we excluded ants, springtails (Collembola), and arachnids (with the exception of trombidiid spiders whose egg and larval life stages occur in soil) from our analysis.

The design of the experiment involved repeated sampling from the same set of turf samples over a protracted period, so a random variable (turf I.D.) was included in all models to avoid the problem of temporal pseudo-replication. In addition, arthropod count data were non-normally distributed, so generalised linear mixed models (GLMMs) were used to model the effects of the experimental treatments on temporal variation in arthropod abundance. All statistical analyses were carried out using R (R Development Core Team 2011). The performance of competing candidate models was compared using Akaike's Information Criterion, corrected for small sample size (AICc; Burnham & Anderson, 2002). Smaller values of AICc indicate better statistical fits. Two statistics were obtained for each model: $\Delta\mathrm{AIC}_i$ (the difference in AICc between model *i* and the best model) and $w\mathrm{AIC}_i$ (Akaike weight), which indicates the likelihood that each model is the best approximation relative to all the other models in the model set. The models were ranked by $\Delta\mathrm{AIC}_i$ and the most plausible models were defined as those with $\Delta\mathrm{AIC}_i \leq 2$.

Sciaridae (colloquially known as "fungus gnats") made up over 80% of all arthropods caught. These small flies are well known garden pests, and flourish in damp turf (Keates et al. 1989, Meers and Cloyd 2005). It is unclear whether sciarids are a component of wheatear diet and therefore we analysed counts of Sciaridae in separate analyses to those of other arthropod families. This was because the extreme dominance of sciarids in the sticky-trap samples, together with their strong association with wet turf, was likely to mask results from other taxa.

Arthropod abundance varied over time in a clearly non-linear manner. We used zero-inflated GLMMs (with a Poisson error distribution and log link function) using the R package “GLMM.admb” (ADMB Project 2009) with week number represented as a categorical variable.

Sciarid abundance was also zero-inflated, and in addition had some very large counts from individual turf samples. The residual distribution was normalised by square root transformation of sciarid abundance. We used a zero-inflated GLMM with a negative binomial distribution (and log link function), using GLMM.admb. To model arthropod size, we used a GLMM with a Poisson distribution (and log link function) implemented in GLMM.admb.

RESULTS

Across all 72 turf samples and 19 weeks of the experiment, a total of 2,752 individual arthropods emerged and were captured, of which 85.0% were of the dipteran family Sciaridae. Other Diptera accounted for 10.7% of the individuals, the remaining 4.3% comprising individuals of Trombidiformes (Arachnida), Collembola, and the Insecta orders Lepidoptera, Hymenoptera, Orthoptera, Coleoptera, Hemiptera, Dermaptera and unidentified insects. A summary of the taxa captured is given in Table S1 (Supporting Information).

Effects of warming and soil moisture on abundance and phenology of non-sciarid arthropod taxa

Temperature treatment and soil water content were both found to affect the emergence of non-sciarid arthropods over time. Temperature and soil water content also exhibited interactive effects on abundance. The only plausible model (with ΔAICc ≤ 2) to explain numbers of emerging arthropods was the model including all pairs of 2-way interactions between warming treatment, soil water content and week (Table 5.2, Model 1). The AIC weight of c. 0.99 of this model indicated very strong support for these interactions as explanatory terms.

The strong support for the warming x week interaction indicated effects of warming on the phenology of arthropod emergence. Specifically, warmed turf samples produced more arthropods than unwarmed turf in the first 9 weeks – particularly in the elevated moisture treatment – then produced fewer arthropods than unheated turf from week 11 onwards (Fig. 5.2a, c and e). Despite these shifts in the timing of emergence, peak emergence occurred in week 7 in both warmed and ambient turf. Furthermore, across all weeks, the mean number of non-sciarid arthropods per trap (± SE) was very similar in warmed and ambient turf (0.60 ± 0.07 and 0.61 ± 0.06 respectively), indicating that warming alone had very little effect on the total number emerging across the study period.

Table 5.2. Results of AICc selection of models of non-Sciaridae arthropod abundance. Interactions are indicated by x and include all lower order terms as well. $\Delta AICc_i$ is the difference in AICc between model *i* and the best model and $wAICc_i$ is the Akaike weight. Turf ID included as a random effect.

model ID	dependent variable	fixed effects[2]	df	$\Delta AICc_i$	$wAICc_i$
1	abundance[1]	warming x water, warming x week, water x week	38	0	0.987
2		warming x week	18	9.7	0.008
3		warming x water, warming x week	22	11.7	0.003
4		warming x week, water	20	12.2	0.002
5		water x week	27	41.8	< 0.001
6		water x week, warming	28	43.9	< 0.001
7		warming x water, water x week	30	44	< 0.001
8		week	9	47.2	< 0.001
9		warming x week	10	49.3	< 0.001
10		water, week	11	49.6	< 0.001
11		warming x water, week	14	51.4	< 0.001
12		warming, water, week	12	51.7	< 0.001
13		warming x water	6	391.7	< 0.001
14		none	1	392.2	< 0.001
15		warming	2	394.2	< 0.001
16		water	3	395.4	< 0.001
17		warming, water	4	397.3	< 0.001

[1] number of non-Sciaridae invertebrates emerging per turf, per sampling period

[2] fixed effects: warming = warming treatment (+ 2ºC or ambient), water = mean soil water content, week = sampling week, none = intercept-only model.

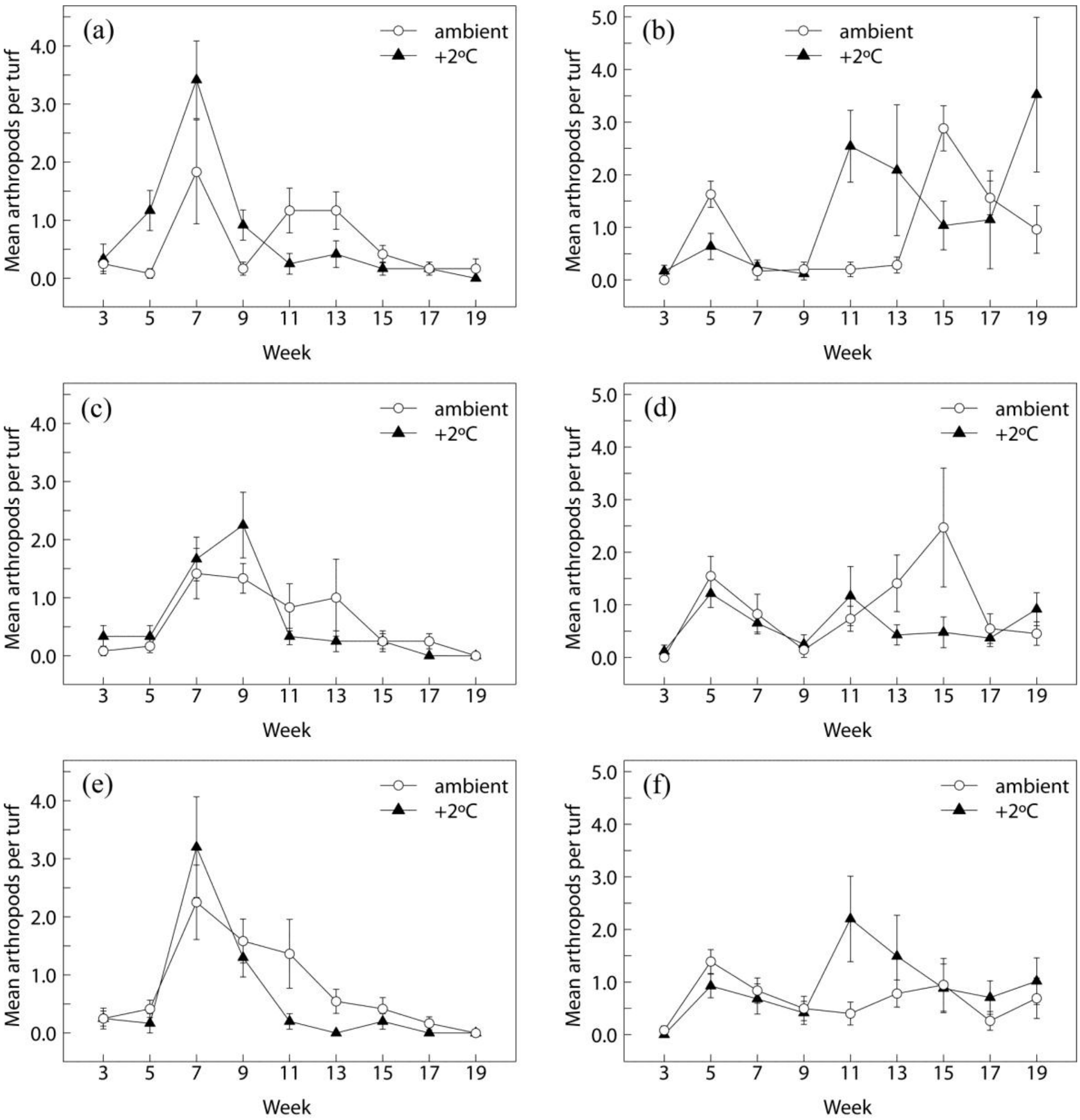

Fig. 5.2. Mean (± 1 SE) abundance of arthropods emerging from turfs over time, by warming treatment (+ 2 ºC and ambient control) and soil moisture treatment: (a) non-Sciaridae at elevated soil moisture (> 12%; wet), (b) Sciaridae at elevated soil moisture (> 12%; wet), (c) non-Sciaridae at medium soil moisture (9–12%; control), (d) Sciaridae at medium soil moisture (9– 12%; control), (e) non-Sciaridae at reduced soil moisture (< 9%; dry) and (f) Sciaridae at reduced soil moisture (< 9%; dry). Sciarid abundances were square root transformed.

The warming x soil water content interaction term indicated that warming had a larger positive impact on non-sciarid arthropod abundance in the elevated moisture treatment, relative to other moisture treatment groups (Fig. 5.2a, c and e).

The soil water content x week interaction term indicated that the effect of soil moisture on non-sciarid arthropod abundance varied significantly over time. From the first measurement of the moisture treatment (week 3) until week 9, emergence from wet turf and dry turf rose relative to control turf (Fig. 5.2a, c and e).

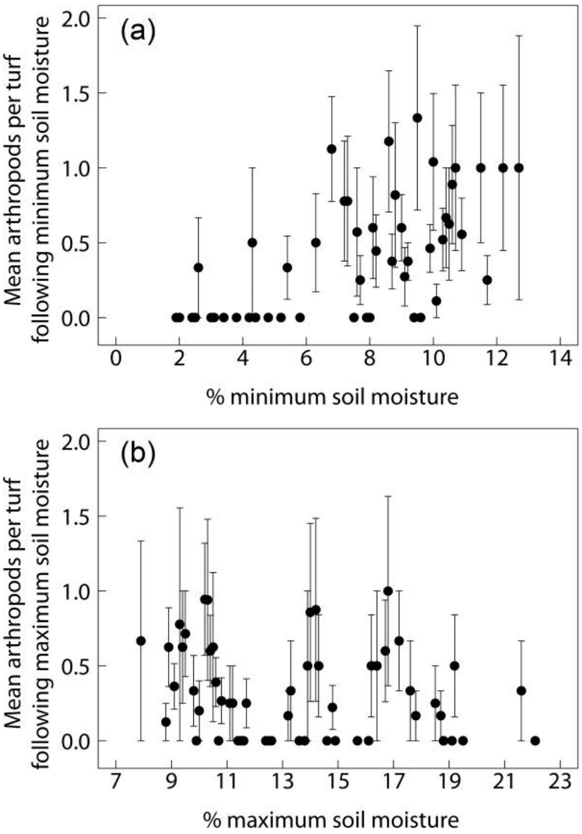

Fig. 5.3. Mean (± 1 SE) abundance of arthropods emerging per turf per sampling period, starting from the week of (a) minimum % soil moisture and (b) maximum % soil moisture for each individual turf.

Numbers of arthropods per turf per sampling occasion were similar between the wet, control and dry soil water content groups (mean ± SE of 0.68 ± 0.09, 0.60 ± 0.08 and 0.68 ± 0.10, respectively). Across all samples and weeks, turf which dried out to lower than approximately 6% soil water content had very little or no emergence of non-sciarid arthropods in the week of minimum soil water content or subsequent weeks (Fig. 5.3a). There was no evidence for a similar pattern in turf that experienced very high maximum levels of soil water content (Fig. 5.3b). Overall, only extremely low levels of soil water content had a great effect upon abundance.

Effects of warming and soil moisture on abundance and phenology of the Sciaridae

Warming and soil moisture were found to affect the emergence of Sciaridae primarily through interactions with time, indicating effects on Sciaridae phenology as well as overall abundance. There appeared to be multiple peaks of emergence of Sciaridae (Fig. 5.2b, d and f), in accordance with this family's multivoltine life history. There were three plausible models to explain Sciaridae abundance, each including the warming treatment x week interaction term (Table 5.3, Models 19–21). AIC weights indicated very strong support for this interaction (summed AIC weights > 0.99). Soil water content and the interaction of warming and soil moisture treatment each appeared in one model (Table 5.3, Models 20–21). Warming appeared to advance second peaks of emergence of Sciaridae (which are multivoltine), but not first peaks (Fig. 5.2b, d and f).

The interaction between warming treatment and soil moisture treatment indicated that Sciaridae abundance was increased under warm conditions with elevated soil moisture (Fig. 5.2b), relative to other treatments (Fig. 5.2d and f). Soil moisture treatment was also reasonably well supported by the data. Overall, over 1.7 times as many Sciaridae emerged from warmed turf relative to ambient turf (mean ± SE per sample; warmed: 4.71 ± 1.32; ambient: 2.57 ± 0.60). Over 2.2 times as many Sciaridae emerged from elevated soil moisture turfs relative to control or dry turfs (mean ± SE per sample; elevated: 5.92 ± 1.86; control: 2.63 ± 0.87; dry: 2.21 ± 0.45).

Table 5.3. Results of AICc selection of models of Sciaridae abundance. Interactions are indicated by x and include all lower order terms as well. $\Delta AICc_i$ is the difference in AICc between model *i* and the best model and $wAICc_i$ is the Akaike weight. Turf ID included as a random effect.

model ID	dependent variable	fixed effects[2]	df	$\Delta AICc_i$	$wAICc_i$
19	abundance[1]	warming x week	19	0	0.457
20		warming x water, warming x week	23	0.7	0.329
21		warming x week, water	21	1.6	0.207
22		warming x water, warming x week, water x week	39	9.7	0.004
23		warming x week, water x week	37	10.7	0.002
24		week	10	15.1	< 0.001
25		water, week	12	15.1	< 0.001
26		warming x water, week	15	15.2	< 0.001
27		warming, week	11	15.9	< 0.001
28		warming, water, week	13	16.2	< 0.001
29		water x week	28	23.7	< 0.001
30		warming x water, water x week	31	24.2	< 0.001
31		water x week, warming	29	24.8	< 0.001
32		warming x water	7	90.2	< 0.001
33		water	4	90.3	< 0.001
34		none	2	91.4	< 0.001
35		warming, water	5	91.7	< 0.001
36		warming	3	92.4	< 0.001

[1] number of individual Sciaridae insects emerging per turf, per sampling period.

[2] fixed effects: warming = warming treatment (+ 2ºC or ambient), water = mean soil water content, week = sampling week, none = intercept-only model.

Table 5.4. Results of AICc selection of models of arthropod body length. Interactions are indicated by x and include all lower order terms as well. $\Delta AICc_i$ is the difference in AICc between model *i* and the best model and $wAICc_i$ is the Akaike weight. Turf ID included as a random effect.

model ID	dependent variable	fixed effects[1]	df	$\Delta AICc_i$	$wAICc_i$
34	body length	warming x week	16	0	0.727
35		warming x week, water	18	3.3	0.141
36		warming x water, warming x week	20	5.4	0.048
37		warming, week	9	5.6	0.044
38		week	8	7.2	0.019
39		warming, water, week	11	8.7	0.010
40		warming x water, week	13	9.6	0.006
41		water, week	10	9.8	0.005
42		none	1	27.3	< 0.001
43		warming	2	28.5	< 0.001
44		water	3	29.6	< 0.001
45		warming x water	6	30.2	< 0.001
46		warming, water	4	31.2	< 0.001
47		warming x week, water x week	32	51.2	< 0.001
48		water x week	24	58.4	< 0.001
49		water x week, warming	25	59.1	< 0.001

[1] fixed effects: warming = warming treatment (+ 2ºC or ambient), water = mean soil water content, week = sampling week, none = intercept-only model.

Effects of warming and soil moisture on arthropod size

Warming was found to increase the mean size of emerging arthropods (all taxa combined) over the first 11 weeks (except for week 3), after which mean arthropod size was greater in the ambient treatment (Fig. 5.4). The only plausible model to explain weekly mean arthropod body length included the interaction warming x week (Table 5.4, Model 34). AIC weights indicated very strong support for inclusion of the warming x week interaction term (summed weights = c. 0.92). Across the experiment as a whole, however, there was little difference in the size of arthropods emerging from warmed and ambient turf (mean body length ± SE of 4.24 mm ± 0.23 mm and 4.00 mm ± 0.19 mm, respectively).

Arthropod sampling at the field site

The arthropod families captured on sticky traps and in pitfall traps at the field sampling site during week 13 are listed in Table S5.1 (Supporting Information). All families of invertebrates captured on sticky papers at the sample site were recorded emerging from experimental turf samples, except the spider family Thomisidae, which does not have a soil-based life-cycle. Pitfall traps contained mainly Coleoptera, of which most were carabids. Of 11 families captured in pitfall traps at the field site, only four were caught on sticky traps emerging from experimental turf samples.

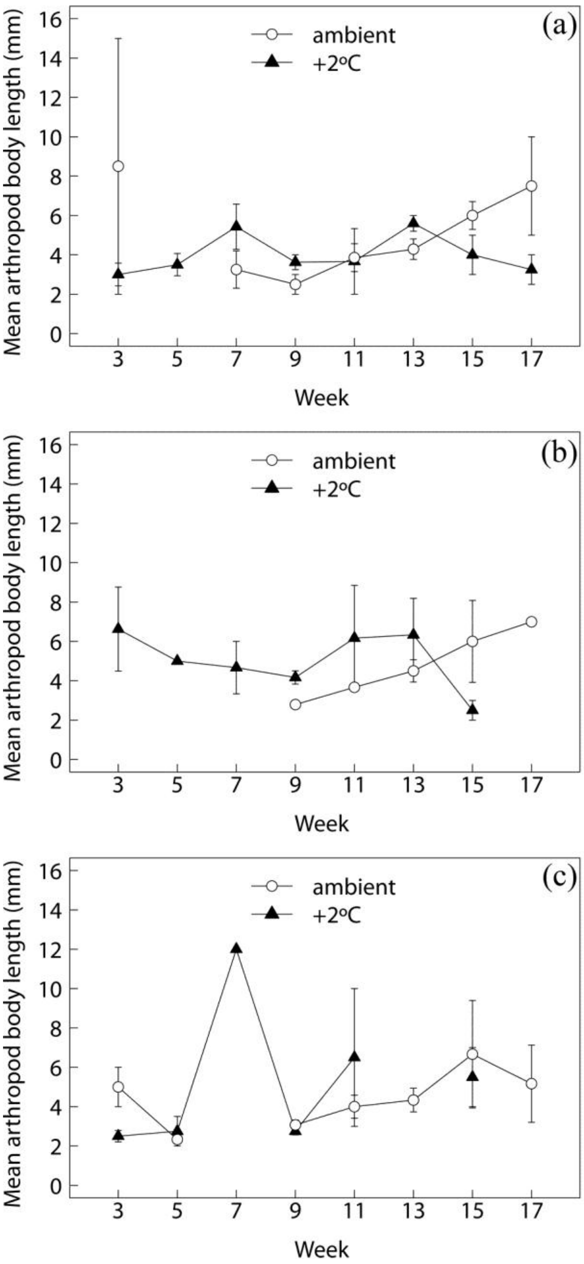

Fig. 5.4. Mean (± 1 SE) body length (mm) of arthropods emerging from warmed (+ 2 ºC) and ambient temperature turf samples at three soil moisture treatments; (a) elevated (> 12%; wet), (b) medium (9–12%; control) and (c) reduced (< 9%; dry).

DISCUSSION

The most recent climate change projections for the UK suggest that summers in Wales will become warmer and drier, relative to a 1961–1990 baseline. Predictions are that summer mean temperature in Wales will increase by approximately 2 ºC by the 2080s, while mean summer precipitation will fall by about 20% over the same period (Murphy et al. 2009). Our results suggest that these predicted climatic changes will have impacts on upland soil arthropod abundance and phenology in Wales, which could, in turn, affect higher trophic levels (such as migratory birds).

Effects of warming and soil moisture on arthropod phenology and abundance

Arthropod phenology

In our study, warming by 2 °C alone had little effect on dates of peak emergence of non-sciarid emergence but increased the height of these peaks. Warming (especially in combination with elevated soil moisture) tended to increase the abundance of non-sciarid arthropods emerging early on (from mid-March until early May), though the time of peak emergence remained unchanged at week 7 (late April). Warming alone resulted in an advance of late emergence peaks of Sciaridae, relative to their emergence from turf kept at ambient temperature, though there was no advance of first Sciaridae emergence peaks. The unchanged timing of peak emergence of arthropods (non-sciarids and first peaks of sciarids) contrasts with the widely observed trend for advancement of spring phenology in a wide range of plant and animal taxa, due to warming (Peñuelas et al. 2002, Walther et al. 2002, Parmesan 2006), although the shifted relative distribution of abundance towards early emergence under warmed conditions are in accordance with these studies.

By the last week of the experiment, emergence of all arthropods except Sciaridae and – in very small numbers – Tineidae (Lepidoptera) had stopped altogether. Emergence of Sciaridae, on the other hand, increased throughout the experiment, particularly in warmed turf with elevated moisture soil. This, together with the observation that the Sciaridae were the only family to have more than two separate peaks of abundance, suggests that the Sciaridae were the only family sampled which produced more than one generation. High peaks of sciarid abundance were not followed by much lower emergence, and emergence across all weeks was far higher from warmed, moist turf. The advancement of later peaks relative to first peaks in the warmed turf, but not in control turf, suggests that sciarids develop faster and shorten inter-generation intervals in warmer weather.

Soil moisture was found to have an important effect on the phenology of upland arthropods. Immediately after the separation of water treatment groups by differential watering and drying regimes, soil with high (> 12%) soil water content produced more arthropods than mid-level (9-12%) or low (< 9%) soil water content. As there was only a minimal delay between watering and this difference in emergence, it is likely that water acted as an emergence cue, rather than a cue to end diapause.

Few studies have focused on the effects of soil moisture on invertebrate phenology; however our findings support the hypothesis of Tauber (1998) and results for tipulids (Carroll et al. 2011) that in some habitats, moisture is likely to play an important role in insect phenology. The changes investigated in our experiment are relatively short-term (intra-annual) effects, but it is clear that longer-term changes in temperature and moisture lead to changes in plant community structure and composition

(Yang et al. 2011), which will in turn affect the communities of insect herbivores feeding on them (Bale et al. 2002).

Arthropod abundance

When soil moisture levels fell to about 6% and below, subsequent arthropod emergence fell considerably. This indicates that prolonged periods of drought (leading to drying of soil), which are predicted to increase in frequency under future climate change (IPCC 2007), could significantly reduce the abundance of arthropods in upland grasslands. Drought in particular, might be of concern in the uplands where much agricultural grassland, used by foraging birds, has been artificially drained (Amar et al. 2011). Few turf samples in the present study reached these very low water content values, however, so statistical inference is difficult. Moisture has been shown previously to play a significant role in the abundance and vertical distribution within the soil of arthropods, especially Diptera, which experience high mortality in dry conditions (Coulson 1962, Briones et al. 1997). For example, warming during the late summer (August) in peatland ecosystems correlates negatively with abundance of the dipteran family Tipulidae (a keystone prey taxa of many upland birds) the following spring (Pearce-Higgins et al. 2010). In contrast to dry conditions, there was no evidence that the wettest conditions led to increased mortality of arthropods yet to emerge from the turf samples.

Aside from the driest levels of soil moisture, there was little difference between the soil moisture treatments in the overall abundance of emerging non-sciarid arthropods. This suggests that upland soil arthropods are resistant to quite broad fluctuations of soil moisture. These arthropods appear to be strongly negatively affected once the soil water content falls below a certain threshold (approximately 6% water content in our study). These thresholds of low soil water content appear to be reached in UK peatlands during hot summers (Pearce-Higgins et al. 2010). Carroll et al. (2011) found that reversing drainage procedures in upland bogs, to increase soil water content, increased Tipulidae abundance over a period of 2 years. Numbers of Sciaridae were greatly increased in the elevated soil moisture treatment group. This finding is consistent with previously published data on sciarids (Keates et al. 1989, Meers and Cloyd 2005).

Arthropod size

Arthropods were, on average, larger in warmed turf than ambient turf during the first 15 weeks of trapping, then larger in ambient turf in subsequent weeks. This indicates that in years with hotter summers, overall arthropod biomass is likely to be even higher than predicted by abundance alone early in the northern wheatear breeding season, but lower towards the end. Increased temperature was not likely to be causing increases in individual body size, since the effects of elevated temperature had only a phenological effect, rather than an effect on mean arthropod size over the whole study period. It is more likely that warming simply caused species of larger arthropods to emerge earlier.

Food availability to breeding northern wheatears

Northern wheatears arrive in the uplands of NW Europe from mid-March to early April (Cramp 1988). Based on our results, sciarids are expected to be the most abundant arthropods emerging from soil at this time. However, these insects are very small (< 3 mm) so other arthropod taxa may be more energetically worthwhile prey. Our results indicate that sciarids are unlikely to be affected by warming at the time of wheatear arrival, whilst total abundance of other arthropods is expected to be higher. During this pre-breeding period, the combination of rainfall and temperature is likely to be an important factor determining the availability of soil-emerging arthropods, with total abundance of arthropods being highest when soil is damp and warm. For birds which have arrived early enough, a warm but wet spring might therefore provide an opportunity to increase breeding productivity by breeding early, hence providing increased possibilities for multiple-breeding attempts (by initiating a second brood, or by simultaneous polygyny) (Chapter 3).

Egg-laying in northern wheatears breeding in northwest Europe takes place from mid April to early June, with chicks hatching 10 to 15 days later (Cramp 1988). Coinciding with wheatear egg-laying, the peak emergence of non-sciarid arthropods occurred in late April in the present study. In warmed and dry soil, this period of peak abundance ended abruptly in early May, whereas in ambient, wet soil, it continued until early June, suggesting that in warm dry years, food availability to insectivorous birds in the uplands will be lower during the critical period when nestlings are being provisioned by their parents. Peak emergence of Sciaridae in the present study coincided approximately with this provisioning period, but occurred two weeks earlier in warmed soil at the beginning rather than the middle of June. As sciarids are perhaps more likely to be fed to very young wheatear chicks because of their small size (Cramp 1988), and because Diptera in general are more important to the diet of chicks than adults (Pearce-Higgins 2010), an abundance of sciarids may be beneficial to breeding wheatears with newly-hatched chicks. As with the other arthropods, dry and warm conditions resulted in low abundance of sciarids. Warming temperatures and reduced summer rainfall is therefore predicted to negatively affect migratory upland birds via a reduction in food availability.

Methodological considerations

Members of all families of arthropods previously found to be included in northern wheatear diet (Cramp 1988, Pearce-Higgins 2010) were recorded as part of the present study, except Curculionidae (weevils). Tipulids, an important food resource for wheatears and other upland birds (Buchanan et al. 2006, Pearce-Higgins 2010), were however very rare in our turf samples. This was likely to be due to the patchy local distribution of tipulids, related to the distribution of food plants such as mosses and liverworts (Coulson 1962). Other taxa important in northern wheatear diet were absent from our analysis, due to their life cycle not including a soil-based stage. In particular, Lepidoptera are very important to the diet of young wheatears (Cramp 1988), yet only a few individual lepidopterans, belonging to one family (Tineidae), were included in our dataset.

The sticky traps in our experiment sampled almost all the same families as were captured by sticky traps at the field site from which we collected our turf samples. Pitfall trapping at the field location revealed that our sticky traps were inadequate for sampling of Coleoptera. The most frequent Coleoptera family captured at the field site was Carabidae, but these constitute only a small proportion of wheatear diet (Pearce-Higgins 2010). Overall, despite the fact that arthropods sampled as part of the present study make up only part of the arthropod community in upland grassland, their abundance is still important for foraging northern wheatears (Pearce-Higgins 2010). Major changes in the abundance and phenology of these arthropods, are therefore likely to have consequences for breeding productivity, migratory fuelling and annual survival of wheatears and other long-distance migratory songbirds.

Conclusion

As initially hypothesised, our experiment demonstrated important changes in arthropod abundance and phenology, associated with warming and changes in soil water content. Climate-driven changes in the timing of peaks in the availability of arthropod biomass, with which migratory birds normally synchronise their breeding, can lead to birds mistiming their reproductive efforts with regards to resource availability (Strode 2003, Both 2010). Mismatching between breeding events and peak food availability is now thought to be one of the major problems facing Afro-Palearctic migratory birds, as shown in detailed studies of the pied flycatcher (Both et al. 2006; Both and Visser 2001; Both 2010; Both and Visser 2005; Møller et al. 2008). Similarly, the northern wheatear, a well-studied model species of migratory bird (Schmaljohann and Dierschke 2005, Arlt and Pärt 2007, Delingat et al. 2008, Low et al. 2010), has been shown to be sensitive to changes in food availability across its annual cycle (Chapters 2–4). The phenology of the arthropods emerging from grassland turf samples in the present study suggests that the window of high food availability to upland grassland birds such as the northern wheatear will be shorter and earlier during warmer and drier summers, as are predicted to become more frequent in Wales over the next century. If this is the case, then the risk of mismatch of peak arthropod abundance with the breeding period of northern wheatears and other upland migrants will increase.

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REFERENCES

ADMB Project. 2009. AD Model Builder: automatic differentiation model builder. Developed by David Fournier and freely available from admb-project.org.

Amar, A., M. C. Grant, G. M. Buchanan, I. M. W. Sim, J. M. Wilson, J. W. Pearce-Higgins, and S. Redpath. 2011. Exploring the relationships between wader declines and current land-use in the British uplands. Bird Study 58:13-26.

Arlt, D., and T. Pärt. 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. Ecology 88:792-801.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8:1–16.

Bale, J. S., and S. A. L. Hayward. 2010. Insect overwintering in a changing climate. The Journal of Experimental Biology 213:980-94.

Both, C. 2010. Food availability, mistiming, and climatic change. Pages 129-147 *in* A. P. Møller, W. Fiedler, and P. Berthold, editors. Effects of Climate Change on Birds. Oxford University Press, Oxford.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81-83.

Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296-8.

Both, C., and M. E. Visser. 2005. The effect of climate change on the correlation between avian life-history traits. Global Change Biology 11:1606-1613.

Briones, M. J. I., P. Ineson, and T. G. Piearce. 1997. Effects of climate change on soil fauna; responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment. Applied Soil Ecology 6:117-134.

Buchanan, G. M., M. C. Grant, R. A. Sanderson, and J. W. Pearce-Higgins. 2006. The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. Ibis 148:615-628.

Buse, A., and J. Good. 1996. Synchronisation of larval emergence in winter moth (*Operophtera brumata* L.) and budburst in pedunculate oak (*Quercus robur* L.) under simulated climate change. Ecological Entomology 21:335-343.

Butterfield, J. 1976. Effect of photoperiod on a winter and on a summer diapause in two species of cranefly (Tipulidae). Journal of Insect Physiology 22:1443-1446.

Cannon, R. J. C. 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. Global Change Biology 4:785-796.

Carroll, M. J., P. Dennis, J. W. Pearce-Higgins, and C. D. Thomas. 2011. Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. Global Change Biology 17:2991-3001.

Conder, P. 1989. The Wheatear. Christopher Helm, London.

Cotton, P. A. 2003. Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences 100:12219-12222.

Coulson, J. C. 1962. The Biology of Tipula subnodicornis Zetterstedt, with Comparative Observations on *Tipula paludosa* Meigen. Journal of Animal Ecology 31:1-21.

Coulson, J. C., J. C. Horobin, J. E. C. Butterfield, and G. R. J. Smith. 1976. The maintenance of annual life-cycles in two species of Tipulidae (Diptera); a field study relating development, temperature and altitude. Journal of Animal Ecology 45:215-233.

Cramp, S. (Ed.). 1988. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Volume V: Tyrant flycatchers to thrushes. Oxford University Press, Oxford.

Crick, H. Q. P. 2004. The impact of climate change on birds. Ibis 146:48–56.

Delingat, J., F. Bairlein, and A. Hedenström. 2008. Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in northern wheatears (*Oenanthe oenanthe*). Behavioral Ecology and Sociobiology 62:1069-1078.

Dunn, P. O., and D. W. Winkler. 1999. Climate change has affected the breeding date of tree swallows throughout North America. Proceedings of the Royal Society B: Biological Sciences 266:2487-2490.

Gordo, O., and J. J. Sanz. 2006. Temporal trends in phenology of the honey bee *Apis mellifera* (L.) and the small white *Pieris rapae* (L.) in the Iberian Peninsula (1956-2004). Ecological Entomology 31:261-268.

Helmuth, B., J. G. Kingsolver, and E. Carrington. 2005. Biophysics, physiological ecology, and climate change: does mechanism matter? Physiology 67:177-201.

Holden, J., L. Shotbolt, A. Bonn, T. P. Burt, P. J. Chapman, A. J. Dougill, E. D. G. Fraser, K. Hubacek, B. Irvine, M. J. Kirkby, M. S. Reed, C. Prell, S. Stagl, L. C. Stringer, A. Turner, and F. Worrall. 2007. Environmental change in moorland landscapes. Earth-Science Reviews 82:75-100.

IPCC. 2007. Summary for policymakers. Page *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate Change 2007: The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge.

Jenni, L., and M. Kéry. 2003. Timing of autumn bird migration under climate change: advances in long–distance migrants, delays in short–distance migrants. Proceedings of the Royal Society B: Biological Sciences 270:1467-1471.

Keates, S. E., R. N. Sturrock, and J. R. Sutherland. 1989. Populations of adult fungus gnats and shore flies in British Columbia container nurseries as related to nursery environment, and incidence of fungi on the insects. New Forests 3:1-9.

Low, M., D. Arlt, S. Eggers, and T. Pärt. 2010. Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. Journal of Animal Ecology 79:214–224.

Marshall, M. R., R. J. Cooper, J. A. DeCecco, J. Strazanac, and L. Butler. 2002. Effects of experimentally reduced prey abundance on the breeding ecology of the red-eyed vireo. Ecological Applications 12:261–280.

Masters, G. J., V. K. Brown, I. P. Clarke, J. B. Whittaker, and J. A. Hollier. 1998. Direct and indirect effects of climate change on insect herbivores: Auchenorrhyncha (Homoptera). Ecological Entomology 23:45–52.

Mazerolle, D. F., K. W. Dufour, K. A. Hobson, and H. E. den Haan. 2005. Effects of large-scale climatic fluctuations on survival and production of young in a Neotropical migrant songbird, the yellow warbler *Dendroica petechia*. Journal of Avian Biology 36:155-163.

Meers, T. L., and R. A. Cloyd. 2005. Quantitative sampling method for fungus gnat (Diptera: Sciaridae) eggs in soilless growing media. Journal of Economic Entomology 98:1399-1403. Entomological Society of America.

Murphy, J. M., D. M. H. Sexton, G. J. Jenkins, B. B. B. Booth, C. C. Brown, R. T. Clark, M. Collins, G. R. Harris, E. J. Kendon, R. A. Betts, S. J. Brown, K. A. Humphrey, M. P. McCarthy, R. E. McDonald, A. Stephens, C. Wallace, R. Warren, R. Wilby, and R. Wood. 2009. UK Climate Projections Science Report: Climate change projections. Exeter, UK.

Musolin, D. L. 2007. Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. Global Change Biology 13:1565–1585.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences 105:16195-16200.

Nagy, L. R., and R. T. Holmes. 2005. Food limits annual fecundity of a migratory songbird: an experimental study. Ecology 86:675–681.

Van Noordwijk, A. J., R. H. McCleery, and C. M. Perrins. 1995. Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. Journal of Animal Ecology 64:451-458.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society B: Biological Sciences 271:59-64.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology and Systematics 37:637-669.

Pearce-Higgins, J. W. 2010. Using diet to assess the sensitivity of northern and upland birds to climate change. Climate Research 45:119-130.

Pearce-Higgins, J. W., P. Dennis, M. J. Whittingham, and D. W. Yalden. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. Global Change Biology 16:12-23.

Perrins, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242-255.

Peñuelas, J., I. Filella, and P. E. Comas. 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. Global Change Biology 8:531–544.

Pollard, E., D. Moss, and T. J. Yates. 1995. Population trends of common British butterflies at monitored sites. Journal of Applied Ecology 32:9-16.

R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rodenhouse, N. L., and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding black-throated blue warblers. Ecology 73:357-372.

Schmaljohann, H., and V. Dierschke. 2005. Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*. Journal of Animal Ecology 74:131-138.

Strode, P. K. 2003. Implications of climate change for North American wood warblers (Parulidae). Global Change Biology 9:1137–1144.

Tauber, M. J. 1998. Moisture, a vital but neglected factor in the seasonal ecology of insects: hypotheses and tests of mechanisms. Environmental Entomology 27:523-530.

Tryjanowski, P., S. Kuźniak, and T. H. Sparks. 2005. What affects the magnitude of change in first arrival dates of migrant birds? Journal of Ornithology 146:200-205.

Visser, M. E., L. J. M. Holleman, and P. Gienapp. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147:164-72.

Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B: Biological Sciences 272:2561-9.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Yang, H., M. Wu, W. Liu, Z. Zhang, N. Zhang, and S. Wan. 2011. Community structure and composition in response to climate change in a temperate steppe. Global Change Biology 17:452-465.

SUPPORTING INFORMATION

Table S5.1. Arthropod taxa captured by sticky-trap after emerging from experimental turf samples and at the field sampling site, and by pitfall traps (field site only). Numbers of individuals are recorded for experimental turfs. Presence of taxa within samples at the field site is indicated with an x. UNK = not identified to taxonomic level of that column.

			Experimental turfs	Field site	
Class	Order	Family	Sticky traps	Sticky traps	Pitfall traps
Arachnida	Araneae	Lycosidae	0		x
Arachnida	Araneae	Thomisidae	0	x	x
Arachnida	Opiliones	Phalangiidae	0		x
Arachnida	Trombidiformes	Trombidiidae	2		x
Collembola	UNK	UNK	8		
Insecta	Coleoptera	Cantharidae	1		x
Insecta	Coleoptera	Carabidae	0		x
Insecta	Coleoptera	Elateridae	0		x
Insecta	Coleoptera	Geotrupidae	0		x
Insecta	Coleoptera	Staphylinidae	3		x
Insecta	Coleoptera	UNK	1		
Insecta	Dermaptera	UNK	1		
Insecta	Diptera	Cecidomyiidae	13	x	
Insecta	Diptera	Chironomidae	5		
Insecta	Diptera	Dolichopodidae	89		
Insecta	Diptera	Fanniidae	28		
Insecta	Diptera	Psychodidae	5		
Insecta	Diptera	Sciaridae	1369	x	
Insecta	Diptera	Tabanidae	5	x	
Insecta	Diptera	Tipulidae	1		
Insecta	Diptera	UNK	149		
Insecta	Hemiptera	Aphrophoridae	56	x	
Insecta	Hemiptera	UNK	5		
Insecta	Hymenoptera	Braconidae	1	x	
Insecta	Hymenoptera	Cephoidea	1		
Insecta	Hymenoptera	Diapriidae	6		
Insecta	Hymenoptera	Formicidae	0		x
Insecta	Hymenoptera	Gasteruptiidae	0	x	
Insecta	Hymenoptera	Platygasteridae	2		
Insecta	Lepidoptera	Tineidae	10		
Insecta	Orthoptera	Acrididae	6		
Insecta	UNK	UNK	4		

CHAPTER 6. Discussion

Discussion

The impact of climate change on individual species and on biodiversity as a whole has become an increasingly dominant topic of ecological research over the last 20 years. There remains, however, much that we do not know. Current research tends to concentrate on observations of correlations between climate variables and various ecological factors, such as the timing of migration (Robson and Barriocanal 2011) and population distribution shifts (Sharma et al. 2009). Predictions are often based on extrapolations from the effects of climate within the current range of variation, or from bioclimatic envelope modelling (e.g. Huntley et al. 2007), which uses climate thresholds within the current distribution of a species to predict its future distribution based on projections of these climate variables within space and time. At large scales, the current distributions of a number of species have been successfully simulated with bioclimatic envelopes (Beerling et al. 1995, Pearson 2002, Huntley et al. 2007). Bioclimatic envelope modelling of future species distributions has, however, been criticised because they ignore much of the complexity of ecological communities, such as inter-specific interactions (Davis et al. 1998). For migratory species, a bioclimatic approach to modelling future distributions may be inadequate because they often utilise locations many kilometres apart that may differ in rates and / or direction of climate change. Furthermore, the different stages of the annual cycles of migratory species are inextricably inter-linked and changes in one stage (e.g. breeding) may reflect changing conditions during another stage (e.g. over-wintering). A major research priority is to move beyond simply describing associations and to establish a more mechanistic and experimental approach to understanding the biological impacts of climate change, by identifying the mechanisms by which climate change impacts biodiversity (Møller et al.

2010, Pearce-Higgins and Gill 2010, Wingfield et al. 2011). By understanding the mechanisms, it may be possible to appreciate the reasons why some species adapt to climate change while others do not (Wingfield et al. 2011) and to devise effective mitigation and conservation strategies. In this thesis, I have attempted to address this gap in our knowledge by studying the mechanisms by which climate change impacts on a long-distance migratory bird, the northern wheatear.

In Chapter 1, I outlined the ways in which climate change is thought to affect migratory taxa. Long-distance migrants are likely to be especially vulnerable to the effects of climate change, as their ability to complete their annual cycle depends on environmental conditions (including weather, habitat quality and food availability) at locations many kilometres apart. Climate change therefore has fitness implications for migrants at their breeding grounds (e.g. affecting fecundity), wintering grounds (affecting survival) or during migration (affecting both survival and subsequent fecundity). Furthermore, ecological conditions at one stage of the annual cycle can have impacts on subsequent stages via carry-over effects (Marra et al. 1998, Norris et al. 2004).

A common theme of recent scientific literature in this subject area is the suggestion that food availability is one of the primary mechanisms by which climate change impacts migratory taxa. For example, changes in temperature and moisture affect the development and survival of the invertebrate prey of migratory songbirds, both directly and via impacts on primary productivity (Dell et al. 2005, Smith et al. 2010, Carroll et al. 2011). As well as changes in overall abundance and distribution of their food supply, migratory songbirds also have to adjust their timing of migration to match the shifting phenology of their food during breeding periods in seasonal environments (Pearce-Higgins et al. 2005, Both et al. 2006). Declines in abundance of some long-distance migratory birds – and other migrant taxa – may have been caused by constraints preventing them advancing arrival on breeding grounds in synchrony with advancing phenology of their food supplies (Beaugrand et al. 2003, Both et al. 2006, Møller et al. 2008).

In Chapters 2, 3 and 4, I used food supplementation of wheatears to simulate climate-driven increases in food availability at breeding, wintering and stopover sites. The food supplementation was not intended to mimic directly the expected ecological response to climate change, which, in seasonal environments, is predicted to involve a shift in distribution of peaks in resource availability, as well changes in overall abundance (Chapter 5). Rather, by supplementing food across whole breeding seasons and migratory fuelling periods, I was able to highlight aspects of wheatear performance that are currently limited by food availability. The most important of these were migratory fuelling, number of breeding attempts and annual survival (due to changes in food availability at the breeding grounds). These are thus the factors most likely to be affected by climate-linked changes in food availability, whether that is an increase or a decrease.

In Chapter 5, I described manipulations of temperature and soil moisture levels of turf samples from wheatear habitat to measure the effects of these climate-linked environmental variables on the abundance and phenology of the wheatear's arthropod prey. Warming by 2 ºC caused a higher peak of arthropod emergence, especially in combination with elevated moisture. This lead to a reduction in arthropods emerging after the peak of emergence, relative to turf kept at ambient temperature. Abundance of emerging arthropods was dramatically reduced when turfs dried to lower than approximately 6% soil water content. Summer droughts are predicted to occur with increasing frequency in the UK and other northern temperate regions during the next 100 years (IPCC 2007). The present study provides experimental evidence that climate change is likely to cause declines in emergence of upland grassland arthropods, via reductions in soil moisture. This builds on field observations and experiments in upland peatlands, which indicated that climate change and artificial drainage cause declines in tipulid emergence (Pearce-Higgins et al. 2010, Carroll et al. 2011).

In Chapter 2, I tested the hypothesis that changing food availability would affect the body mass regulation of two subspecies of northern wheatear (*O. o. oenanthe* and *O. o. leucorhoa*) with contrasting migration strategies. I examined the effects of an increase in food availability during migratory fuelling periods of both subspecies at shared wintering and stopover locations, as well as at the onset of autumn migration. The trans-Atlantic sea-crossings of *O. o. leucorhoa* are one of the most extreme examples of long-distance songbird migration, requiring them to double their lean body mass in fuel in the form of fat and muscle. *O. o. oenanthe* are ecologically very similar, but migrate in shorter flight stages. Both subspecies, however, must fly across the Sahara desert twice annually, where there are few foraging opportunities. By studying two closely-related and ecologically similar subspecies, the importance of migration strategy in determining the impact of changing food supply on body mass regulation could be tested. For *O. o. oenanthe*, I also tested the hypothesis that body mass regulation during the breeding season would be affected by an increase in food availability.

Both subspecies increased their body mass in response to food supplementation during migratory fuelling periods, but the magnitude of this increase varied by subspecies and location. Food supplementation had a large positive impact on body mass of both subspecies in the autumn on Fair Isle, indicating quite strong food limitation (under current climatic and foraging conditions) on their ideal fuelling strategy. I did not expect a difference between the subspecies at this location in the autumn, as they both face an identical onward journey to reach their wintering grounds. Summers in the UK are predicted to become warmer and drier, conditions which, when these conditions were experimentally simulated, led to lower arthropod emergence during the post-fledging period (Chapter 5), in accordance with field observations of lower tipulid abundance after drought (Pearce-Higgins et al. 2010). Since the addition of food demonstrated food limitation on autumn migratory fuelling on Fair Isle, reduction of food abundance is likely to limit fuelling rates further, as well as possibly affecting post-breeding moult. As migration is likely to be the period when most mortality of migratory birds occurs (Sillett and Holmes 2002), limitation on fuelling due to falling arthropod prey abundance is likely to reduce survival rates of long-distance migrant birds, such as northern wheatears.

Northern wheatears breeding at high latitudes such as Fair Isle and Sweden rarely have multiple breeding attempts (except for replacement clutches after nesting failure), but this aspect of breeding productivity was increased by food supplementation (Chapter 3). First broods were little affected by the feeding experiment, except for some evidence that chicks grew larger when food availability was increased. These results suggest that climate change may affect breeding productivity of northern wheatears primarily by affecting behavioural decisions over multiple breeding attempts. It was not possible to test whether second broods were more successful amongst fed birds than control birds, as control birds never produced a second brood. Further south, second brooding is more common; for example, approximately 50% of wheatear pairs on Skokholm have second broods (Conder 1989). If arthropod emergence peaks become higher but narrower, as my results in Chapter 5 suggest, first broods are unlikely to be significantly affected, but rates of second brooding may decline. Rates of polygyny during the first brood period may increase, however, due to a higher peak of arthropod abundance (Chapter 3). Simultaneous polygyny is therefore a means by which individual male wheatears can increase their annual reproductive output (at the expense of rival males) if foraging conditions permit. However, an increase in polygyny need not result in higher productivity at the population level, if the number of females is the limiting factor to the total number of reproductive attempts among the whole population.

Timing of clutch initiation was an important factor determining breeding productivity of northern wheatears (Chapter 3). Timing of breeding is constrained by arrival date in migratory songbirds, which is affected by departure date from wintering grounds and the fuelling conditions experienced at wintering grounds and *en route*. Supplementation of food supply of wintering northern wheatears showed that migratory fuel accumulation is currently limited by food availability (Chapter 2). Rainfall variation in the Sahel correlates with over-winter survival and spring migration timing, possibly because of its effect on arthropod abundance (Baillie and Peach 1992, Boano et al. 2004, Saino et al. 2007), where wheatears and many other Afro-Palaearctic migratory songbirds over-winter. Models of climate change are inconclusive regarding the direction of changes in future Sahel rainfall (Hulme et al. 2001). If food supply increases in the Sahelian wintering grounds due to higher rainfall, this may facilitate earlier departures of migratory birds, allowing them to track advancing phenology of arthropod emergence in their breeding grounds. Conversely, decreasing rainfall in the region is likely to lower arthropod abundance, reducing the potential of migrants to respond to advancing phenology of food supplies in their breeding grounds by increasing fuelling rates.

Environmental conditions in the non-breeding season of migratory birds are undoubtedly important determinants of population sizes (Marra et al. 1998, Sillett and Holmes 2002, Norris et al. 2004a). The results of this study suggest that climate-linked changes in breeding season food availability can affect survival of adults and juveniles. Predictions of drier summers in the UK (Murphy et al. 2009), combined with the results of Chapter 5 and other studies (Coulson et al. 1976, Pearce-Higgins et al. 2010), suggest that food availability during the post-fledging period is likely to decline in future, which will be likely to reduce fledgling survival. The direction of change in food availability in the Sahel, which is currently difficult to predict because of uncertainties over future rainfall (Hulme et al. 2001), will determine whether this will be exacerbated or buffered by changes in over-winter survival.

This study has identified some of the key mechanisms by which climate change is likely to affect northern wheatears, but it also suggests a number of important questions. While this study has examined short-term impacts of simulated climate changes on northern wheatears and their arthropod prey, what will be the longer-term effects of warming and moisture level changes? For example, what will be the relative importance of increases in climate fluctuations and changes in mean temperature and rainfall on arthropod abundance and phenology? How will competition between resident and migratory birds be affected by climate change? Will changes in survival rates in one stage of the annual cycle be buffered by density-dependent effects at other stages of the annual cycle? What is the extent of phenotypic and genetic flexibility in the migration strategies of long-distance migrants, which although reasonably flexible in timing in relation to current environmental conditions, are under genetic controls over general timing, destination and route? How much genetic variation in migration strategy exists to allow a rapid evolutionary response to climate change? As ecological conditions in the African wintering grounds are implicated in population limitation of many Afro-Palaearctic migratory birds (Baillie and Peach 1992, Sanderson et al. 2006, Wilson and Cresswell 2006), future research effort should focus on the effects of changing climate in this region on wintering birds.

In addition to climate change, food availability to wheatears and other migrant birds is affected by land-use changes. Changes in land use and management, particularly agricultural intensification, have been implicated in the declines of wheatears observed in Europe. Wheatears are associated with unimproved, often sheep grazed, grassland (Woodhouse et al. 2005) and breeding success and survival is highest in areas with short grass swards, where prey density and foraging success are highest (Tye 1992, Pärt 2001a, 2001b, Low et al. 2010). High-density stocking of sheep reduces arthropod abundance, however (Dennis et al. 2008). Soil moisture is an important determinant of soil invertebrate abundance. Extensive drainage of peatlands has occurred in the UK and elsewhere in northern Europe, causing reductions in the abundance of invertebrates such as tipulids. Climate warming is likely to cause further reductions of moisture-sensitive invertebrate species by increasing evaporation from the soil (Coulson et al. 1990). Management interventions, such as drain blocking, that increase the moisture levels of peatlands are likely to increase the populations of tipulids and other invertebrates (Carroll et al. 2011). This, in turn, should lead to increases in the populations of predators that feed on them, such as wheatears. Land-use change is likely to differ from climate change in that overall food availability is affected rather than primarily the phenology of food availability. In that respect, the experiments in Chapters 2- 4 are arguably better representations of the effects of land-use change than of climate change. Changing food availability is the most important mechanism underlying both of these environmental changes, and so this thesis addresses the consequences of both issues.

In this study, I compared the impact on body mass regulation of increased food availability on *O. o. oenanthe* and *O. o. leucorhoa* during migratory fuelling periods. This highlighted how migration distance may be a factor explaining the response of migratory birds to climate-driven changes in food availability. It would have been desirable to extend the food manipulation experiments on breeding *O. o. oenanthe* to *O. o. leucorhoa*. The long migrations across the North Atlantic of *O. o. leucorhoa* may have consequences on other life history stages. For example, the costs to survival of late reproduction may be amplified because reduced fuelling efficiency of late migrating birds, due to dwindling food resources late in the Arctic and sub-Arctic summer/autumn, are likely to have more severe impacts when thousands of open ocean must be crossed without stopping. Because of the differences in migration journey between the two subspecies, the condition of breeding adults on arrival may differ. This possibility, combined with possible differences in the duration of peaks of arthropod abundance on the breeding grounds, may mean that *O. o. leucorhoa* are less flexible in their reproductive decisions than *O. o. oenanthe*. Such extreme contrasts of migration strategy between ecologically and phylogenetically similar species can help to highlight how migration strategies have co-evolved with other aspects of life history.

Climate changes expose migrants to new environmental conditions, to which they must adapt (Stenseth et al. 2002). Selective pressure for evolutionary change will occur if the range of climate (and thus food) variability exceeds the birds’ current phenotypic plasticity. Indeed phenotypic plasticity, combined with genetic variance, contributes to the phenotypic variation on which selection can act, facilitating evolutionary change. Some migratory birds are showing a decreased tendency to migrate or even radical changes in migration direction, which has been attributed to recent climate change. A small but growing number of blackcaps (*Sylvia atricapilla*) breeding in south central Europe for example, have stopped migrating to the Mediterranean, wintering instead in southern Britain (Berthold 1995, Fiedler 2003). These birds arrive earlier on the breeding grounds in spring than the birds continuing to winter in the Mediterranean, which has lead to assortative mating, and hence could lead to sympatric speciation (Bearhop et al. 2005). Such changes in migratory behaviour may be less likely to occur in species that migrate across large ecological barriers, such as wheatears and other Afro-Palaearctic migrants crossing the Sahara desert, because the opportunities for gradual shifts in wintering distributions are physically limited by the desert margin. The evolutionary history of migratory taxa clearly has a strong influence on current strategies. For example, northern wheatears breeding in Alaska or Greenland and eastern Canada still migrate to sub-Saharan Africa; some of the most extreme migrations of any songbird, in terms of total distance and distance across inhospitable barriers, respectively. Other species breeding sympatrically with these populations migrate shorter distances, probably reflecting the evolution of their migration strategies.

For example, other migratory songbirds breeding alongside northern wheatear in Canada winter in the Neotropics or southern USA, rather than crossing the Atlantic to reach Europe / Africa. Climate change may impact on the migration of birds with different evolutionary histories in unpredictable ways. By increasing or decreasing food availability, climate change can lead either to new locations being utilised by migrants (for breeding, wintering or stopping over), or to locations becoming unsuitable. Either scenario would be likely to influence selection pressures on stopover, fuelling and departure decisions, leading to adaptation of migratory strategies. The extent to which this can be achieved may depend on the level of existing genetic variability in the populations, as well as current levels of phenotypic flexibility.

This study has used an experimental approach to address an important gap in our knowledge of biotic impacts of climate change; the mechanisms underlying these impacts. Climate change is a global problem, and by focusing on a long-distance migratory bird, I have been able to assess how climate may affect species populations in geographically and climatically contrasting locations. This project emphasises that although climate change may act globally, it can be investigated locally by manipulating key climate-linked variables, to understand the causal mechanisms by which individual organisms, populations and ecological communities may be affected.

REFERENCES

Baillie, S. R., and W. J. Peach. 1992. Population limitation in Palearctic-African passerine migrants. Ibis 134:120-132.

Bearhop, S., W. Fiedler, R. W. Furness, S. C. Votier, S. Waldron, J. Newton, G. J. Bowen, P. Berthold, and K. Farnsworth. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. Science 310:502-4.

Beaugrand, G., K. M. Brander, J. A. Lindley, S. Souissi, and P. C. Reid. 2003. Plankton effect on cod recruitment in the North Sea. Nature 426:661-664.

Beerling, D. J., B. Huntley, and J. P. Bailey. 1995. Climate and the distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surfaces. Journal of Vegetation Science 6:269-282.

Berthold, P. 1995. Microevolution of migratory behaviour illustrated by the Blackcap *Sylvia atricapilla*: 1993 Witherby Lecture. Bird Study 42:89-100.

Boano, G., A. Bonardi, and F. Silvano. 2004. Nightingale *Luscinia megarhynchos* survival rates in relation to Sahel rainfall. Avocetta 28:77-85.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81-83.

Carroll, M. J., P. Dennis, J. W. Pearce-Higgins, and C. D. Thomas. 2011. Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. Global Change Biology 17:2991-3001.

Conder, P. 1989. The Wheatear. Christopher Helm, London.

Coulson, J. C., J. C. Horobin, J. E. C. Butterfield, and G. R. J. Smith. 1976. The maintenance of annual life-cycles in two species of Tipulidae (Diptera); a field study relating development, temperature and altitude. Journal of Animal Ecology 45:215-233.

Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. N. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391:783–785.

Dell, D., T. H. Sparks, and R. L. H. Dennis. 2005. Climate change and the effect of increasing spring temperatures on emergence dates of the butterfly *Apatura iris* (Lepidoptera: Nymphalidae). European Journal of Entomology 102:161–167.

Dennis, P., J. Skartveit, D. I. McCracken, R. J. Pakeman, K. Beaton, A. Kunaver, D. M. Evans, 2008. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. Journal of Applied Ecology 45:279-287.

Fiedler, W. 2003. Recent changes in migratory behaviour of birds: a compilation of field observations and ringing data. Pages 21-37 *in* P. Berthold, E. Gwinner, and E. Sonnenschein, editors. Avian migration. Springer, Berlin Heidelberg New York.

Hulme, M., R. Doherty, T. Ngara, M. New, and D. Lister. 2001. African climate change: 1900-2100. Climate Research 17:145–168.

Huntley, B., P. M. Berry, W. Cramer, and A. P. McDonald. 2007. Modelling present and potential future ranges of some European higher plants using climate response surfaces. Journal of Biogeography 22:967-1001.

IPCC. 2007. Summary for policymakers. Page *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate Change 2007: The Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge.

Low, M., D. Arlt, S. Eggers, and T. Pärt. 2010. Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. Journal of Animal Ecology 79:214–224.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884-1886.

Murphy, J. M., D. M. H. Sexton, G. J. Jenkins, B. B. B. Booth, C. C. Brown, R. T. Clark, M. Collins, G. R. Harris, E. J. Kendon, R. A. Betts, S. J. Brown, K. A. Humphrey, M. P. McCarthy, R. E. McDonald, A. Stephens, C. Wallace, R. Warren, R. Wilby, and R. Wood. 2009. UK Climate Projections Science Report: Climate change projections. Exeter, UK.

Møller, A. P., W. Fiedler, and P. Berthold (Eds.). 2010. Effects of Climate Change on Birds. Oxford University Press, New York.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences 105:16195-16200.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society B: Biological Sciences 271:59-64.

Pärt, T. 2001a. The effects of territory quality on age-dependent reproductive performance in the northern wheatear (*Oenanthe oenanthe*). Animal Behaviour 62:379-388.

Pärt, T. 2001b. Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. Proceedings of the Royal Society B: Biological Sciences 268:2267-2271.

Pearce-Higgins, J. W., P. Dennis, M. J. Whittingham, and D. W. Yalden. 2010. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. Global Change Biology 16:12-23.

Pearce-Higgins, J. W., D. W. Yalden, and M. J. Whittingham. 2005. Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). Oecologia 143:470–476.

Pearce-Higgins, J. W., and J. A. Gill. 2010. Commentary: Unravelling the mechanisms linking climate change, agriculture and avian population declines. Ibis 152:439-442.

Pearson, R. 2002. SPECIES: A Spatial Evaluation of Climate Impact on the Envelope of Species. Ecological Modelling 154:289-300.

Robson, D., and C. Barriocanal. 2011. Ecological conditions in wintering and passage areas as determinants of timing of spring migration in trans-Saharan migratory birds. Journal of Animal Ecology 80:320-31.

Saino, N., D. Rubolini, N. Jonzén, T. Ergon, A. Montemaggiori, N. C. Stenseth, and F. Spina. 2007. Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. Climate Research 35:123-134.

Sanderson, F. J., P. F. Donald, D. J. Pain, I. J. Burfield, and F. P. J. Van Bommel. 2006. Long-term population declines in Afro-Palearctic migrant birds. Biological Conservation 131:93–105.

Sharma, S., S. Couturier, and S. D. Côté. 2009. Impacts of climate change on the seasonal distribution of migratory caribou. Global Change Biology 15:2549-2562.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296-308.

Smith, J. A. M., L. R. Reitsma, and P. P. Marra. 2010. Moisture as a determinant of habitat quality for a nonbreeding Neotropical migratory songbird. Ecology 91:2874-2882.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292-1296.

Tye, A. 1992. Assessment of territory quality and its effects on breeding success in a migrant passerine, the wheatear *Oenanthe oenanthe*. Ibis 134:273-285.

Wilson, J. M., and W. Cresswell. 2006. How robust are Palearctic migrants to habitat loss and degradation in the Sahel? Ibis 148:789-800.

Wingfield, J. C., J. Patrick Kelley, F. Angelier, O. Chastel, F. Lei, S. E. Lynn, B. Miner, J. E. Davis, D. Li, and G. Wang. 2011. Organism–environment interactions in a changing world: a mechanistic approach. Journal of Ornithology:1-10.