When Climate is Changing: Effects of Phenology and Local Climate on Individual Fitness

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Abstract

The fitness impacts of climate change on seasonal breeding organisms is, in part, linked to local climatic effects on phenology (i.e. the timing of major life events, such as breeding and migration) and how these relate to temporal changes in resource distribution. Thus, in this thesis we examine relationships between phenology, measures of fitness (reproduction and survival) and local climate for a long-distance migratory bird species, the northern wheatear (*Oenanthe oenanthe*).

There was a seasonal fitness decline in this population, but the relative contribution of different reproductive components to this decline varied. Because declines in these fitness components were driven by different factors this suggests climate change is unlikely to affect fitness components equally. This unequal susceptibility of different fitness components to climate change was further demonstrated by different responses in reproduction and survival to rainfall, and that these effects were age-, sex- and time-dependent. During the past 20 years, wheatears have advanced their migration to arrive and begin breeding ~8 days earlier than in the early 1990s. Regardless, this change in migration and breeding phenology may be lagging behind current climate change because birds are breeding increasingly later relative to the progression of spring. One factor potentially contributing to this phenological mismatch is limited plasticity in the arrival-breeding interval, arising from constraints on how much the interval can be reduced after migration. Another constraint on the ability for birds to advance their breeding time is the cost of reproduction carried over from one breeding season to the next. This impacts on individual fitness through delays in breeding phenology and the fitness loss associated with seasonal fitness declines.

Overall, this thesis shows that to avoid underestimation of potential effects of climate change on population demography, all fitness components and their drivers need to be considered. In addition, it highlights potential constraints preventing individuals from optimally adjusting their breeding time in order to track environmental change. Such knowledge is crucial if we are to make informed decisions regarding the management of populations in the future.

Keywords: Weather, habitat quality, individual quality, nest predation, carry-over effects, pre-breeding period, precipitation, survival, reproductive performance, nestling

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The question is, are we happy to suppose
that our grandchildren may never be able
to see an elephant except in a picture book?

Sir David Attenborough

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Öberg, M., Pärt, T., Arlt, D., Laugen, A. T. and Low, M. (2014). Decomposing the seasonal fitness decline. *Oecologia* 174(1), 139-150.

II Öberg, M., Arlt, D., Pärt, T. and Low, M. Delayed timing of breeding as a cost of reproduction (manuscript).

III Öberg, M., Low, M., Pärt, T., Arlt, D. and Knape, J. Phenological adjustments to spring temperature: effects on the arrival-breeding interval (manuscript).

IV Öberg, M., Pärt, T., Arlt, D., Laugen, A. T., Eggers, S. and Low, M. Rainfall during parental care affects multiple fitness components (manuscript).

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The contribution of Meit Öberg to the papers included in this thesis was as follows:

I Developed research questions and design together with ML, TP, DA and ATL. Contributed to collection of long-term data. Performed statistical analysis together with ML. Main author with guidance from co-authors.

II Developed research questions and design together with ML, TP and DA. Contributed to collection of long-term data. Performed statistical analysis together with ML. Author together with ML, with guidance from TP and DA.

III Developed research questions and design together with JK, ML, TP, and DA. Contributed to collection of long-term data. Performed statistical analysis. Main author with guidance from co-authors.

IV Developed research questions and design together with ML, TP, DA, SE and ATL. Contributed to collection of long-term data. Performed statistical analysis. Main author with guidance from co-authors.

1 Introduction

1.1 Climate change

Climate change has resulted in an increase in the global average temperature by 0.85°C over the last century (Figure 1) and there is now strong support for an anthropogenic influence on this change (IPCC 2013). Climate change is predicted to further increase temperatures, alter precipitation patterns and increase the frequency and intensity of extreme weather events (IPCC 2013).

Past and future patterns of climatic change are of a complex nature due to the high degree of spatial and temporal heterogeneity (Figure 2); temperature change has been and will be greater in some areas than in others and precipitation is expected to increase in already wet areas and decrease in arid regions (IPCC 2013). The rate of change also differs between, winter, spring summer and autumn seasons (IPCC 2013).

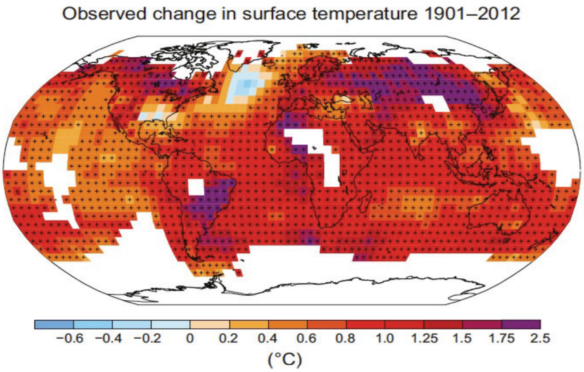

Figure 1. Map of the observed surface temperature change from 1901 to 2012 derived from temperature trends determined by linear regression from one data set. Trends have been calculated where data availability permits a robust estimate. Other areas are white. Grid boxes where the trend is significant at the 10% level are indicated by a + sign. The figure is taken from the Fifth Assessment Report of the Intergovernmental Panel on Climate Change Working Group 1 Summary for Policymakers (IPCC 2013).

Climate change has been shown to influence a broad range of ecological systems in terms of spatial and temporal patterns of population, community and ecosystem dynamics (Walther et al. 2002; Parmesan & Yohe 2003; Root 2003) and may lead to extinction of species (Parmesan 2006). Thus, climate change poses an enormous challenge for nature conservation, especially as climate change effects are likely to interact with other human-caused stressors such as habitat loss and land-use changes.

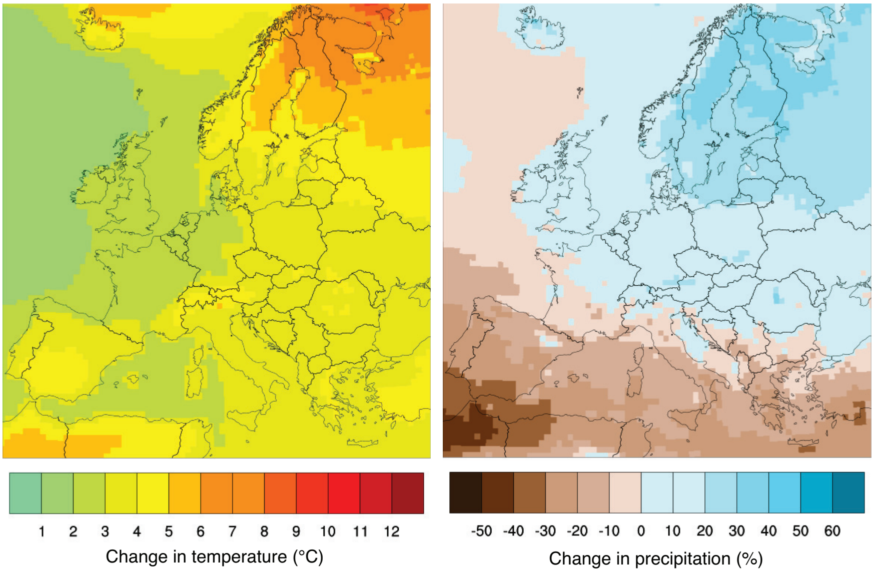

Figure 2. Illustration of the high degree of spatial variation in expected changes, using Europe as an example. Maps show the expected changes according to climate scenario RCP 8.5 in, a) temperature and b) precipitation for years 2071-2100 compared to 1971-2000 (SMHI 2014).

1.2 Phenology

The most commonly observed response attributed to climate change are shifts in phenology – the timing of periodic life-cycle events – such as earlier leaf unfolding in trees, flowering in plants, appearance of insects and reproduction in birds (Walther et al. 2002; Parmesan & Yohe 2003; Root et al. 2003). But why is timing so important? Species breeding in seasonal environments commonly show a strong relationship between breeding time and fitness, with individual fitness often declining as the season progress (e.g. Perrins 1965, 1970; Hochacka 1990; Cushman et al. 1994; Öberg et al. 2014). The seasonal fitness decline has been under the scrutiny of research for several decades, with studies focusing on both adaptive and proximate mechanisms. Deteriorating environmental conditions is one such proximate mechanism, with changes in food availability as the main driver (Perrins 1970; Hedgren & Linnman 1979), although other environmental conditions also may play a role (e.g. increasing nest predation risk or prevalence of parasites; Smith 1993; Naef-Daenzer et al. 2001; Götmark 2002). The importance of these drivers may, however, differ depending on which measure of fitness is analysed (e.g. organisms may trade-off one fitness component against another) and the contribution of that fitness component to lifetime reproductive success. Therefore, to fully understand how climate change may impact breeding-time-fitness relationships, we need more knowledge on how different drivers of seasonal reproductive declines interact with different fitness components, and how these fitness components contribute to the overall seasonal fitness decline (Paper I).

Furthermore, in seasonal environments food abundance is often expected to display a seasonal peak, which is why fitness may strongly depend on matching the timing of reproduction to the food peak (Perrins 1965, 1970; Both et al. 2006). Earlier progression of spring as predicted with climate change (Figure 3) may cause asynchrony between trophic levels if these differ in their rate of phenological response to warmer springs. The response of higher trophic level species such as birds and mammals tend to lag behind the response at lower trophic levels such as plants and insects (Both et al. 2009; Thackeray et al. 2010), thus leading to an ecological 'mismatch' between the timing of reproduction and the peak of food availability (Both et al. 2006; Both et al. 2010). One outcome being reduced reproductive output and population growth rate (Both et al. 2006; Møller et al. 2008; but see Reed et al. 2013).

1.2.1 Why study migratory species?

Migratory species are of particular interest because their yearly cycle consists of several energetically demanding stages (e.g. migration, breeding, moult) in geographically separate areas (Robinson et al. 2009). They may therefore not only be susceptible to detrimental effects of climate change at several locations, but the asymmetry in change between areas (Figure 2) may also cause asynchrony in the timing of the yearly cycle. Because of the sequential nature of the life-cycle stages, migratory species may be less

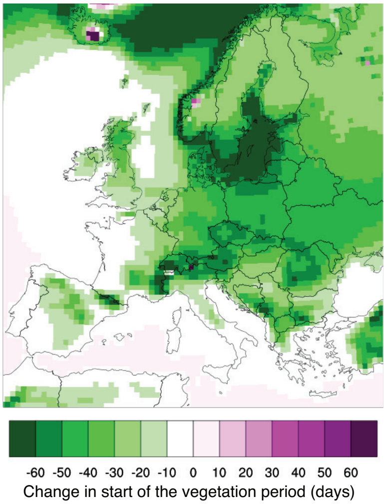

Figure 3. Expected changes in start of the vegetation period according to climate scenario RCP 8.5 for years 2071-2100 compared to 1971-2000 (SMHI 2014).

flexible in the timing of some stages because of constraints imposed by previous or future stages (Wingfield 2008). Long-distance migratory species rely on both endogenous (Gwinner 2003) and environmental cues (Gordo et al. 2005; Gordo & Sanz 2007) for departure from their wintering area, but these cues are not directly linked to climate in the breeding area. As they approach the breeding area during migration organisms may increasingly rely on local environmental cues to fine tune their arrival (Ahola et al. 2004; Hüppop & Winkel 2006), but spatial and temporal variation in climate change is likely to result in large variations in this arrival adjustment (Both et al. 2004; Hüppop & Winkel 2006; Both & te Marvelde 2007). Because departure from the wintering area and migration speed may be influenced by factors independent of the breeding area, it has been suggested that arrival to the breeding ground may be the greatest constraint on plasticity in breeding time for migratory species ('arrival constraint hypothesis'; Both & Visser 2001; Sanz et al. 2003). However, breeding time is not simply a function of arrival, but also the interval between arrival and beginning of breeding. Thus, to understand how well populations track environmental change by adjusting their breeding time requires an understanding of factors influencing both arrival and the arrival-breeding interval. If there is little flexibility in arrival times or if the advancement in arrival time is insufficient, individuals can potentially reduce the length of the arrival-breeding interval (a.k.a. pre-laying period) to achieve earlier breeding. This, however, depends on if the arrival-breeding interval is influenced by environmental variables related to climatic conditions (e.g. weather and food availability), as it may act as a constraint if largely determined by variables that are non-climatic in their origin (e.g. age, photoperiod). Although many studies have shown advancements in breeding time with increasing temperatures (Visser et al. 2009; Schaper et al. 2012; Caro et al. 2013; but see Nager & Noordwijk 1992) or food availability (Nilsson & Svensson 1993; Nager et al. 1997), these studies are generally limited to resident species (e.g. great tits *Parus major* or blue tits *Parus caeruleus*). There is, however, no *a priori* reason to expect that such effects can be translated to the arrival-breeding interval in migratory species due to their largely different life histories. Despite the potential influence the arrival-breeding may have on the ability of populations' to adjust their breeding time under climate change, the influence of climatic variables on the arrival-breeding interval has received little attention. (Paper III).

1.2.2 The cost of reproduction

The yearly cycle of migratory species is not a simple 'linear' process with separately defined and independent life stages: there are interactions, overlaps and trade-offs (Wingfield 2008; Williams 2012). A core assumption in life-history theory is the trade-off between current and future reproduction (the cost of reproduction; Williams 1966). Although reproductive costs are initiated during breeding, they may influence subsequent reproductive decisions because previous reproductive effort can affect individual condition (so called 'carry over effects', Norris 2005, Harrison et al. 2010), or through the organism modifying its current reproduction in light of future reproductive output (Williams 1966; Stearns 1992). In seasonal breeders these reproductive carry-over effects may be partly driven by constraints operating on the timing of breeding: i.e. organisms breeding later in one season may not have enough time to recover their condition before the beginning of the next breeding period. This should be particularly evident in migratory species that face large seasonally linked energetic costs outside of breeding. In birds, for example, individuals face a series of energetically demanding stages in their yearly life cycle in addition to breeding (e.g. moulting new plumage, migration) that may limit an individual's ability to compensate for additional or late breeding energy expenditure (Wingfield 2008). Several studies have experimentally shown that reproductive costs may lead to reduced survival and reproductive success the following season (e.g. Lindén & Møller 1989; Nilsson & Svensson 1996; Brinkhof et al. 2002), but despite the potential impact costs of reproduction may have on subsequent stages combined with the importance of timing in migratory species, few have investigated the influence of reproductive costs on timing in the following breeding season (Paper II).

1.3 Direct effects of local climate

The response of organism’ phenologies to increasing spring temperatures has gained much focus, but predicted changes in rainfall patterns may also have potential consequences for phenology through delays in breeding in wet springs (Senapathi et al. 2011), or more directly for reproductive output as persistent or heavy rainfall may influence juvenile growth rates (Siikamäki 1996; Veistola et al. 1997; Dawson & Bortolotti 2000) and increase offspring mortality (e.g. Siikamäki 1996; Dawson & Bortolotti 2000; Franklin et al. 2000; Rodríguez & Bustamante 2003; Arlettaz et al. 2010). This is because rainfall may cause changes in prey activity / food availability (Avery & Krebs 1984), altered foraging patterns (Veistola et al. 1997; Dawson & Bortolotti 2000; Radford et al. 2001) and/or increased energy demands (Keller & van Noordwijk 1994; Siikamäki 1996; Veistola et al. 1997). However, negative effects of rainfall on reproduction may not only be expressed as nestling mortality, as reduced foraging opportunities during rainfall (especially for insectivorous species) is likely to influence the condition of both young and their parents. Thus, examinations of population impacts of rainfall patterns need to consider long-term effects on individuals, such as reduced juvenile survival to the next year (Lindén et al. 1992; Naef-Daenzer et al. 2001; Low & Pärt 2009) and increased costs of reproduction in adults (Linden & Møller 1989; Stearns 1992). Despite this, studies investigating longer-term effects of rainfall during nestling feeding on juvenile and adult survival are largely lacking (Paper IV). Furthermore, if the goal is to make predictions of how populations respond to on-going climate change it will require information on relationships between rainfall and vital rates; especially for insectivorous birds breeding in northern temperate regions where mean precipitation and extreme precipitation events are likely to increase in this region (IPCC 2013).

2 Thesis aims

The impact of climate change on population demography is clearly of a complex nature and before we can fully understand how populations may respond to such large-scale environmental change we need more basic knowledge of the influence of phenology and local climate on individual fitness. The primary aim of this thesis was therefore to gain a deeper understanding of the relationships between phenology (i.e. the timing of arrival and breeding), multiple fitness components (i.e. nest success, clutch size, fledging success, recruitment success and adult survival) and local weather variables (i.e. rainfall, temperature and thermal sums), and how these relationships interact with habitat quality, individual quality and nest predation risk in a migratory bird species. Figure 4 illustrates these inter-relationships and their direct and indirect links to the potential influence of climate change.

The specific aims for each paper were to:

I Analyse breeding time effects on different reproductive components and adult survival and their relative contribution to the overall seasonal decline in reproduction. This will provide crucial knowledge on the relative and absolute importance of different fitness components in terms of the timing of breeding (i.e. phenology) and thus also the relative importance of the potentially different drivers behind seasonal fitness declines.

II Investigate if effects of breeding time and effort in one year carry-over to affect the bird's breeding time and fitness in the subsequent breeding season. If costs carry-over from one year to the next and influence timing of breeding, this may partly determine how much individuals can advance their breeding in response to warmer springs.

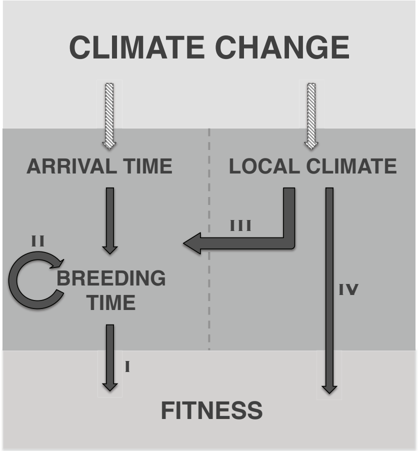

Figure 4. Schematic representation of the relationship between phenology, local climate in the breeding area and fitness. Roman figures represent the chapters in this thesis where these relationships are addressed.

III Describe temporal changes in arrival and breeding time relative to long-term climatic changes at the breeding ground, and analyse the effects of local climate on the arrival-breeding interval – with an aim to identify constraints on these phenologies. With climate change, migratory populations are at the risk of becoming mismatched in their timing of breeding to the seasonal peak of food availability. Plasticity in arrival and the arrival-breeding interval is important in determining the ability of populations to track environmental change and adjust their breeding time accordingly.

IV Investigate the effects of rainfall during the nestling period on reproductive output, recruitment and adult survival probability. In northern temperate regions, mean precipitation and extreme precipitation events are likely to increase with future climate change (IPCC 2013). Thus, knowledge on the impact of rainfall on multiple fitness components is potentially as important as temperature on understanding the fitness consequences for populations resulting from climate change.

3 Methods

3.1 Study Species

The northern wheatear (*Oenanthe oenanthe*; hereafter 'wheatear') is an insectivorous, long-distance migratory passerine that breeds in cavities in open farmland habitats. It is a ground-foraging species that prefers short (<15 cm) or sparse ground vegetation (hereafter 'field layer'; Conder 1989). This habitat has higher prey availability (Tye 1992), lower nest predation rates (Pärt 2001a), higher fledgling production (Pärt 2001b) and higher adult survival (Low et al. 2010) than habitats with tall and dense ground vegetation.

3.2 Study area and population

Our study area is a 60 km^2 heterogeneous agricultural landscape situated southeast of Uppsala in southern central Sweden (59°50' N, 17°50' E; Figure 5). The area consists of a mixture of forest, crop fields, pastures, farmyards and villages where 230 territory sites have been occupied by wheatears at least once since 1993 when the yearly monitoring started. Each year 120-180 pairs breed in the area. In a smaller core area (~40km^2, 150 sites, 80-90 pairs per year) each territory site has been visited at least every second-to-fifth day throughout the breeding season to collect detailed data on phenology and demographic parameters.

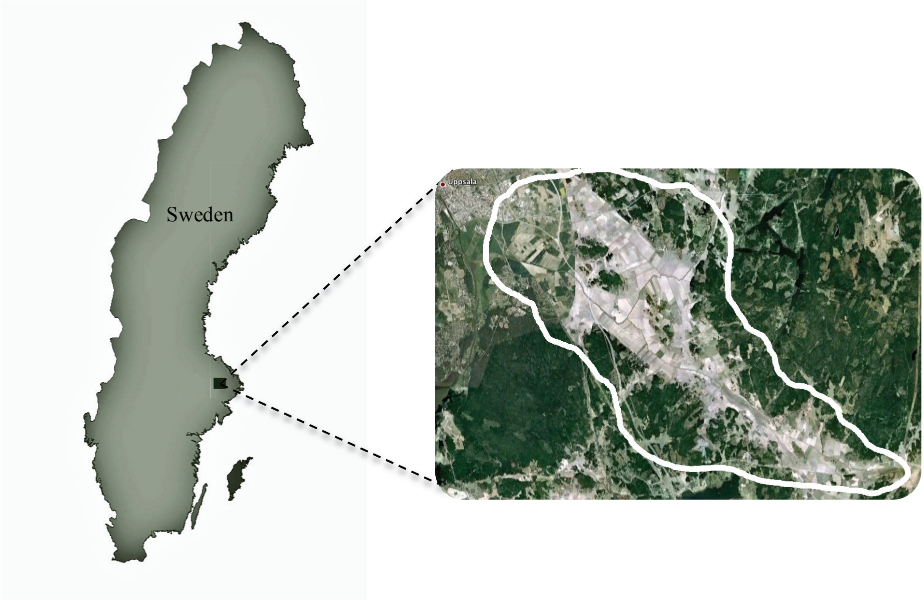

Figure 5. Location of the study area south-east of the city of Uppsala, Sweden.

Wheatears in this population build their nests in stone piles (80%) or under roof tiles of farm buildings (20%). Nest predation is the major cause of breeding failure in this system (approximately 85% of all failures; Pärt 2001a), with partial depredations very rare (< 2 % of all depredations; T Pärt & D Arlt, unpublished data). Nests under roof tiles suffer much lower predation rates than those in stone piles at ground level, primarily because they are fully or partly protected from the key nest predators in our system (all ground-living): weasel (*Mustela nivalis*), red fox (*Vulpes vulpes*), badger (*Meles meles*), domestic cat (*Felis catus*), stoat (*Mustela erminea*), rat (*Rattus norvegicus*) and adder (*Vipera berus;* Pärt & Wretenberg 2002; Schneider et al. 2012).

Breeding pairs usually produce one brood per season, although second breeding attempts may occur after failed first attempts (~20% of all failed attempts) or after successful breeding (~5% of all successful attempts). For each breeding attempt we recorded clutch size (number of eggs when nest found during incubation or chicks within 2 days of hatching), hatching date (calculated from chick age based on pictures of nestlings of known age), number of fledged young (number of ringed chicks minus number of dead chicks in the nest after time of fledging) and nest success (nest success vs. failure; Arlt & Pärt 2007; Arlt & Pärt 2008). We determined a breeding attempt successful if we had observed one or more fledged chicks or heard intense warning calls from parents at the time of fledging (young ≥15 days old).

We ringed nestlings and adults with a unique combination of colour-rings and a numbered metal ring (adults from 57% of all breeding attempts, nestlings from approx. 90% of all successful breeding attempts). We aged adult birds as yearling or older based on their plumage characteristics or known history (Pärt 2001a). We have used age as a proxy for individual quality as reproductive performance often increases with age (Sæther 1990; Forslund & Pärt 1995) and old females tend to select high quality habitats (Arlt & Pärt 2008; Decker et al 2012). Recruitment and apparent adult survival was determined by re-sighting of ringed birds in subsequent years. To minimize the potentially confounding effect of dispersal on survival, we only estimated recruitment success and apparent survival for breeding attempts in the core part of the study area, using the surrounding 2 km area as a buffer zone for re-sighting of individuals (Arlt & Pärt 2008; Arlt et al. 2008). Re-sighting probability for adults in this population is high (mean ± SE: males 0.98 ± 0.01; females 0.89 ± 0.03) and not influenced by habitat or age (Low et al. 2010); thus our apparent survival estimates based on return rates are not biased by habitat or age specific differences in re-sighting probabilities.

We categorized territories according to field layer height (FLH; see also Pärt 2001a; Arlt & Pärt 2007; Low et al. 2010) based on the proportion of short (≤5cm) and high (>5 cm) field layers measured at different stages during the breeding season. Short territories have a permanently short field layer throughout the breeding season on at least 0.25 ha [i.e. the minimum territory size] within 50 m of the nest site (farmyards and grazed pastures) while tall territories have a growing field layer during the breeding season (spring- and autumn-sown crop fields, ungrazed pastures and unmanaged grasslands; see Arlt & Pärt 2007). Breeding adult wheatears experience a habitat-specific difference in workload where birds breeding in tall field layer habitats have higher daily energy expenditure (~20% higher than for birds breeding in short field layer habitats) due to longer foraging flights (Low et al. 2010).

3.3 Phenology

In this thesis we have used individual arrival and breeding times as measures of phenology and we have also calculated the time between these, the arrival-breeding interval.

The arrival date was defined as the date when an individual was first observed in the study area (relative to 1 May; Papers II-III). We only included arrival data during years (1994-1998 and 2002-2012) and areas where territories were frequently visited (every second to fifth day during the arrival period, mid-April to 25th May).

Breeding time was defined as the date the first egg was laid (i.e. egg-laying date 'ELD'; May 1st=1; Papers I-IV), and was estimated for all breeding attempts based on chick hatching dates (88% of all breeding attempts) or observations of breeding behaviour (12 % of all breeding attempts; see Öberg et al. 2014; Paper I). We assumed an incubation period of 13 days and if clutch size was unknown we used a clutch size of six (population mean ± SD, 6.12 ± 0.75 for all years).

The arrival-breeding interval (Papers II-III) was calculated as number of days between arrival date and egg-laying date. Observations were excluded if arrival date was less than 7 days earlier than egg-laying date, because this is the minimum time required to build a nest and start egg laying (Conder 1989; Moreno 1989).

3.4 Fitness components

We have used five fitness components in Papers I, II and IV: (i) nest success – successful if fledging at least 1 young, while failed if 0 fledged young, (ii) clutch size - number of eggs when nest found during incubation or chicks within 2 days of hatching, (iii) fledging success – number of fledged young per egg laid, (iv) recruitment success – number of recruits per fledged young and (V) female and male adult survival to the next breeding season. When estimating effects of factors (e.g. breeding time or rainfall) on different reproductive components it is important that these components are conditional upon the previous step, e.g. that recruitment success is only calculated for attempts where young have been successfully fledged. This was particularly important when comparing the relative contribution of different reproductive components to the overall seasonal decline in recruited young (Paper I).

In papers I and III we have only analysed first breeding attempts because reproductive performance of second attempts may be confounded due to costs connected to re-laying (Hansson et al. 2000; but see Paper II). Although sample sizes have differed for these fitness components throughout the different papers, sample sizes have generally been ~ 600 for clutch size, ~ 1450 for nest success, ~ 500 for fledging success, ~ 700 for recruitment success and ~ 700 for male and female survival respectively (but see Paper II where individuals needed to be matched across breeding seasons).

3.5 Local climate

We obtained data on daily average temperature and local daily rainfall (mm) from the Ultuna Climate Station (59°82’ N, 17°65’ E; http://grodden.evp.slu.se/slu_klimat/index.html). In paper III we have also used thermal sums as an indicator of spring phenology (Nietschke et al. 2007; Hodgson et al. 2011; Saino et al. 2011). Plant and arthropod development early in the season is strongly determined by degree days, i.e. days with influential temperature above a threshold (base) temperature where development rate for arthropods is zero at the threshold and below; thus insect phenology models are usually based on accumulated degree days (i.e. number of degree days above the threshold required to complete development; Hodgson *et al.* 2011; Nietschke *et al.* 2007). We therefore used thermal sum as an indicator of spring phenology. We calculated degree days as $DD = T_{mean} - T_{base}$, where T_{mean} = daily mean temperature, T_{base} = base temperature, and calculated thermal sum for each day as the accumulated sum of positive degree days starting on January 1. We chose the threshold, T_{base}, to be 5 °C because this is the threshold used by the Swedish Metrological and Hydrological Institute to analyse the start of the growing season in agricultural areas (SMHI 2013; Persson *et al.* 2007).

3.6 Statistical analysis

In general, we considered three factors when deciding which statistical approach to use for the different questions in this thesis: (i) selection of the appropriate model form to determine the relationship between the response and explanatory variables of interest (i.e. the statistical test), (ii) a way of determining which combination of explanatory variables best represented the patterns in the data (i.e. model selection), and (iii) a way of calculating the parameter estimates of the explanatory variables and their associated uncertainties. The main part of the analyses was performed in R (R Development Core Team 2012), while analyses on adult survival in Paper I were performed using the multi-state module in MARK (version 5.1; White & Burnham 1999).

3.6.1 Selecting the type of statistical model

We used two general model forms in this thesis: (i) the generalized linear mixed model (GLMM) that contains both fixed and random effects (papers I-IV) and (ii) the Cox proportional hazards regression model (paper III; Cox 1972). In papers I, II and IV we modelled the different response variables as either Poisson or binomial variables (or both for zero-inflated models) because the data were discrete (e.g. clutch size) and could often be considered as arising from a binomial process ('successes' per number of 'trials'; e.g. fledging success = number of chicks fledged per number of eggs laid), while temporal trends in arrival and breeding time in paper III were modelled using a Gaussian distribution because of their continuous nature and the shape of the distribution. We used GLMMs because our data were sampled across almost two decades and contained repeated measures of individuals; this allowed us to include individual and year as random effects to account for between-individual and between-year variation, and observation-level random effects to account for overdispersion when required. The advantage of including terms as random effects not only saves degrees of freedom, but also allows us to make more general inferences from our models (Zuur et al. 2007).

A common approach when analysing effects of climatic variables on phenology or fitness is to use a fixed period of time over which measurements of the climate variable are averaged (e.g. averaged daily mean temperature in a specific month). This can be used to explain between-year variation in the variable of interest, but is unable to explain any of the within-season variation. This level of detail is, however, needed if we fully want to understand the effect of local climate on reproductive decisions and consequences. By using a Cox proportional hazards regression in paper III, we could instead use observational data with daily measures of climate variables for each individual arrival-breeding interval. This way, we could analyse how daily measures of temperature, thermal sum and rainfall affected the probability that a female would initiate egg laying after arrival (i.e. factors influencing the arrival-breeding interval).

3.6.2 Information theoretic approach

In papers I, III and IV we used an information theoretic approach (Burnham & Anderson 2002), which is a very useful framework for analyzing observational and correlative data that are a common feature of ecological datasets (like the data sets used in this thesis). Using Akaike's information criterion (AIC) we can compare the strength of support for a range of models – with one option being the full set of possible models – and use model comparisons to gain insight in to the absolute and relative importance of variables of interest. This has the advantage of avoiding arbitrary significance thresholds (e.g. P-value<0.05) and avoids some of the problems associated with stepwise model selection (e.g. reliance on a single final best model; Wittingham et al. 2006). Using multi-model inference, we can instead acknowledge that there may be several competing models that have a similarly good fit and allow this uncertainty to influence parameter estimates (Burnham & Anderson 2002).

3.6.3 Bayesian approach

In papers I and II we used a Bayesian framework for generating parameter estimates and their uncertainties (i.e. their posterior distributions) from generalized linear mixed model structures, using a Markov Chain Monte Carlo (MCMC) Gibb's sampler. We created models based on results in previous analyses that used multi-model inference (Low et al. 2010; Öberg et al. 2014). The advantage of using a Bayesian approach in these cases was that by deriving posterior distributions we could get probability distributions of model parameters, rather than point estimates. This allowed us to more easily calculate probabilities for group-level differences that properly accounted for the uncertainties in model predictions of the factors of interest. This is possible because all derived variables (e.g. the difference between groups [Paper II], or predictions at different time periods [Paper I]) in a Bayesian analysis have their own posterior distribution, allowing probabilities for specific events (e.g. is the parameter estimate for the difference between groups >0) to be directly calculated from the distribution.

3.6.4 Frequentist approach

In paper III we used parameter estimates from a single Cox proportional hazards model (Cox 1972). Including too many variables and risking over-fitting is rarely a problem with this type of model (Allison 2010); instead problems generally arise if important parameters are not included in the model. How this influences parameter estimates and uncertainty when using multi-model inference is unclear, which is why we instead used a frequentist approach. Instead of focusing solely on an arbitrary significance threshold (e.g. P-value<0.05), we also consider effect sizes, their direction and confidence intervals when interpreting the importance of different parameters. P-values are useful in such models because they provide information on model suitability; if many parameters in the model are highly significant (P-value < 0.0001) it indicates that the model may lack important parameters or interactions or that it is not fulfilling important model assumptions.

4 Results and Discussion

In this thesis we investigate the relationship between local climate, phenology and fitness to increase our understanding of how these relationships may influence population demography. This is particularly important if we want to be able to model population responses to large-scale environmental changes.

4.1 Relating phenology to fitness

4.1.1 The seasonal fitness decline (Paper I)

Although seasonal fitness declines for northern temperate breeding species have been well studied, most studies have focused on only a subset of reproductive components (e.g. Perrins 1965; Winkler & Allen 1996). Different reproductive components, however, are likely to differ in their contribution to the overall seasonal decline in fitness, with this being important for two reasons: (i) accurate estimates of fitness declines need to be based on all fitness components that contribute to the decline, not simply those easiest to measure, and (ii) because seasonal declines in different fitness components could be driven by different factors, the importance of these drivers will be dependent on the contribution of the particular reproductive component to fitness. In Paper I we show that four mutually exclusive reproductive fitness components (i.e. nest success, clutch size, fledging success and recruitment success) all declined with breeding time (i.e. egg-laying date). Although there were apparent large seasonal declines in nest success and clutch size, the decline in recruitment success contributed most (~50%) to the overall seasonal decline in expected production of local recruits (i.e. the common fitness measure we used for comparison; Figure 6). This was followed by nest success and clutch size (each ~20%) and fledging success (~10%). Adult survival, on the other hand, appeared not to be influenced by breeding time, suggesting that early breeders are not trading-off their survival for higher reproductive success.

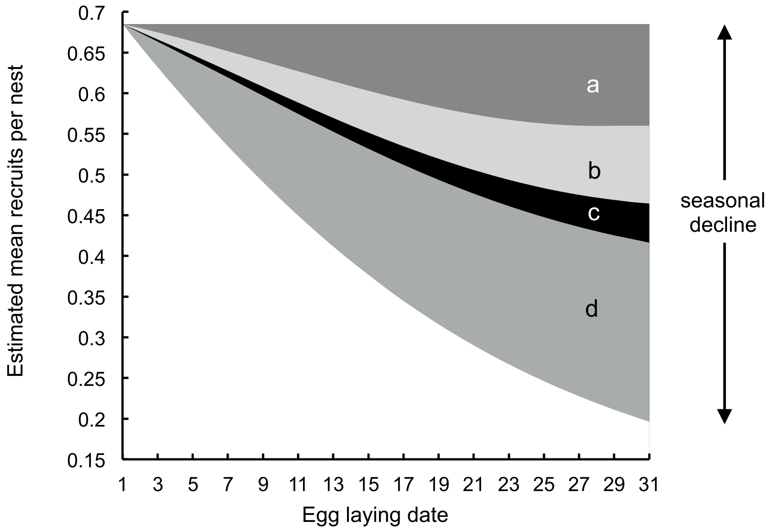

Figure 6. Estimated contribution of the different reproductive components (a nest success, b clutch size from successful nests, c fledging success, d recruitment success) to the seasonal decline in reproduction as expressed in mean recruits per nest. The horizontal top of the coloured area represents the number of recruits if there was no seasonal decline after day 1; the bottom of the coloured area represents the seasonal decline as estimated from this study. Egg-laying date refers to the day of laying the first egg where 1 is the 1^{st} May.

As nest success is primarily determined by nest predation in this population (~85% of all nest failures are caused by nest predation; Pärt 2001a) this suggest that nest predation rates increase during the season. Nest predation was thus the second most important contributor to the overall seasonal fitness decline. Because we could largely account for seasonal changes in individual quality (through female age) and habitat quality (through field-layer height; tall vs. short), our results in Paper I provide strong evidence that the seasonal decline in fitness of wheatears is, at least at a proximate level, driven by a combination of increasing nest predation rates and the deterioration of other environmental conditions (e.g. declining food availability, increasing parasite loads, post-fledging predation) on the production and recruitment of young. This is further supported by additional analyses (Pärt et al. unpublished data) that show seasonal changes in female and territory quality have little relationship between phenology and reproductive output in this system. However, the relationship between phenology and clutch size may be more likely an adaptive response (sensu Drent & Daan 1980; Rowe et al. 1994; Brommer et al. 2002) to deteriorating conditions for producing young (e.g. increasing predation risk) because food conditions generally improve with date in early spring when egg laying occurs, before declining during chick rearing and independence.

4.1.2 Costs of reproduction (Paper II)

Because breeding time clearly had a large impact on individual fitness in this population, we investigated whether costs of reproduction from one year can carry-over to influence the timing of breeding (and hence fitness) in the following season (Paper II). To investigate this we used data on individuals for which we had breeding records for two consecutive years and divided them into three groups that differed in their effort and timing of breeding in year 1 (i.e. a 'natural experiment'): (i) successful breeders, that invested reproductive effort in a single successfully fledged brood; (ii) failed breeders (that did not renest), that invested less in breeding and finished breeding earlier than successful breeders and birds that renested after failure; and (iii) renesters (i.e. failed breeders that did renest), that invested more than at least failed breeders and finished breeding later in the season compared to both successful and failed breeders. We then analysed how these group differences affected their phenology (and related reproductive output) the following breeding season. Our results show that the main carry-over effect of previous breeding history was apparent in the timing of arrival and breeding. Females with less effort and earlier breeding completion in year 1 (i.e. failed breeders), tended to arrive earlier and breed earlier when compared to other breeders (i.e. successful breeders & renesters). Similarly, females spending potentially more effort and finishing breeding later in one season (i.e. renesters) tended to arrive later in the following season when compared to birds that only had one breeding attempt (i.e. successful & failed breeders).

Reproductive output in the following breeding season (measured by the number of fledged chicks) differed between the three groups, but this was largely a result of the different breeding times between the three groups (i.e. the relationship between phenology and fitness: see 4.1.1). The possibility that high reproductive effort and late completion of breeding may be costly was also suggested by slightly reduced survival rates to the next year for renesting females.

Why is it that an individual's ability to compensate for additional or late breeding energy expenditure may be limited? Studies have shown that individuals that complete breeding early have more time to prepare their physiology and condition before migration (Mitchell et al. 2012a, b) and avoid an overlap between breeding and moult (Nilsson & Svensson 1996, Siikamaki 1998, Mitchell et al. 2012b) than later breeders; this, in turn, is expected to improve survival during and post-migration (Nilsson & Svensson 1996).

Furthermore, individuals that arrive early to the wintering grounds may be at an competitive advantage to those arriving later and thus be able to start earlier when it is time to migrate back to the breeding grounds in the next year (Marra et al. 1998, Norris et al. 2004).

4.2 Relating phenology to local climate: temporal changes in phenology and flexibility in the arrival-breeding interval (Paper III)

In Papers I and II we show that breeding time is very important in terms of fitness (see 4.1). But with increasingly warmer springs, plants and arthropods (i.e. lower trophic level organisms) are expected to respond to these changes more rapidly than higher trophic level organisms (e.g. wheatears) that rely on these resources for food and shelter (Both et al. 2009; Thackeray et al. 2010). Thus, bird populations are at increasing risk of mismatching their timing of breeding to the peak of food availability unless they are able to track these lower trophic level changes by adjusting their breeding time accordingly. In Paper III we show that as spring temperatures have increased during the past two decades, individuals in our study population have advanced both their arrival and breeding time and reduced the arrival-breeding interval. Despite this however, there is evidence that they are not able to ‘keep up’ with the current rapid changes in environmental conditions because in 2012 they were arriving and breeding at a relatively much later time in the progression of spring development than they did in 1994 (i.e. at almost twice as high thermal sums; Figure 7).

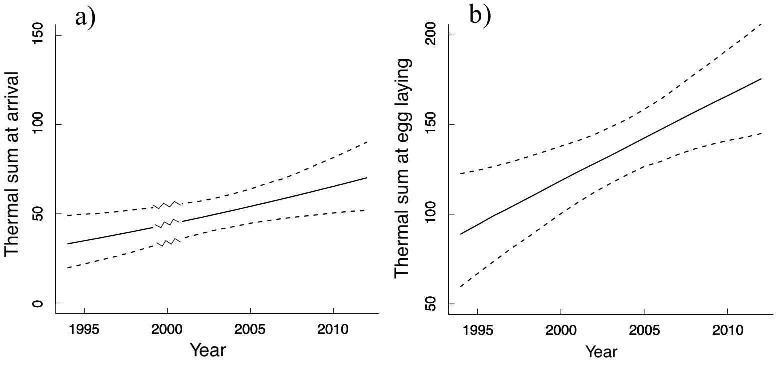

Figure 7. Temporal trends in (a) thermal sums at arrival and (b) thermal sums at egg laying, with thermal sums used as an indicator of spring phenology. Lines show model predictions with their associated 95% CIs. Zigzag lines in (a) indicate years where arrival data are missing.

This relatively later arrival and breeding (in terms of thermal sums) despite the birds arriving and breeding earlier suggests the population could be becoming increasingly mismatched with its breeding food supply (Saino et al. 2011; although we cannot be certain without data on food phenology). In recent years the seasonal fitness decline in this population (Paper I & section 4.1 above) has been reduced in its magnitude, with an overall fitness decline in the population. This is in line with such a view that the population is becoming mismatched with its food supply, although other explanations are also possible (Arlt et al. unpublished manuscript). How is it then that there has only been a weak reduction in the arrival-breeding interval when a greater reduction could lead to earlier breeding and potentially better matching to the peak of food abundance?

Although the arrival-breeding interval is a plastic trait, there is evidence that its plasticity is limited by constraints. Early arriving individuals had longer arrival-breeding intervals than those arriving later (when local feeding conditions are better), suggesting that plasticity may be linked to energetic stress. Constraints in trait plasticity are further demonstrated by the strong influence of the thermal sum (i.e. spring progression) on the expression of the length of arrival-breeding interval, and how this relationship has changed with recent warmer springs. Higher thermal sums did not reduce the arrival-breeding interval to the same extent in 2012 as in 1994 despite thermal sums at arrival and egg laying having become almost twice as high in 2012 as in 1994, suggesting constraints on how much the interval can be reduced. One possibility is that there has been decreased selection for early breeding in recent years (Arlt et al. unpublished manuscript), resulting in little benefit in reducing the arrival-breeding interval compared to potential costs of speeding up phenology. Similarly, an evolutionary response may be undetectable during this timeframe if selection for early breeding is low.

4.3 Relating local climate to fitness: the effect of rainfall (Paper IV)

There is a strong relationship between phenology and fitness, and between local climate and phenology in this population (Papers I-III: sections 4.1 & 4.2 above). Local climate, however, may also have more direct effects on fitness. In Paper IV we show that increasing rainfall was related to direct losses of fledglings at the nestling stage, and also longer-term effects on both recruitment and adult survival.

Daily rainfall reduced parental visitation rates by ~22% during days with heavy rainfall (>20 mm; Figure 8a). This is similar to rainfall effects on provisioning rates shown in other studies (e.g. Dawson & Bortolotti 2000;

Radford et al. 2001; Geiser et al. 2008; Arlettaz et al. 2010). Such a reduction in visitation rates would suggest that nestlings receive less food during rainfall (unless the reduction in visitation rates is compensated for by changes in load size; Grieco 2002).

Rainfall had a negative effect on fledging success (Figure 8b), with older chicks being more sensitive than young. This could be related to a higher energy demand for older nestlings and that younger nestlings may be protected from adverse weather by brooding by the female (Conder 1989; Radford et al. 2001). The magnitude of the rainfall effect was also greater earlier in the season than later, which could be linked to the often larger clutches produced by early breeders (Paper I), potentially requiring an effort beyond the parent's

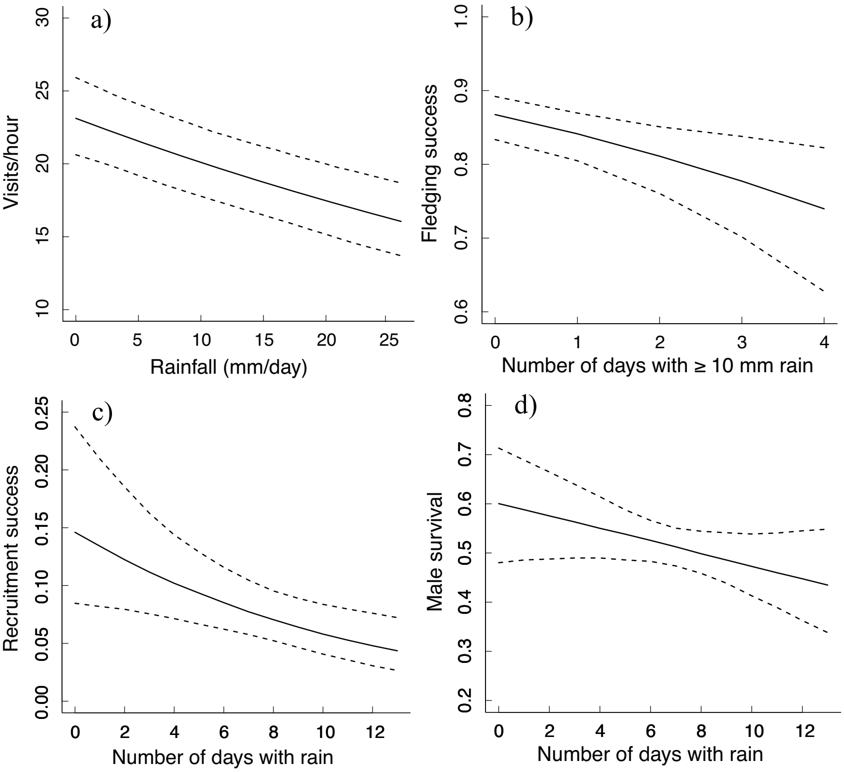

Figure 8. Relationship between a) hourly visitation rates and daily amount of rainfall during day of visitation, b) fledging success (number of fledged young per egg laid) and number of days with ≥10 mm of rain during the later part of the nestling period, c) recruitment success (number of recruits per fledged young) and number of days with >0 rain during the entire nestling period and d) male apparent survival and number of days with >0 rain during the entire nestling period. Lines are model predictions with their associated 95% CIs.

capacity when feeding young during poor environmental conditions thus causing brood reduction through nestling mortality (Siikamäki 1996). If this is true, differences in fitness between early and late breeders may disappear in years with heavy rain early in the season, reducing advantages of early breeding (Paper I).

Recruitment success (Figure 8c) was, however, more sensitive to rainfall when nestling were younger. It is not clear why younger nestling would be more sensitive to rainfall (could be an artefact of differential mortality in the later nestling stage, see fledging success above), but recruitment success may be affected by rainfall through reduced growth rates of the nestlings (Conder 1989; Keller & van Noordwijk 1994; Siikamäki 1996; Veistola et al. 1997; Dawson & Bortolotti 2000). Fledging body condition has been shown to strongly affect probability of juvenile survival to the next year (Sullivan 1989; Lindén et al. 1992; Naef-Daenzer et al. 2001; Low & Pärt 2009)

We show in Paper IV that male survival (Figure 8d) was more sensitive than female survival to increased rainfall during the period of nestling care. This could be because of differences in parental duties when weather becomes adverse. In this species, only females brood the young (Conder 1989) and when raining the female may increase her time spent brooding young and ectothermic nestlings to protect them from chilling (Radford et al. 2001). This could in turn explain the reduction in visitation rates during rainfall and why female survival was not reduced as with males. It furthermore may explain why male survival tended to be more sensitive to rainfall when nestlings were young, as the male may be forced to increase their effort during rainfall to compensate for the reduced provisioning rates of females.

4.4 The impact on land-use on phenology and fitness

Ground vegetation is a good indicator of habitat quality in this system, with short or sparse vegetation (e.g. spring-sown crops) having higher prey availability (Tye 1992; Low et al. 2010), lower nest predation (Pärt 2001a), higher fledgling production (Pärt 2001b), higher population growth (Arlt et al. 2008) and higher adult survival (Low et al. 2010) than habitats with tall and dense ground vegetation (e.g. autumn-sown crops). However, with earlier springs and longer growing seasons there is a general expectation that autumn-sown crops will become more common in Swedish agricultural systems. This has potential implications for demography in this population because of the strong effect of field layer height on reproductive output (Paper I). Tall field layer habitats had lower nest success from predation, with the effect of field layer becoming more pronounced as the season progressed. If birds continue arriving and breeding later relative to the spring progression (Paper III), this suggests that not only will birds have a lower fitness in general because of advancement in seasonal fitness declines, but those birds that are increasingly forced to breed in poorer quality habitat resulting from land-use changes will suffer disproportionately higher fitness losses that would be expected from land-use changes alone. In addition, increased extreme rainfall events and their negative relationship to fledgling and recruitment success (Paper IV) could further compound fitness losses from poorer quality habitats by further reducing food availability in those habitats (Low et al. 2010; Paper IV).

5 Conclusions and implications for future research

The primary aim of this thesis was to better understand how local climate and phenology affects individual fitness. By increasing our basic knowledge of these relationships, we can start working towards predicting how population demography may be influenced by climate change.

An essential question that needs to be answered before we can start making predictions on changes in population demography in relation to climate change is - which fitness components should we actually study? Our results in Paper I clearly show that an apparent large seasonal decline in a single fitness component does not necessarily mean that this is the one that contributes the most to the overall production of recruited young. As these fitness components also differ in their determinants they may be differentially affected by a changing climate. The importance of studying multiple fitness components is further shown in Paper IV where increasing rainfall not only affected reproduction and survival, but these effects were age-, sex- and time-dependent. Most studies of rainfall effects focus on nestling survival, but here we show that rainfall has longer-term effects influencing both recruitment success and male survival. Clearly, the sensitivity of different fitness components to climate change differ and by focusing on single or few components there is a risk that we may underestimate potential effects of climate change on population demography.

Paper III shows that wheatears have advanced their arrival to the breeding grounds and to some extent reduced the arrival-breeding interval. Still, they seem to breed later relative to the progression of spring during the late years of the study. Possible explanations for the relatively small reduction in the arrival-breeding interval may be constraints on how much the interval can be reduced or because of a reduced selection for early breeding. Constraints could be linked to reduced flexibility in the arrival-breeding interval, but as we have seen in Paper II costs may have their main impact in timing and thus constrain the ability of individuals to advance their timing. The question, however, remains to be answered - is there really a need for advancing breeding at all? Selection for early breeding has been reduced in recent years resulting in lower benefits for breeding early that have to be balanced with potential costs associated with advancing breeding. It could be that the population is lagging behind the peak of their main food supply, but studies that have been able to show evidence for mismatches are often done on birds relying on single insect species with clear abundance peaks for feeding young. Wheatears, on the other hand, feed their young with several different types of insect prey and the food provisioned to nestlings appears to change the as chicks grow older (personal observations). The type of food provisioned (and its quality) may furthermore depend on time in the season and habitat type (e.g. habitats surrounded by crops fields vs. forest), which is why measuring food abundance may prove quite difficult; not only do we need to carefully consider what species to measure, we also need to consider when and where we measure them and if insects species may differ in quality as a food source.

Thus, a shift in the peak of food abundance in response to a warming climate may be an over-simplification in a system like this and because responses of insects are likely to be of a more complex nature than just phenological shifts, the abundance of insects during the bird's breeding season may be very difficult to predict.

In Paper II we showed that females that renested after a failed attempt produced clutches similar to the expected seasonal fitness decline (Paper I) and that there are costs associated with the production of a second clutch (in the following year's timing of breeding). Although not considered in Papers I and III, the production of replacement clutches after failure may have implications for our findings there as well. Because time is a limiting factor, early breeders have a higher probability of renesting after failure (Öberg M., unpublished data). This has implications for the seasonal fitness decline as early breeders that fail have the chance of compensating for the failed clutch by producing a replacement clutch, hence achieving a higher fitness than those failing late. This reasoning also applies to Paper III regarding the reduced selection for earlier breeding; early breeding may still be beneficial in terms of production of replacement clutches after failure. However, as there are costs associated with producing a replacement clutch, it implies that carry-over effects from one season to the next also may influence the decision on whether to renest after failure or not. Thus, although renesting individuals have the fitness benefits of producing a replacement clutch, it also comes at a cost of delayed breeding (and possibly reduced survival) in the following year, while failed individuals are able to arrive and breed earlier the next season with the potentially higher fitness it entails. Costs of producing a replacement clutch hence need to be weighed against benefits of earlier breeding the next season and a general probability of surviving to the next season. Thus, the possibility of producing a replacement clutch after failure is an important fitness measure that should be considered when estimating potential impacts of climate change on fitness and population growth.

Lastly, this thesis highlights the importance of habitat quality and that we should aim to not investigate climate change effects in isolation, but also consider other environmental changes, such as land-use changes, that are likely to interact with climate change and potentially have large influences on population demography.

References

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

Allison, P. (2010) *The Reviewer's Guide to Quantitative Methods in the Social Sciences*. Ed. Hancock, G. & Mueller, R. Pp 413-425. Routledge, New York.

Arlettaz, R., Schaad, M., Reichlin, T.S. & Schaub, M. (2010) Impact of weather and climate variation on Hoopoe reproductive ecology and population growth. *Journal of Ornithology*, 151, 889–899.

Arlt, D. & Pärt, T. (2007) Nonideal breeding habitat selection: a mismatch between preference and fitness. *Ecology*, 88, 792–801.

Arlt, D. & Pärt, T. (2008) Post-breeding information gathering and breeding territory shifts in northern wheatears. *Journal of Animal Ecology*, 77, 211–219.

Arlt, D., Forslund, P., Jeppsson, T. & Pärt, T. (2008) Habitat-specific population growth of a farmland bird. *PLoS ONE*, 3, e3006.

Avery, M. I., & Krebs, J. R. (1984) Temperature and foraging success of Great Tits *Parus* major hunting for spiders. *Ibis*, 126, 33-38.

Both, C. & te Marvelde, L. (2007) Climate change and timing of avian breeding and migration throughout Europe. *Climate Research*, 35, 93–105.

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

Both, C., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E.V., Jarvinen, A., Metcalfe, N.B., Nyholm, N.E.I., Potti, J., Ravussin, P.A., Sanz, J.J., Silverin, B., Slater, F.M., Sokolov, L.V., Torok, J., Winkel, W., Wright, J., Zang, H. & Visser, M.E. (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society B: Biological Sciences*, 271, 1657–1662.

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

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

Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J. & Foppen, R.P.B. (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B: Biological Sciences*, 277, 1259–1266.

Brinkhof, M.W.G., Cavé, A.J., Daan, S. & Perdeck, A.C. (2002) Timing of current reproduction directly affects future reproductive output in european coots. *Evolution*, 56, 400–411.

Brommer, J.E., Pietiäinen, H. & Kokko, H. (2002) Cyclic variation in seasonal recruitment and the evolution of the seasonal decline in Ural Owl clutch size. *Proceedings: Biological Sciences*, 269, 647–654.

Burnham, K. P. & Anderson, D. R. (2002) *Model Selection and Multi-model Inference – a Practical Information Theoretical Approach*, 2nd edn. Springer-Verlag, New York

Caro, S.P., Schaper, S.V., Dawson, A., Sharp, P.J., Gienapp, P. & Visser, M.E. (2013) Is microevolution the only emergency exit in a warming world? Temperature influences egg laying but not its underlying mechanisms in great tits. *Combined Special Issues: NASCE 2011 and ISARN 2011 The Inaugural Meeting of the North American Society for Comparative Endocrinology (NASCE) and the 7th International Symposium on Amphibian and Reptilian Endocrinology and Neurobiology (ISAREN)*, 190, 164–169.

Conder, P. (1989) *The wheatear*. Helm, London.

Cox, D. R. (1972) Regression models and life tables. *Biometrics*, 39, 67-77.

Cushman, J.H., Boggs, C.L., Weiss, S.B., Murphy, D.D., Harvey, A.W. & Ehrlich, P.R. (1994) Estimating female reproductive success of a threatened butterfly: influence of emergence time and hostplant phenology. *Oecologia*, 99, 194–200.

Dawson, R.D. & Bortolotti, G.R. (2000) Reproductive success of American Kestrels: the role of prey abundance and weather. *The Condor*, 102, 814–822.

Decker, K.L., Conway, C.J. & Fontaine, J.J. (2012) Nest predation, food and female age explain seasonal declines in clutch size. *Evolutionary Ecology*, 26, 683-699.

Drent, R.H. & Daan, S. (1980) The prudent parent: energetic adjustments in avian breeding. 1–28.

Forslund, P & Pärt, T. (1995) Age and reproduction in birds – hypotheses and tests. *Trends in Ecology and Evolution*, 10, 374-378.

Franklin, A.B., Anderson, D.R., Gutiérrez, R.J. & Burnham, K.P. (2000) Climate, habitat quality, and fitness in Northern Spotted Owl populations in Northwestern California. *Ecological Monographs*, 70, 539–590.

Geiser, S., Arlettaz, R. & Schaub, M. (2008) Impact of weather variation on feeding behaviour, nestling growth and brood survival in Wrynecks Jynx torquilla. *Journal of Ornithology*, 149, 597–606.

Gordo, O. & Sanz, J.J. (2007) The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. *Journal of Ornithology*, 149, 199–210.

Gordo, O., Brotons, L., Ferrer, X. & Comas, P. (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.

Götmark, F. (2002) Predation by sparrowhawks favours early breeding and small broods in Great Tits. *Oecologia*, 130, 25–32.

Grieco, F. (2002) How different provisioning strategies result in equal rates of food delivery: an experimental study of blue tits *Parus caeruleus*. *Journal of Avian Biology*, 33, 331–341.

Gwinner, E. (2003) Circannual rhythms in birds. *Current Opinion in Neurobiology*, 13, 770–778.

Hansson, B., Bensch, S. & Hasselquist, D. (2000) The quality and the timing hypotheses evaluated using data on Great Reed Warblers. *Oikos*, 90, 575–581.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. (2010) Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, 80, 4–18.

Hedgren, S. & Linnman, Å. (1979) Growth of Guillemot *Uria aalge* chicks in relation to time of hatching. *Ornis Scandinavica*, 10, 29–36.

Hochachka, W. (1990) Seasonal decline in reproductive performance of Song Sparrows. *Ecology*, **71**, 1279–1288.

Hodgson, J.A., Thomas, C.D., Oliver, T.H., Anderson, B.J., Brereton, T.M. & Crone, E.E. (2011) Predicting insect phenology across space and time. *Global Change Biology*, 17, 1289–1300.

Hüppop, O. & Winkel, W. (2006) Climate change and timing of spring migration in the long-distance migrant Ficedula hypoleuca in central Europe: the role of spatially different temperature changes along migration routes. *Journal of Ornithology*, 147, 344–353.

IPCC (Intergovernmental Panel on Climate Change). (2013) Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Keller, L. F. & van Noordwijk, A. J. (1994) Effects of local environmental conditions on nestling growth in the Great Tit *Parus major*. *Ardea*, 82, 349-362.

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

Lindén, M., Gustafsson, L. & Pärt, T. (1992) Selection on Fledging Mass in the Collared Flycatcher and the Great Tit. *Ecology*, 73, 336–343.

Low, M. & Pärt, T. (2009) Patterns of mortality for each life-history stage in a population of the endangered New Zealand stitchbird. *Journal of Animal Ecology*, 78, 761–771.

Low, M., Arlt, D., Eggers, S. & Pärt, T. (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., Hobson, K.A. & Holmes, R.T. (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *New Series*, 282, 1884–1886.

Mitchell, G.W., Newman, A.E.M., Wikelski, M. & Ryan Norris, D. (2012a) Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study. *Journal of Animal Ecology*, 81, 1024–1033.

Mitchell, G.W., Wheelwright, N.T., Guglielmo, C.G. & Norris, D.R. (2012b) Short- and long-term costs of reproduction in a migratory songbird. *Ibis*, 154, 325–337.

Møller, A. P., Rubolini, D. & Lehikoinen, E. (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.

Moreno, J. & Hillström, L. (1992) Variation in time and energy budgets of breeding wheatears. *Behaviour* 120, 11-39.

Naef-Daenzer, B., Widmer, F. & Nuber, M. (2001) Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging date. *Journal of Animal Ecology*, 70, 730–738.

Nager, R.G. & Noordwijk, A.J.V. (1992) Energetic limitation in the egg-laying period of Great Tits. *Proceedings: Biological Sciences*, 249, 259–263.

Nager, R.G., Ruegger, C. & Noordwijk, A.J.V. (1997) Nutrient or energy limitation on egg formation: a feeding experiment in Great Tits. *Journal of Animal Ecology*, 66, 495–507.

Nietschke, B. S., Magarey, R. D., Borchert, D. M., Calvin, D. D. & Jones, E. (2007) A developmental database to support insect phenology models. *Crop Protection*, 26, 1444-1448.

Nilsson, J.-Å. & Svensson, E. (1993) Energy constraints and ultimate decisions during egg-laying in the Blue Tit. *Ecology*, 74, 244–251.

Nilsson, J.-Å. & Svensson, E. (1996) The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proceedings: Biological Sciences*, 263, 711–714.

Norris, D.R. (2005) Carry-over effects and habitat quality in migratory populations. *Oikos*, 109, 178–186.

Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W. & Ratcliffe, L.M. (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings: Biological Sciences*, 271, 59–64.

Öberg, M., Pärt, T., Arlt, D., Laugen, A. & Low, M. (2014) Decomposing the seasonal fitness decline. *Oecologia*, 174, 139-150.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics*, 37, 637-639.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.

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.

Pärt, T. & Wretenberg, J. (2002) Do artificial nests reveal relative nest predation risk for real nests? *Journal of Avian Biology*, 33, 39-46.

Perrins, C.M. (1965) Population fluctuations and clutch-size in the Great Tit, *Parus-major*. *Journal of Animal Ecology*, 34, 601-647

Perrins, C.M. (1970) The timing of birds‘ breeding seasons. *Ibis*, 112, 242–255.

Persson, G., Bärring, L., Kjellström, E., Strandberg, G. & Rummukainen, M. (2007) Climate indices for vulnerability assessments. *SMHI Rapporter RMK*, 111. http://www.smhi.se/polopoly_fs/1.2096!RMK111%5B1%5D.pdf

Radford, A. N., McCleery, R. H., Woodburn, R. J. W. & Morecroft, M. D. M. (2001) Activity patterns of parent Great Tits *Parus major* feeding their young during rainfall. *Bird Study* 48, 214-220.

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, http://www.R-project.org/

Reed, T.E., Jenouvrier, S. & Visser, M.E. (2013) Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, 82, 131–144.

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

Rodríguez, C. & Bustamante, J. (2003) The effect of weather on Lesser Kestrel breeding success: can climate change explain historical population declines? *Journal of Animal Ecology*, 72, 793–810.

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

Rowe, L., Ludwig, D. & Schluter, D. (1994) Time, condition, and the seasonal decline of avian clutch size. *The American Naturalist*, 143, 698–722.

Saether, B.E. (1990) Age-specific variation in reproductive performance of birds. *Current Ornithology,* 7, 251-283.

Saino, N., Ambrosini, R., Rubolini, D., Hardenberg, von, J., Provenzale, A., Huppop, K., Huppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M. & Sokolov, L. (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, 278, 835–842.

Sanz, J.J., Potti, J., Moreno, J., Merino, S. & Frías, O. (2003) Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Global Change Biology*, 9, 461–472.

Schaper, S.V., Dawson, A., Sharp, P.J., Gienapp, P., Caro, S.P. & Visser, M.E. (2012) Increasing temperature, not mean temperature, is a cue for avian timing of reproduction. *The American Naturalist*, 179, E55–E69.

Schneider, N.A., Low, M., Arlt, D. & Pärt, T. (2012) Contrast in edge vegetation structure modifies the predation risk of natural ground nests in an agricultural landscape (ed DM Evans). *PLoS ONE*, 7, e31517.

Senapathi, D., Nicoll, M.A.C., Teplitsky, C., Jones, C.G. & Norris, K. (2011) Climate change and the risks associated with delayed breeding in a tropical wild bird population. *Proceedings of the Royal Society B: Biological Sciences*, 278, 3184–3190.

Siikamäki, P. (1996) Nestling growth and mortality of Pied Flycathcers *Ficedula hypoleuca* in relation to weather and breeding effort. *Ibis*, 138, 471-478.

Siikamaki, P. (1998) Limitation of reproductive success by food availability and breeding time in pied flycatchers. *Ecology*, 79, 1789–1796.

SMHI website, 2013. Sveriges Meteorologiska och Hydrologiska Institut. http://www.smhi.se (accessed 2013-12-27).

SMHI website, 2014. Sveriges Meteorologiska och Hydrologiska Institut. http://www.smhi.se (accessed 2014-01-10).

Smith, H.G. (1993) Seasonal Decline in Clutch Size of the Marsh Tit (Parus palustris) in Relation to Date-Specific Survival of Offspring. *The Auk*, 110, 889–899.

Stearns, S. C. (1992) *The evolution of life-histories*. Oxford University Press, Oxford, U.K.

Sullivan, K.A. (1989) Predation and starvation: age-specific mortality in juvenile Juncos (*Junco phaenotus). Journal of Animal Ecology*, 58, 275–286.

Thackeray, S.J., Sparks, T.H. & Frederiksen, M. (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16, 3304-3313.

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

Veistola, S., Lehikoinen, E. & Eeva, T. (1997) Weather and breeding success at high latitudes – the Pied Flycatcher *Ficedula hypoleuca* and the Siberian Tit *Parus cinctus*. *Ornis Fennica*, 74, 89-98.

Visser, M.E., Holleman, L.J.M. & Caro, S.P. (2009) Temperature has a causal effect on avian timing of reproduction. *Proceedings of the Royal Society B: Biological Sciences*, 276, 2323–2331.

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

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

Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. (2006) Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, 75, 1182–1189.

Whittow, G. C. (Ed.), (2000) *Sturkie's avian physiology.* Academic Press, New York.

Williams, G. C. (1966) Natural selecetion, the cost of reproduction and a refinement of Lack's principle. *American Naturalist*, 100, 687-690.

Williams, T.D. (2012) Hormones, life-history, and phenotypic variation: Opportunities in evolutionary avian endocrinology. *Combined Special Issues: NASCE 2011 and ISARN 2011 The Inaugural Meeting of the North American Society for Comparative Endocrinology (NASCE) and the 7th International Symposium on Amphibian and Reptilian Endocrinology and Neurobiology (ISAREN)*, 176, 286–295.

Wingfield, J.C. (2008) Organization of vertebrate annual cycles: implications for control mechanisms. *Philosophical Transactions: Biological Sciences*, 363, 425–441.

Winkler, D.W. & Allen, P.E. (1996) The seasonal decline in Tree Swallow clutch size: physiological constraint or strategic adjustment? *Ecology*, 77, 922–932.

Zuur, A.F., Ieno, E.N. & Smith G.M. (2007) *Analysing Ecological data.* Springer, New York.

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