

# **The impacts of climate change on the ecology of a migrant wetland warbler**

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Thesis submitted for the degree of Doctor of Philosophy

School of Biological Sciences

September 2014

## Summary

Climate-change has the potential to affect migratory birds by altering prey availability across their annual cycle. Observational and experimental approaches were used to understand the causes and consequences of these changes on the breeding productivity, mass regulation and survival of a wetland bird; the Eurasian reed warbler *Acrocephalus scirpaceus*. Climatic influences on wetland invertebrate populations were assessed by monitoring natural and experimentally-induced variations in temperature. Further increases in early spring temperatures are likely to result in earlier availability of prey resources. The responses of breeding birds to changes in their prey were tested with food supplementations, which advanced egg-laying dates, reduced the laying interval and incubation duration, and increased nestling growth rate. These effects enable earlier first fledglings and increase the opportunity for second breeding attempts within the peak invertebrate prey window. The consequences of prey availability on wintering body condition were tested by comparing resources and energy reserves in contrasting habitats in West Africa during the non-breeding period. Birds occupying prey-rich habitats maintained lower body reserves than conspecifics occupying prey-poor dry-scrub habitats, consistent with strategic buffering of reserves against starvation in food-poor habitat. These results suggest how reed warblers are able to survive in lower quality habitats and potentially avoid density-dependent mortality associated with drought as observed in other wetland migrants. Analysis of long term (>30 year) weather effects on survival revealed measureable but minor impacts, suggesting reed warblers are very adaptive to environmental change. Overall, this study provides strong support for climate-driven advance in spring invertebrate availability and identifies the reed warbler breeding and survival parameters most affected by increases to prey availability. This study provides an integrated and original understanding of the mechanisms which may underlie current levels of population growth in what appears to be one of the few long-distance migratory European songbird species currently benefiting from climate-change.

## Acknowledgements

This thesis sets out an investigation into changes in the environment and how it affects a group of little-noticed European breeding birds. Persistent changes in climate have been shown to have consequences for many Palearctic-African migrant birds and it is only by exploring the populations of common, and seemingly unremarkable, species such as reed warblers that we can understand the extent of such consequences. As is so often the case for such subjects, much of the time spent collecting data in various parts of this species domains has been with great pleasure and sense of privilege, despite the soggy feet, constant harassment from biting insects and health threats from various gut and blood parasites. While it is tempting to think that the birds might have gained some sort of insight to the human condition during this study, it was quite clear that their involvement in this project was of great inconvenience to them.

This study has taken me, my wife, son, colleagues, supervisors, friends and volunteers to a number of fantastic places in the UK, Portugal and Senegal where we have enjoyed a great many experiences with wildlife, culture and landscapes. That said, herein, there will be no descriptive appreciation of the wetland environment, for (in the words of Philip Brown and Majorie Gwen Davies 1949) “in a reedbed there is nothing mysterious about what rises up from that bosom..it is a persistent stink of sulphureted hydrogen”. Indeed, reedbeds may be picturesque, but they do stink.

This research is funded by the **European Social Fund Knowledge Economy Skills Scholarship** project, with support from The Wildlife Trust for South and West Wales, Eco-explore community interest company and Cardiff University, School of Biosciences.

I have received considerable support from Cardiff Harbour Authority, Vale of Glamorgan County Borough Council, Bridgend county Council, Dow Corning Ltd and the staff of Kenfig Nature Reserve.

I am grateful to a number of individuals too many to list here, but I must particularly mention the following people for considerable assistance in one way or another.

Rob Thomas; for his friendship, endless reassurance, patience and tact.

Hefin Jones; for his honesty, generosity and special access to his outlooks.

Ian Vaughan; for maintaining perspective, supplying the voice of reality and for his kind treatment of my developing statistical expertise.

Rob Parry; for providing refuge and rooting the thesis in the realms of application, engagement and communication.

Richard Facey; for remaining the fiercest advocate of the project.

Renata Medeiros; invaluable genetic assistance and encouragement.

Jez Smith; for his optimism and dedication at home and away.

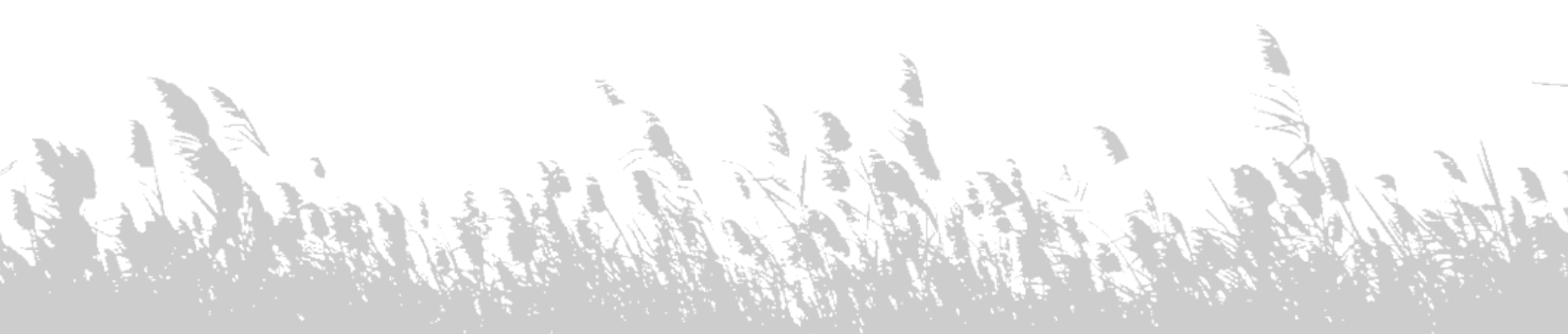
All in the office for sharing their R scripts, interesting insights to ‘outdated concepts’ and components of their lunch.

To all final year, professional training year and masters students Liam Doyle, Todd Jenkins, Jason Lewis, Jordan Beasley, Lizzie Grayshon, Owen Griffith, Laura Robertson, Amie-Beth Sabin, Hayley Roberts and Ed Suitters; for their assistance with data collection and invertebrate identification:

Dave Bull; A teacher, friend and vector of Acrocephalidaephilia of which I am now irreversibly infected. I dedicate this thesis to him.

Finally, and mostly, it remains only to state that this work could not have been done without the support and understanding of my wife, family and friends.

This is all your fault (Thank You).



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# **Chapter 1**

## **Impacts of climate change on the Eurasian reed warbler *Acrocephalus scirpaceus***

## 1.0 Introduction

The evidence for rising atmospheric concentrations of greenhouse gases is unequivocal and is linked to significant changes in climate systems, including rises in air temperatures across the world (Rosenzweig *et al.* 2007; IPCC 2013). Although the patterns of climate change are complex, it is the trend of rising temperature that is most geographically widespread and temporally consistent on a global scale (Warren *et al.* 2010). Predicting the consequences of rising temperatures, and other aspects of climate change, on the world's ecosystems has over the last two to three decades become the most active and rapidly evolving field of ecological research (Walther *et al.* 2002; Pearce-Higgins *et al.* 2011; Bellard *et al.* 2012). The major challenge for biologists attempting to predict and detect effects on ecological communities is in separating the complexity of interactions within and between the biotic and abiotic components (Harrington *et al.* 1999). As a consequence, many studies only test the effects of climate change on a single species or a single trophic level (e.g. Bale *et al.* 2002; Root *et al.* 2003). More recently, studies have started to span trophic levels to provide clearer predictions of the effects of temperature on species, for example, by considering the impacts of climate change on the phenology and availability of their prey and condition of their habitats (Schweiger *et al.* 2008; Tylianakis *et al.* 2008; Van der Putten *et al.* 2010).

In many ecosystems, birds and their trophic resources provide a tractable and informative model for understanding the integrated effects of climate change (Parmesan and Yohe 2003). Birds are a useful subject for such studies as their behaviour and ecology is generally well understood, they are mobile, highly sensitive and are able to respond rapidly to changes in their environment (Furness and Greenwood 1993; Gregory and Van Strien 2010). Their reliance on appropriate nesting and foraging resources links them directly to any changes in the trophic levels below them. This approach is further complicated when considering migratory organisms that rely on several ecosystems which, in the case of trans-Saharan

migrant birds, are often thousands of kilometres apart (Chernetsov 2005; Both *et al.* 2010). So far, this field of research has largely relied on observations and post-hoc interpretation of correlations between climate, behaviour and demographics across the birds' migratory ranges, which have provided important insights about long term trends but, are limited in revealing the causal mechanisms underlying the observed ecological changes. In light of the importance of trophic relationships in influencing demographic change (Pearce-Higgins *et al.* 2010), further insights into the mechanisms driving changes in the population dynamics of a particular species may be revealed by considering the responses of the phenology and availability of its prey species to climate variation, as well as the responses of the focal species itself.

In this study, the mechanisms and consequences of climate-driven changes in the prey resources of a long-distance migrant bird, the Eurasian reed warbler *Acrocephalus scirpaceus* (hereafter 'reed warbler'; Plate 1.1), are assessed using a combination of observational and experimental approaches.

Firstly, the study examines the availability of invertebrate prey groups in the habitats used by breeding and wintering reed warblers, and tests the responses in emergence timing to natural and experimentally manipulated temperature changes (Chapters 2-3). These studies will reveal the relationship between temperature (and other facets of weather) and the availability of invertebrate prey, and indicate the likely effect of projected levels of climate warming on the prey resources of reed warblers in the future. Secondly, the impact of these changes on the reed warblers' body mass regulation, breeding productivity and survival will be tested using experimental manipulations of food availability (Chapters 4-6).



**Plate 1.1.** Breeding (adult female) Eurasian reed warbler at Cardiff Bay Wetland Reserve in July 2014. Photo credit: Peter Howlett



The aim of this introductory chapter is to review and summarise the current literature on the mechanisms and impacts that changes to invertebrate prey populations have on migratory insectivore birds and to provide the justification and organisation of the research described in this thesis.

### *1.1 The effects of climate change on migratory insectivore birds*

There is growing evidence that birds are already adapting to the effects of recent climate change (Chase 2013; Vedder *et al.* 2013). The past thirty years have seen temperate bird species advancing their spring migration and breeding dates (Crick *et al.* 1997; Brown *et al.* 1999; Walther *et al.* 2002; Root *et al.* 2003; Dunn 2004; Both *et al.* 2004; Tryjanowski *et al.* 2005; Sheldon 2010; Crick and Sparks 2010) and exhibiting distribution shifts pole-wards

and to higher altitudes (Pearson *et al.* 2002; Thomas *et al.* 2004; Pimm 2009; Pearce-Higgins *et al.* 2010). There are several mechanisms mediated by climate change that have wide-ranging effects on birds and lead to marked differences in the intensity of impact between regions and species (Mustin *et al.* 2007). For example, evidence from recent studies suggest that climate fluctuations have the potential to affect the availability of prey resources for insectivorous birds (Pearce-Higgins *et al.* 2010; Bradbury *et al.* 2011; Seward *et al.* 2012). Since food supply can limit aspects of survival and fecundity in birds (Martin 1987; Arcese 1989; Hoodless *et al.* 1999; Both and Visser 2005; Studds and Marra 2011; Pearce-Higgins and Bradbury 2011; Seward *et al.* 2012), such changes may represent a key mechanism driving population change.

Despite the potential importance of invertebrate prey limitation for breeding birds, the knock-on effects of climate-mediated changes in prey populations on bird ecology is little studied (Arcese and Smith 1988; Sillett *et al.* 2000; Bayly 2006; Marshall *et al.* 2010). Changes in phenology of prey species have important implications for the timing of energetically-demanding life-history events such as breeding, moulting and migration (Møller and Hobson 2004; Both *et al.* 2010; Pearce-Higgins 2010; Van der Putten *et al.* 2010). Breeding success and nestling development of several species of migratory birds have been shown to depend on synchronising the hatching of chicks with the local peak in invertebrate emergence (Lack 1950; Marshall 1950; Immelmann 1971; Pearce-Higgins and Yalden 2004; Visser *et al.* 2006; Drent 2006). After all, the breeding period requires large quantities of food to support the energetic activities of egg production, incubation and nestling provisioning; it is therefore a period when birds are likely to be strongly responsive to changes in food availability.

An advance (i.e. a shift to earlier timing) in the peak of invertebrate availability (e.g. due to climate warming) reduces the period between the arrival of birds on the breeding grounds (assuming that arrival date does not change) and the optimal breeding date. This is due to the invertebrate abundance curve shifting forward, rather than increasing the length of the emergence period and increasing net abundance, resulting in corresponding declines in invertebrate abundance earlier in the season. The consequences of failure to adapt to such shifts in prey phenology have been well-studied in highly seasonal habitats such as temperate broadleaved woodland (Visser *et al.* 1998; Both *et al.* 2004; Both *et al.* 2006), Arctic tundra (Tulp and Schekkerman 2008) and upland moorland (Pearce-Higgins 2010), in bird species with breeding strategies that rely on close synchrony with short-lasting seasonal peaks in invertebrate availability. In broadleaved woodland, the duration of the invertebrate food peak is limited by the period of edibility of the early leaf buds for caterpillars, which is culminated by the production of chemical defences such as phenolics (Dury *et al.* 1998). The consequences of mismatch include reductions in egg quality (Bolton *et al.* 1992; Ramsay and Houston 1997), clutch size (Illera and Diaz 2006; Preston and Rotenberry 2006), incubation attendance (Eikenaar *et al.* 2003), lower nestling provisioning rate (Both 2010; Bańbura *et al.* 2011), fewer broods (Sanz 2003) and loss of adult body condition (Nagy *et al.* 2007). The resulting changes in breeding productivity are thought to be a major cause of decline among long-distance migrant species, whose departure timing from their wintering grounds is regulated by day length, and hence unrelated to climate variation, limiting their ability to adjust to local breeding conditions (Visser and Both 2005; Sanderson *et al.* 2006; Robinson *et al.* 2009; Both *et al.* 2010). The strength of these impacts varies between species (Sanz 2003; Visser *et al.* 2003; Both *et al.* 2004), between breeding seasons, and may also be influenced by local factors such as predation pressure, competition, and climatic conditions (Dunn *et al.* 2011).

While extensive research has been carried out on food limitation in breeding birds, few studies have investigated experimentally the impacts of changes in food availability on breeding productivity in long-distance migrant passerines, or investigated the different mechanisms by which overall breeding productivity may be altered. The effect of increases in food availability on parental investment in egg quality, clutch size and provisioning rate of nestlings are well-studied in game birds and waterfowl (Boutin 1990; Hoodless *et al.* 1999), but less so in altricial species. Experimentally increasing food availability leads some species to increase egg size (e.g. Eurasian blue tit *Cyanistes caeruleus*: Ramsay and Houston 1997) and in some cases, clutch size (e.g. Canary Islands stonechat *Saxicola dacotiae*: Illera and Diaz 2006; wrenit *Chamaea fasciata*: Preston and Rotenberry 2006), which indicates that the immediate food resources are limiting to both the production and quality of eggs (Nooker *et al.* 2005). Supplementary fed great tit *Parus major* nestlings grew faster than control nestlings (Banbura *et al.* 2011). Greater prey availability for parents and nestlings is therefore likely to be beneficial for nestling growth rates, which could accelerate fledging and thus reduce the period of vulnerability to predation and adverse weather conditions. There is less evidence that nestlings are fed more frequently with higher food availability, as parents are considered to adjust their provisioning rates to local food availability (Svensson and Nilsson 1995; Cook and Hamer 1997; Dewey and Kennedy 2001). Positive associations between clutch size and food availability have been widely observed and confirmed experimentally (Yom-Tov 1974; Dijkstra *et al.* 1982; Illera and Diaz 2006; Preston and Rotenberry 2006). A study by Eikenaar *et al.* (2003) on Australian Reed Warbler *A. australis* found that increased food availability for adults resulted in higher incubation attendance, which reduced the period of incubation and vulnerability to predation. A larger pre-incubation energy reserve ensures maintenance of body condition throughout incubation, reducing foraging requirements and subsequent costs to nest attendance, consequently reducing incubation period, and increasing hatching success (Norberg 1981a; Drent *et al.* 1985; Lifjeld and Slagsvold 1986; Afton and Paulus 1992; Williams 1996). Greater adult

body reserves are also associated with larger chick size; female parents with larger incubatory masses produce fledglings that are larger and in better condition than lighter females (Lifjeld and Slagsfold 1986). Parents in habitats of higher food abundance feed their young at a higher rate than those in habitats of lower food abundance and have a reduced foraging time. These findings indicate that breeding productivity, individual lifetime fitness and population growth may be limited by parental body condition (and ultimately by food availability; Etterson *et al.* 2011).

Adults must balance their investment in any single nesting episode against the increased physiological stress and reduced adult survival incurred by such an investment, to maximise offspring recruitment across the parent's lifespan (Stearns 1992; Alonso-Alvarez *et al.* 2004). The extent to which adults will improve reproductive output and success before it takes its toll on future survival is an important consideration in the likely response to increases in food availability.

The direct consequences of changes to food availability on energetic reserves (stored as body fat and muscle mass) are well-studied in birds and may serve as an important predictor of adult body condition. The direct consequences of food limitation (either by unpredictability or scarcity) include a strategic increase in fat storage as a buffer against starvation (Jenni and Jenni-Eiermann 1987; Ekman and Hake 1990; Bednekoff and Krebs 1995; Witter *et al.* 1995; Gosler 1996; Witter and Swaddle 1997; Cuthill *et al.* 2000) and in extreme food-limited conditions, the loss of stored fat reserves and catabolism of muscle mass (Strong and Sherry 2000). The consequences of experimentally supplemented food can therefore include either decreases (Ratikainen and Wright 2013) or increases (Cucco and Malacarne 1997) in fat storage and muscle mass (Brown and Sherry 2006), depending on the treatment and control conditions.

The associations between prey availability, reproductive success and survival in birds are often cited as key mechanisms by which climate may be capable of driving population change (Martin 1987; Hoodless *et al.* 1999; Both and Visser 2005; Pearce-Higgins *et al.* 2010; Studds and Marra 2011; Fokidis *et al.* 2012; Seward *et al.* 2012). Current predictions of climate change on the breeding grounds in northwest Europe suggest that warmer conditions will occur earlier in the year (Räisänen *et al.* 2004; Rowell 2005), which in temperate wetland habitats may be associated with increases in food availability earlier in the year (Halupka *et al.* 2008). Higher rates of adult survival are associated with years of good environmental breeding conditions, possibly due to reduced levels of the physiological stress which has been shown to increase mortality during subsequent migration or over winter (Alonso-Alvarez *et al.* 2004). Conversely, higher rates of mortality in breeding adult birds are associated with physiological stress during poor environmental conditions (Martin 1987; Williams 1996). Such effects are also likely to be reflected in offspring survival during these years. There is evidence to suggest that birds fledging earlier in the breeding season have higher survival rates than later fledged birds or those hatched during years of poor environmental conditions (Daan *et al.* 1988; Price *et al.* 1988; Møller 1994; Dzus and Clark 1998; Hochachka 1990; Spear and Nur 1994; Verhulst *et al.* 1995). Early fledging may avoid the period of highest nest predation during the middle of the breeding season and give the fledged young a longer period on the breeding grounds, enabling them to gain experience and body reserves, before migration (Perrins 1965; Spear and Nur 1994; Dzus and Clark 1998; McKim-Louder *et al.* 2013).

On the West African wintering grounds, temperatures are predicted to increase and precipitation to decrease over the coming decades (Atkinson *et al.* 2014). This is expected to provide further stress by decreasing the size and quality of suitable habitats where many migrants overwinter, particularly in association with further anthropogenic habitat-loss (Giorgi and Lionello 2008; Zwarts *et al.* 2009).

Across the annual cycle, climate-driven changes to food availability may therefore have the potential to affect breeding performance, recruitment and survival, all of which drive population dynamics.

## 1.2 *Gaps in knowledge*

There is growing evidence that migratory birds are affected by indirect effects of climate-driven changes to habitat quality and food availability (Crick 2004; Pearce-Higgins *et al.* 2010; Seward *et al.* 2013) as well as being affected by climate change directly through the effects of weather. Both short and long-term changes to the abundance and distribution of prey may have a variety of implications for the different stages of the annual cycle for migrant birds. Despite the breadth of studies in this subject, major gaps exist in our knowledge of the effects of climate change on migratory birds; specifically there is a need for:

Gap 1: Consideration of the effects of climate change at multiple trophic levels and how this impacts migratory bird populations (Harrington *et al.* 1999; Van der Putten *et al.* 2010).

Gap 2: Understanding the role of local weather conditions and influence of larger-scale weather systems (e.g. North Atlantic Oscillation or Sahel Precipitation Index) upon the prey resources of birds (Møller *et al.* 2010; Salewski *et al.* 2013).

Gap 3: Testing which traits respond to climate change (e.g. the propensity to exploit temporally abundant food; or to nest earlier in response to better conditions) and why (Møller *et al.* 2004; Møller *et al.* 2010).

Gap 4: Use of experimental approaches rather than descriptive post-hoc interpretations (Møller *et al.* 2004; Møller *et al.* 2010; Pearce-Higgins and Gill 2010; Wingfield *et al.* 2011).

Gap 5: Consideration of climate effects outside the northern temperate breeding areas (Møller *et al.* 2004; Møller *et al.* 2010; Vickery *et al.* 2014).

### 1.3 Study system: *The Phragmites australis* reedbed

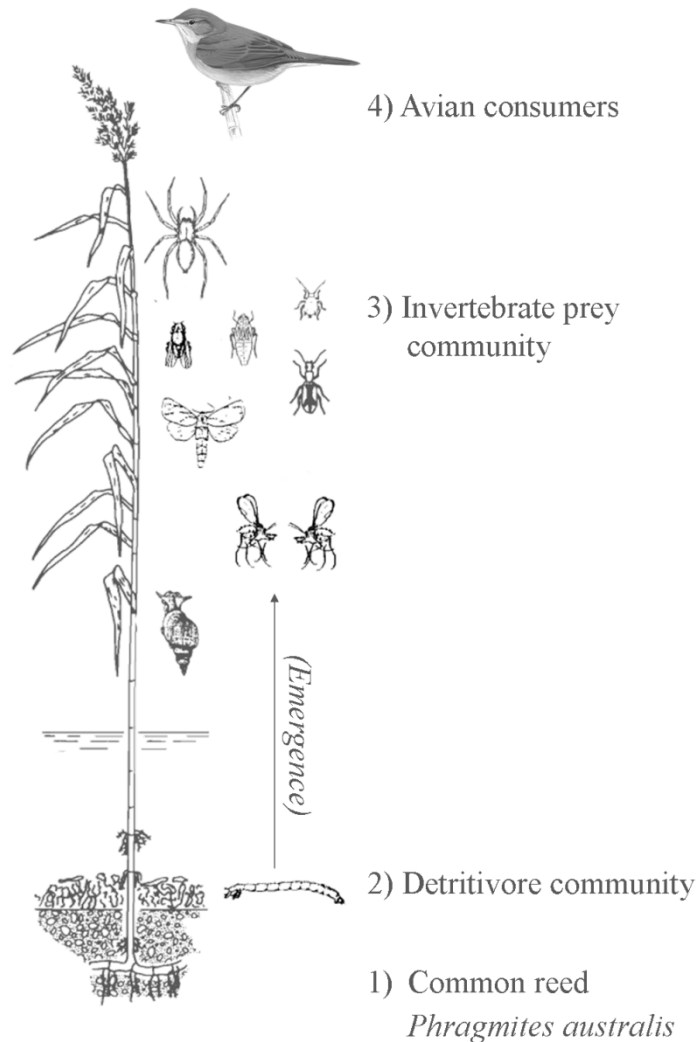
Temperate wetlands are used as breeding habitats by many invertivorous migrant bird species that winter in tropical latitudes (Poulin *et al.* 2002; Zwarts *et al.* 2009). The favourable conditions for breeding in temperate wetlands include long summer days, abundant prey and comparatively low density of interspecific competitors (Alerstam and Lindström 1990; Robinson *et al.* 2009; Newton 2010). Reedbeds are the focus ecosystems for the present study and have been chosen on account of the following characteristics:

1. The relative simplicity of this ecosystem compared to most other ecosystems, makes a multi-trophic level study more tractable.
2. The responsiveness of its dominant plant species, common reed *Phragmites australis*, (hereafter “*Phragmites*”) to changes in temperature, wind, rain and water levels.
3. The biology of the main avian consumer: the reed warbler is well studied, but less is known about how they are affected by changes in the availability of their invertebrate prey.



The focus of the remainder of this literature review is on how climatic variation (primarily elevated temperature and other weather variables), can have cascading impacts across the trophic levels of a relatively simple food chain, comprising the primary plant level (and associated detritus), the invertebrate prey community (including the detritivore community), and its avian consumers (Figure 1.1).

**Figure 1.1.** The primary elements of the reedbed food chain; comprising 1) The dominant plant: *Phragmites australis*; 2) the detritivore community; 3) the invertebrate prey community; and 4) the avian consumers (based on Figure 7a. in Ostendorp (1993)).



Reedbeds and associated marshland habitats often form as the emergent phase of a hydrosere (freshwater sequence of succession) in standing or slow-running water and often form dense, tall stands dominated by *Phragmites* reeds (Jodoin *et al.* 2008; Beemster *et al.* 2010; Kettenring *et al.* 2011). Despite the high productivity of *Phragmites*, which is capable of producing 2 kg/ m<sup>2</sup>/ day (Bedford and Powell 2005; Schmidt *et al.* 2005), very little living plant matter is consumed by herbivorous grazers (Hendricks *et al.* 2011). It is the high

silicate content in *Phragmites* which is considered to be the main deterrent to herbivore attack (Tscharntke 1999). Instead, the invertebrate community obtains most of its basal nutritional resources from benthic algae and detritus (Teal 1962; Tscharntke 1999; Gratton and Denno 2006). The high stem-density (50-200/ m<sup>2</sup>) and fast daily growth rates (e.g. 45 mm/day) of *Phragmites* makes the habitat one of the most productive natural ecosystems in the world (Greenberg and Marra 2005). Reedbeds therefore represent model ecosystems for climate change studies, responding more readily to changes in the environment than less-productive, more seasonal habitats such as temperate deciduous woodlands, Arctic tundra and upland grasslands (Westlake 1963; Engloner 2009).

#### 1.4 *The impacts of climate change on Phragmites; invertebrates and reed warblers*

As a widespread, dominant, economically important plant of wetlands and a pernicious invader outside its native range, *Phragmites* is well-studied (Björk 1967; Haslam 1972a; Clevering and Lissner 1999; Engloner 2009; Wang *et al.* 2013). The tolerance and adaptation of *Phragmites* to a wide range of temperature and soil-water conditions has enabled its prevalence across the world (Haslam 1974; Squires and Vandervalk 1992; Zemlin *et al.* 2000; Pagter *et al.* 2005).

The effects of experimental manipulations of temperature on *Phragmites* growth are well-studied and reviewed by Engloner (2009). The review revealed concurring conclusions from several studies (e.g. Haslam 1974; Oksanen *et al.* 1981; Lee 1990; Raulier *et al.* 2000; Zemlin *et al.* 2000; Warren *et al.* 2010; Lewandowska *et al.* 2011), particularly that increasing temperatures (up to a certain threshold) increases growth and productivity. Haslam (1969; 1971; 1972; 1974) examined responses of other aspects of *Phragmites* biology such as seedling establishment and bud emergence which advanced under small

increases in temperature and drier soil water regimes. Supporting the influence of environmental conditions on reed growth, several other studies have concluded that growth and seasonal productivity is strongly dependent on temperature during either the start or main period of the growing season (Kühl and Kohl, 1992; Zemlin *et al.* 2000). There have, however, been inconsistent findings about the role of temperature on the development of morphological features including the final shoot height, number of inter-nodes (junctions on the stalk between stem sections) and stem diameter (McKee and Richards 1996), and these are also influenced by length of the growing season (Dykyjová and Hradecká 1976; Clevering 1999; Clevering *et al.* 2001; Karunaratne *et al.* 2003; Hansen *et al.* 2007).

An important consideration is the provenance of the *Phragmites* genotypes used in each study, since these may respond differently to environmental changes, due to differences in genetically-determined tolerances. This was addressed by Daniels (1991), in which the growth responses of *Phragmites* grown from seeds and rhizomes from sites with different climatic and soil conditions were found to differ significantly. Further work confirms that growth and other structural characteristics depend both on environment as well as genotype (Koppitz *et al.* 1997; Kühl and Zemlin 2000; Clevering *et al.* 2001; Bastlová *et al.* 2004; Hansen *et al.* 2007). The importance of the environmental and genetically-determined growth responses of *Phragmites* in this investigation is due not to its importance for invertebrates, since the majority of the community does not feed directly upon *Phragmites*, but for the birds that live, forage, roost and nest between its stems. While other vegetation types and habitats are used by reed warblers for these activities during the breeding season, it is *Phragmites* stands that are strongly favoured (Catchpole 1974). While old *Phragmites* stems are used by reed warblers arriving early on their breeding grounds for nest construction, the essential cover and structure of new emergent stems is critical for screening the nest from predators and brood parasites (such as common cuckoo *Cuculus canorus*) as

well as buffering and protecting the nest from wind, sunshine and rainfall (Burger 1985; Moskát and Honza 2000; Batary *et al.* 2004).

The timing of new *Phragmites* shoot emergence and subsequent growth is therefore an important factor in nest initiation in reed warblers (Brown and Davies 1949). Earlier and more rapid reed growth in response to warmer spring temperatures may enable earlier nesting, providing there are sufficient prey numbers available (Schaefer *et al.* 2006; Halupka and Dyrz, 2008; Dyrz and Halupka, 2008).

#### 1.5 *The impacts of climate change on wetland invertebrates as food for reed warblers*

While it is understood that environmental and soil conditions underpin much of the complex variation in reedbed plant communities (Rodwell and Crawley 1995), less is known about the abiotic influences that define the invertebrate community. Reedbeds support a diverse and abundant invertebrate prey community, most of which is dependent on *Phragmites* for one or more stages of their life cycle (Hawke and José, 1996; Tschardtke, 1999). As well as forming the major component of reed warbler diet, this community represents the key link between primary production and the higher trophic levels (Wissinger 1999). The invertebrate community serves important functional roles in wetland ecosystems, including acceleration of benthic detrital decomposition, the release of bound nutrients into solution and the control of host plant species and other invertebrate species (Covich *et al.* 1999; Reed, 2007). *Phragmites* primary production is recycled by a guild of specialist invertebrate detritivores at the mud-surface, feeding on detritus formed by bacterial decomposition of algae and dead emergent macrophytes such as *Phragmites* and bulrush *Typha latifolia* (Cowie *et al.* 1992). In reedbed ecosystems, the larvae of chironomids as well as many other aquatic insects form a major component of the benthic detritivore community (Oliver, 1971).

Following a benthic pupal phase, these insects undergo a metamorphosis into their winged adult form, making a transition from an aquatic to an above-water, semi-terrestrial or terrestrial environment (Walde and Davies, 1984; Reed, 2007). Although these detritivores are important for the economy of the ecosystem by maintaining the flow of energy from the primary producers to the subsequent trophic levels, if they were excluded from such systems, the decomposition rates would be unchanged due to the strength of leaching and microbial pathways (Riley and DeRoia 1989; McArthur *et al.* 1994). Instead the importance of this detritivore community is the consistent emergence of the adult form, providing an abundant prey group for secondary consumers.

A large and growing body of literature has investigated the potential effect of climate change on invertebrates (Kimerle and Anderson 1971; Jacobsen *et al.* 1997; Walther *et al.* 2002; Bale *et al.* 2002; Root *et al.* 2003; Dell *et al.* 2005; Memmott *et al.* 2007; Tylianakis *et al.* 2008; Cornelissen 2011). Although these studies are mostly limited to single trophic-level model systems, they provide important insights into the mechanisms involved and how they drive population dynamics. Not least because of their ectothermy, invertebrates are predicted to be highly sensitive to the effects of rising temperatures (Robinet and Roques 2010; Cornelissen 2011). There is much experimental and observational support for the direct effect of temperature on all stages of pre-adult development in chironomids and other common nematoceran taxa, influencing their hatching success, emergence phenology, metabolism and activity (Ward and Stanford 1979; Sweeney 1984; Iwakuma 1986; Gong *et al.* 2002; P'ery and Garric 2006; Danks 2007). Changes in the availability of invertebrate prey populations are predicted to have important consequences for bird populations (Pearce-Higgins *et al.* 2010)

## 1.6 *Study species: Eurasian reed warbler*

The study will focus on the reed warbler, a long-distance insectivorous migrant passerine that breeds chiefly in mature reedbed habitats of temperate Eurasia (Snow and Perrins, 1998, Procházka *et al.* 2007). Reed warblers are well-studied, not least because they are easily caught in large numbers in mist nets (Bairlein 1998; Leisler *et al.* 2011) but they are also easily manipulated in field experiments (Davies 2011; Stokke *et al.* 2007; Stokke *et al.* 2008). One of the great advantages of studying a well-known species is that long-term databases of breeding data exist which can be compared to test for climate effects (Schaefer *et al.* 2006; Halupka *et al.* 2008; Dyrce and Halupka 2008). The global breeding population is very large (>2,700,000 pairs), with the majority of national population trends stable or increasing (Burfield *et al.* 2004). In the UK, breeding performance has increased, with some suggestion that this may be related to more favourable conditions brought about by improved habitat management practices, recent habitat restoration and creation schemes in Europe and the beneficial response of prey resources to the effects of climate warming (Baillie *et al.* 2013), although the evidence for this is sparse.

Reed warblers reach their northerly range limit in north-west Europe, including the UK, where the synchronised emergence of wetland invertebrates, dominated by Diptera, Hymenoptera and Hemiptera, provide a key food resource for adults and offspring (Catchpole 1973; Hawke and Jose 1996; Grim and Honza 1996; Chernetsov and Manukyan 2000; Grim 2006). The continuous emergence of aquatic insects over the summer months provide a protracted window of invertebrate prey, potentially making reed warblers less likely to suffer the consequences of phenotypic mismatch between the timing of their migration and breeding, and the availability of sufficiently abundant prey to sustain successful breeding (Both 2010; Dunn *et al.* 2011). Reed warblers are thought to feed opportunistically on any invertebrate prey groups available (Cramp 1992), feeding primarily

at middle height (~0.2-2 m) in reeds and the centre of bushes and occasionally on the ground. Breeding adults are typically socially monogamous with both sexes incubating, feeding and brooding the young (Davies and Green 1976; Snow *et al.* 1998). Breeding males maintain small territories (20-100 m<sup>2</sup>) in the breeding season and both adults will travel up to 150 m from their territory to collect food for young (Cramp 1998). Nest initiation is limited by the growth of *Phragmites* as well as the availability of invertebrates, both of which are considered to be influenced by spring temperatures (Brown and Davies 1949; Catchpole 1974; Crick and Sparks 1999; Schaefer *et al.* 2006; Halupka *et al.* 2008).

There is evidence that reed warblers are laying clutches earlier in response to warmer temperatures, thereby extending the length of the breeding period and increasing the likelihood of successful second breeding attempts (Crick and Sparks 1999; Halupka *et al.* 2008). Continental European populations of reed warbler have been reported laying 18 days earlier over the last 33 years, as well as increasing the proportion of second broods from 0-10% in the 1970s and 1980s to 15-30% between 1994 and 2006 (Halupka and Wróblewski 1998; Halupka *et al.* 2008).

Little is known of reed warbler ecology in their wintering grounds. The recoveries (captures of ringed birds) and new captures of reed warblers suggest a wide distribution over the Sahel and Sudan wetlands as well as the occupation of non-wetland habitats such as dry scrub, savannah grassland and saline mangrove (Altenburg and Van Spanje 1989). It is likely that Senegal is an important wintering site for birds from Great Britain (Zwarts *et al.* 2009; Procházka *et al.* 2008). The adverse effect of drought in West Africa is thought to be less severe for reed warblers because they can occupy non-wetland habitats. This is supported by several studies across Europe that show no correlation between long-term population trend and rainfall in the Sahel (Nef *et al.* 1988; Zang and Heckenroth 2001; Weggler 2005; Reif *et*



*al.* 2006; Thaxter *et al.* 2006). However a recent study by Salewski *et al.* (2013) shows some evidence of an association between reed warbler survival and Sahel rainfall values.

## 1.7 Chapter organisation

The current investigation will attempt to address under-studied areas of research into climate effects on migratory bird populations (as specified in *1.3 Gaps in knowledge*) by: considering multiple effects of climate change at different trophic levels (Gap 1), using local and larger-scale weather variation to explain patterns of invertebrate availability (Gap 2), testing the response of traits to climate-change (Gap 3), using an experimental approach (Gap 4), and considering climate effects in the tropical non-breeding areas (Gap 5).

The current study investigated the direct impacts of temperature elevation, as a principle driver of climate change on major intervening trophic links in a *Phragmites*-dominated reedbed system; from primary productivity; the invertebrate prey community; and the response of the avian consumers to these changes. Over the course of the study, the challenge was in isolating the effects of change from the range of confounding seasonal and local variables. The chapters set out in this thesis discuss and investigate some of the potential selection pressures driven by climate change acting on the life history of reedbed warblers breeding in Europe and wintering in the Sahel. Specifically, I tested two core hypotheses;

- 1) “Increases in temperature advance the timing of emergence and growth rate of *Phragmites*, and the timing of emergence and availability of invertebrate prey taxa”.

- 2) “Food availability affects the mass regulation strategy, breeding performance and annual survival rates of reed warblers”.

#### 1.8 *Testing Hypothesis 1:*

A major gap in our understanding of how climate change will affect migratory birds is the lack of information about the 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 invertebrate taxa on which reed warblers feed. The effects of natural and manipulated changes in temperature on *Phragmites* growth and the phenology and abundance of invertebrate prey taxa was assessed using a combination of observational and experimental approaches. In **Chapter 2**, the reedbed invertebrate community was monitored under natural conditions throughout three annual cycles to measure how local and larger-scale weather conditions affect the availability of invertebrate prey resources for breeding reed warblers. These associations were extrapolated using a historical 34-year weather dataset, collected in the same area, to allow assessment of how associations with weather reveal long-term trends in invertebrate prey availability that may have occurred in relation to climate change. In **Chapter 3**, experimental manipulations of temperature were used to explain differences in phenology and growth rate of *Phragmites*, and the emergence and availability of invertebrate prey.

#### 1.9 *Testing Hypothesis 2:*

A series of experimental and observational approaches were used to identify the relationship between prey availability, breeding performance, mass regulation and survival in reed warblers. In **Chapter 4**, a large scale replicated field experiment was undertaken in which the responses of breeding reed warblers to simulated changes in food abundance were

measured. The impacts of changes in food supply were tested on nesting phenology, laying intervals, incubation duration and aspects of reproductive investment and reproductive success. The effects of food availability on mass regulation are tested to reveal evidence of energetic stress or adaptive mass regulation. In **Chapter 5**, I assessed how habitat occupation in the tropical non-breeding grounds affects body condition and how climate change may affect body condition, and hence over winter survival. In **Chapter 6**, I assessed the relative importance of inter-annual variations in weather conditions on the breeding and wintering grounds to the survival of reed warblers breeding in South Wales. In addition, I assessed the impact of changes in food supply at the breeding grounds, on annual survival of juvenile and adult reed warblers. Finally, I bring together all these different types of information in **Chapter 7**, to identify the major traits affected by climate warming, to place these findings within the wider context of climate change impacts on migratory taxa, and to identify future research priorities.

## **Chapter 2**

**Environmental influences on seasonal and short-term variation in potential food resources for breeding Eurasian reed warblers *Acrocephalus scirpaceus***

## Summary

The effects of climate change on the seasonal pattern of invertebrate prey availability may have important consequences for the breeding performance of insectivorous wetland birds. Understanding the influence of short-term (weekly) weather variation on invertebrate phenology, availability and activity is an essential component of understanding and predicting the short- and longer-term consequences of climate change. This study tests the hypothesis that local weather conditions determine both short-term (weekly) and longer term (seasonal and inter-annual) patterns of wetland invertebrate availability by collecting invertebrate activity-density data in a wetland in South Wales over three years and modelling the observed patterns using the local weather measurements air temperature, wind speed and rainfall as predictors. The analysis revealed strong variations in invertebrate availability, particularly among Diptera, in relation to mean air temperature, wind and rain. Chironomidae were the most abundant taxa and showed a strong response to air temperature in their patterns of activity-density. Statistical models were used to “hindcast” invertebrate availability using a local weather dataset spanning 34 years (1980-2013). The hindcasted invertebrate activity-density showed an advance in the date at which a measure of invertebrate activity level was reached (4.8 days earlier over the 34 year period). The threshold ‘growing degree-days’ required for the emergence of two common species of chironomid (*Paratanytarsus grimmii* and *Glyptotendipes paripes*) were reached 12.6 and 18.8 days earlier, respectively, over the 34 year period. The results provide conceptual and empirical support for the influence of rising temperatures on the timing of invertebrate availability in temperate wetland ecosystems. In particular, these patterns indicate that climate-driven increases in temperature earlier in the spring are likely to result in corresponding earlier increases in invertebrate abundance. Such effects on prey availability early in the bird breeding season may affect the breeding performance of a consumer of reedbed invertebrates, the Eurasian reed warbler *Acrocephalus scirpaceus*.

## 2.1 Introduction

Temperate wetlands are used as breeding habitats by many insectivore migrant bird species that winter in tropical latitudes (Poulin *et al.* 2002; Zwarts *et al.* 2009). The favourable conditions for breeding in temperate wetlands include long summer days, abundant prey and comparatively low density of interspecific competitors and are sought at the cost of long-distance migration (Alerstam and Lindström 1990; Robinson *et al.* 2009; Newton 2010). Breeding success and nestling development of several species of migratory birds have been shown to depend on synchronising the hatching of chicks with the local peak in invertebrate emergence (Lack 1950; Pearce-Higgins and Yalden 2004; Visser *et al.* 2006). An advance in the peak of invertebrate availability (e.g. due to climate warming) reduces the period between the arrival of birds on the breeding grounds (assuming that arrival date does not change) and the optimal breeding date. The consequences of failure to adapt to such shifts in prey emergence dates have been well-studied in highly seasonal habitats such as broadleaved woodland, Arctic tundra and upland moorland, in bird species with breeding strategies that rely on close synchrony with short-lasting seasonal peaks in invertebrate availability (e.g. great tit *Parus major*: Visser *et al.* 1998; European pied flycatcher *Ficedula hypoleuca*: Both *et al.* 2004; Both *et al.* 2006; red knot *Calidris canutus*: Tulp and Schekkerman 2008; European golden plover *Pluvialis apricaria*: Pearce-Higgins 2010). Such consequences include reductions to egg quality (Bolton *et al.* 1992; Ramsay and Houston 1997); clutch size (Illera and Diaz 2006; Preston and Rotenberry 2006), lower rates of nestling development (Both 2010), nestling starvation (Visser *et al.* 1998; Visser *et al.* 2003; Both *et al.* 2004; Both *et al.* 2006) and fewer broods (Sanz 2003). The resulting changes in breeding productivity are considered to be a major cause of decline among long-distance migrant species in particular, whose departure from their wintering grounds is regulated by day-length rather than climate, is limiting their ability to adjust to local breeding conditions (Visser and Both 2005; Sanderson *et al.* 2006; Robinson *et al.* 2009; Both *et al.* 2010).

By contrast, breeding birds occupying less seasonal habitats such as *Phragmites australis*-dominated wetlands, where the continuous emergence of aquatic insects over the summer months provide a long window of invertebrate prey emergence, are less likely to suffer the consequences of phenotypic mismatch (Both 2010; Dunn *et al.* 2011). Instead, wetland breeding birds such as Eurasian reed warblers *Acrocephalus scirpaceus* (hereafter ‘reed warblers’) have a relatively long breeding window (between May and July) as a consequence of the protracted emergence of invertebrate prey in wetlands (Halupka *et al.* 2008a). This long period of invertebrate emergence is attributed to the extensive volume of dead plant material available to benthic detritivore invertebrate larvae such as those of Chironomidae, the emerged adults of which form the major component of the prey available to reed warblers (Catchpole 1974; Bibby and Green 1976; Bibby and Thomas 1984; Hoi *et al.* 1995; Grim and Honza 1996; Chernetsov and Manukyan 1999). The starting date of the reed warbler breeding period is considered to be limited by the growth of their nesting plant *Phragmites australis* (hereafter ‘*Phragmites*’) as well as the availability of invertebrates in the spring, both of which are considered to be influenced by spring temperatures (Schaefer *et al.* 2006; Halupka *et al.* 2008a). Since reed warblers typically arrive several weeks in advance of these resources becoming suitable for breeding, any climate-driven advances in their suitability may instead represent an opportunity for reed warblers to breed sooner. The benefits of earlier nesting include earlier nest completion, which has been associated with higher rates of first brood survival (Daan *et al.* 1988; Price *et al.* 1988; Møller 1989; McKim-Louder *et al.* 2013) and greater chances of raising a second brood within the window of high prey availability (Schaefer *et al.* 2006; Halupka *et al.* 2008). Although reedbeds provide a broad window of high prey availability, short-term variations in weather such as heavy rainfall, high winds or droughts have been shown to reduce chick survival (Dyrce *et al.* 1980; Borowiec 1994; Halupka and Wróblewski 1998; Honza *et al.* 1998).

Much experimental and observational research provides support for a direct effect of temperature on all stages of pre-adult development in chironomids and other common nematoceran taxa, influencing their hatching success, emergence phenology, metabolism and activity (Ward and Stanford 1979; Sweeney 1984; Iwakuma 1986; Gong *et al.* 2002; P'ery and Garric 2006; Danks, 2007). Small increases in temperature have been shown to shorten the overall duration of the larval stage by increasing rates of feeding, assimilation and respiration (P'ery and Garric 2006; Eggermont and Heiri 2012). The overall development time required for eggs to develop into emerged adults is determined by the length of time above a critical developmental temperature threshold following winter diapause (i.e. the 'growing degree day' (GDD); Pruess 1983). The timing of adult emergence has the potential to advance if the number of GDDs increases early in the year as a result of warmer spring temperatures (Vannote and Sweeney 1980; Gillooly and Dodson 2000; Nesterovitch and Zwick 2003; Lee *et al.* 2008). Shorter development periods and earlier emergence have the potential to increase the number of invertebrate generations produced per year (Eggermont and Heiri 2012). However, the degree of voltinism may differ spatially in a wetland site where there is a water depth gradient, in which invertebrate populations inhabiting the warmer shallower waters develop faster, emerge earlier and produce more generations than those inhabiting the cooler deeper waters (Jonasson 1965; Maitland *et al.* 1972; Iwakuma 1986).

As well as affecting the timing of emergence and density of invertebrate populations, weather factors such as air temperature, wind and rain determine the activity of invertebrates, which represents their availability to birds (P'ery and Garric 2006). Warmer air temperatures are associated with greater levels of invertebrate activity, particularly in flight, whereas cooler air temperatures, high winds and rainfall are associated with lower activity and retreat into sheltered recesses (such as *Phragmites* leaf sheaths), where they are



less available to foraging birds (Ward and Stanford 1979; Sweeney 1984; Huryn and Wallace 1986; Stites and Benke 1989; Walther *et al.* 2006).

Nevertheless, as with other ecosystems, the effects of density-dependent population processes within reedbeds, such as competition from -and predation and parasitism by- other invertebrates, can buffer temperature-driven increases in invertebrate population processes, so that overall invertebrate availability remains relatively stable (Walde and Davies 1984; Ramirez 2008). Indeed, species-specific competitors, parasitoids, predators and pathogens are integral parts of the reedbed ecosystem and are likely to exhibit their own phenological and demographic responses to temperature, together with– or independently of- their hosts, competitors and prey (Davis *et al.* 1998; Bale *et al.* 2002). The pattern of highly synchronized emergence of aquatic insects is considered to maximise their mating success while minimizing individual predation risk through a brief saturation (“swamping”) of the predator community (Davies 1984; Ramirez 2008; Eggermont and Heiri 2012). Temperature-induced shifts in the timing of emergence may be expected to alter these ecological processes.

In the current study, the hypothesis is tested that air temperature, rainfall and wind speed can each determine short-term, seasonal and between-year availability patterns of wetland invertebrates. In particular, the relationship between the availability (measured as ‘activity-density’, representing a combination of the organisms’ activity level and population density) of wetland invertebrates and weather variables is examined to consider the potential impact of changing climate on this important food source for breeding birds. Since the present study is ultimately concerned with the availability of invertebrate prey for generalist-foraging warblers, a higher-taxon (Order/Family level) approach is used. The patterns are analysed within and between years, based on data collected in a reedbed in South Wales, over three

annual cycles. To understand how short-term effects of weather might be translated into long term trends, statistical models derived from this 3-year period were used to “hindcast” (i.e. retrospectively predict) the timing of historical prey peaks, using real weather parameters from a 34 year weather dataset collected in the same area. These hindcasted values were used to investigate inter-annual variability and long-term trends in invertebrate activity-density that may have occurred in relation to climate change. Historical GDDs were calculated for several species of chironomid known to be present at the study site, to assess whether the timing of emergence is likely to have advanced over the 34-year period due to the minimum GDD value required for development being reached progressively earlier in the year.

## 2.2 Methods

### 2.2.1 Study site

Invertebrate samples and weather data were collected and measured weekly across 147 weeks (between November 2011 and August 2014) at Cardiff Bay Wetland Reserve (CBWR) on the southern edge of the city of Cardiff, Wales, UK (51° 27' 32'' N, 3° 10' 11'' W). The habitat consists of large freshwater pools fringed by dense stands of *Phragmites* interspersed with isolated willow *Salix sp.*, and alder *Alnus glutinosa*. Adjacent terrestrial habitats include semi-natural grassland (dominated by couch grass *Elymus repens*, tall ruderal herbs including rosebay willowherb *Chamerion angustifolium*, and nettle *Urtica dioica*, and dense willow, alder and bramble *Rubus fruticosus* agg. scrub habitat. The site is approximately four hectares in area and supports populations of typical breeding wetland insectivore passerines including reed warbler, sedge warbler *A. schoenobaenus*, Cetti's warbler *Cettia cetti* and reed bunting *Emberiza schoeniclus*.

### 2.2.2 Weather variables

Air temperature, solar radiation, wind speed and rainfall data were collected every 15 minutes by an automated weather station (Davis Instruments Vantage Pro 2, Hayward CA), located 750m from the study site for the duration of the study. On-site water temperature was recorded hourly by *in situ* temperature data loggers (Solinst Level logger Model 3001). A GDD value was calculated for each week, based on a standardised general invertebrate development base temperature of 5°C, as recommended by Pruess (1983). These variables were summarised into weekly averages, with the exception of rainfall and GDD, which are presented as cumulative totals for the week. Weather data (daily means for air temperature, rainfall and wind speed) from Cardiff Bute Park Weather Station (located 2.95 km from the

study site) for the years 1980-2013 were obtained through the UK Meteorological Office (<http://www.metoffice.gov.uk/>).

### 2.2.3 *Invertebrate activity-density*

Although reed warblers feed on a wide variety of organisms, the majority of their prey taxa are represented by Diptera (Davies and Green 1976; Grim and Honza 1996; Grim 2006; King *et al.* 2015). Therefore rather than ensuring that every available prey species is represented in the sampling, the following methodologies provide a standardised means for representing an index of invertebrate prey availability (in terms of “activity-density”) optimised for Diptera. Terrestrial invertebrate samples were collected using double-sided yellow (dry-stick) invertebrate traps (Oecos, UK; <http://www.oecos.co.uk/dry%20stick.htm>). This is a standard technique for studying and monitoring activity-density of Diptera (Black and Krafur 1985; Hogsette *et al.* 1993; Goulson *et al.* 2005). Traps were hung at 1.0-1.5 m above ground level, attached to sticks, reed stems or shrubbery. Each trap was encased in a 10mm wire mesh cage to prevent trapping of small birds, mammals and reptiles while allowing free access to invertebrates<sup>1</sup>. Eight traps were deployed per week, between 12 November 2011 and 6 August 2014. Trap positions were selected to represent the typical range of foraging habitats used by reed warblers, including dense *Phragmites*, reedbed edge, adjacent to deep and shallow water, and mixed scrub. These positions were maintained for the duration of the study. In 2012 the traps measured 10x10cm, but in 2013 and 2014 trap size was reduced to 5x10cm; trap size was taken into account in subsequent analyses. On collection, the traps from both sites were wrapped with clear plastic film for returning to the laboratory, and replaced with new traps in each sampling location. The traps were inspected

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<sup>1</sup> A preliminary study confirmed the presence of the wire mesh cages to have no significant effect on the level of invertebrate activity recorded.

using a 10x hand lens or binocular dissecting microscope (Brunel; 7x- 45x magnification) where necessary. The following taxa were identified to Order level: Araneae (spiders), Coleoptera (beetles), Dermaptera (earwigs), Hemiptera (bugs), Hymenoptera (sawflies and wasps), Lepidoptera (moths and butterflies), Megaloptera (alderflies), Thysanoptera (thrips), Odonata (dragonflies and damselflies) and Psocoptera (barklice). As the most abundant prey Order, Diptera were identified to Family level, including Chironomidae, Culicidae, Dixidae, Mycetophilidae, Psychodidae, Sciaridae, Tipulidae, Trichoceridae, Muscidae and Tachinidae using Tilling (1987), Unwin (1981) and Watson and Dallwitz (2003).

#### 2.2.4 *Statistical analyses*

This study monitors the composition and activity-density of wetland invertebrates over 147 weeks and tests the effects of weather variables (independent variables) on invertebrate activity-density (dependent variable). These effects were investigated using the statistical package R, version 3.1.0 (R Development Core Team, 2013) fitting general linear models (GLMs), generalized linear mixed models (GLMMs), generalized additive models (GAMs) and generalized additive mixed models (GAMMs) using the R packages ‘mgcv’ (Wood 2011), ‘lme4’ (Bates *et al.* 2013) and “nlme” (Pinheiro *et al.* 2013). Candidate models were compared and reduced using the Akaike’s Information Criterion adjusted for small sample sizes (AIC<sub>c</sub>; Burnham and Anderson 2004) to identify the most parsimonious model(s).

#### 2.2.5 *Seasonal and weather-related variation in invertebrate activity-density*

The numbers of invertebrates caught on each sticky trap collected weekly, represent an integrated measure of invertebrate activity and population density levels (‘activity-density’) and serve as a proxy for the magnitude of the ecological processes influencing prey availability to reedbed warblers. Generalized additive mixed models (GAMMs; with

negative-binomial error family and log link function) were used to explain variation in weekly activity-density with the fixed effects of mean air temperature, mean water temperature, total rainfall, mean wind speed, mean solar radiation and mean dew point, year (i.e. “2012”, “2013” or “2014”), and all two way interaction terms (in the full candidate model). These parameters represent the variation in capture rate due to factors which vary over short timescales (i.e. activity). The effect of trap size was controlled for in the model by also including a trap size parameter in the fixed effects. The parameter of date (i.e. week number) is represented as a splined (non-linear) predictor characterising the longer-term, ‘seasonal’ pattern of availability (Hastie and Tibshirani 1990), around which local weather variables may influence week-to-week variation in activity-density. Trap identity was used as a random term to explain spatial and habitat-related differences in activity-density across the study site. On the basis that prey availability may be limiting to the timing of egg laying in birds (Dunn 2004), a ‘minimum prey level’ required for reed warbler breeding attempts to be initiated was estimated by calculating the mean totals of all invertebrate traps during the weeks of the reed warblers’ first egg dates in 2012, 2013 and 2014.

#### 2.2.6 *Hindcasting activity-density using historical weather data*

Data from the 147 weeks were used to fit one model describing invertebrate availability with the same variables used in the GAMM analysis (see 2.2.5 *Seasonal and weather-related variation in invertebrate activity-density*) excluding wind speed, for which data were not available between 1980 and 2006. Using this model, the availability of invertebrates for the years 1980 – 2014 were predicted on the basis of the measured weather data. Because ‘year’ effects cannot be extrapolated outside the sampling period, the mean of the year effects for the four sampling years were used in the predictions. The year effect determines variation in overall population level between years, but not the seasonal patterns within years.

The dates on which the estimated minimum prey activity-density for reed warbler breeding initiation was reached, based on the invertebrate capture predictions for each hypothetical trap on each week of the years between 1980 and 2006 were analysed for an overall trend, using a generalized additive model (GAM) using year as a splined (non-linear) predictor and the North Atlantic Oscillation (NAO) index value as a term to explain additional variation as a result of large-scale climatic fluctuations (Hurrell and Trenberth 2010).

#### 2.2.7 Growing degree days GDD

Although invertebrates were either identified to the level of ‘family’ or ‘order’ in the present study, for the purposes of understanding the biological implications of warming spring temperatures, two species of chironomid (considered likely to be present in the diet of reed warblers at the CBWR study site, by a separate genetic analysis, see King et al. 2015) were selected for a study of their growing degree day (GDD) responses to observed temperature variations. *Paratanytarsus grimmii* and *Glyptotendipes paripes* are two species, whose GDDs were calculated using the averaging method by subtracting the species-specific minimum development temperature threshold (MDTT) (*C. grimmii*: 7.9°C (Olsen et al. 2003); *G. paripes*: 9°C (Lobinske et al. 2002) from the mean of minimum (MIN) and maximum (MAX) temperature for each day (Nugent 2005):

$$\left[ \frac{MAX+MIN}{2} \right] - MDTT.$$

The dates on which the developmental requirement for each of these species (294 GDD for *C. grimmii*) and (717 GDD for *G. paripes*) were achieved in each year for the period between 1985 and 2014 (based on historical daily maximum and minimum daily temperatures) were estimated and compared. The theoretical maximum number of generations for these species each year was then estimated by dividing the accumulated maximum GDD for each year by the required developmental GDD from egg to adult. The

trend of advancing GDD value and number of generations with year were analysed initially using GAMs (to test for non-linearity) and GLMs (where GAMs revealed no support for non-linearity).

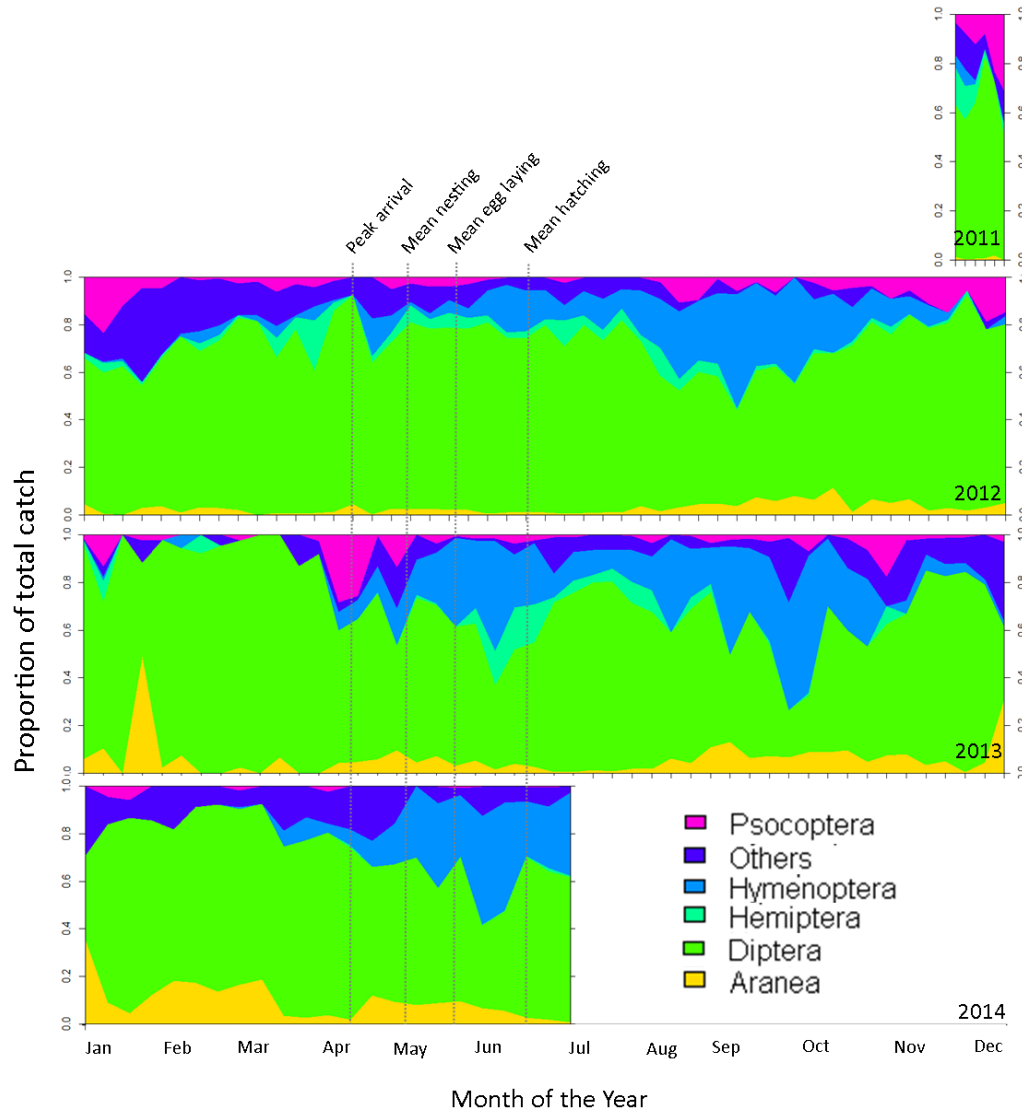
## 2.3 Results

### 2.3.1 *Invertebrate community composition*

Invertebrate monitoring revealed a high proportion of Diptera (mean proportion calculated across all individual weekly samples from each trap location =  $67.8\% \pm 1.5\%$ ) followed by Hymenoptera ( $11.1\% \pm 1.2\%$ ), Aranea ( $5.1\% \pm 0.6\%$ ), Psocoptera ( $4.4\% \pm 0.6\%$ ), Hemiptera ( $2.9\% \pm 0.4\%$ ), unknown groups ( $4.2\% \pm 0.4\%$ ; unidentifiable due to incomplete specimens) and several other orders including Odonata, Lepidoptera, Trichoptera, Collembola, Coleoptera, Thysanoptera, Dermaptera and Megaloptera which each made up less than 1% of the total number of individuals sampled (Figure 2.1). Of the Diptera, Chironomidae represented  $54.6\% \pm 0.9\%$ , followed by Sciaridae ( $10.9\% \pm 0.2\%$ ), Psychodidae ( $8.3\% \pm 0.2\%$ ), Mycetophilidae ( $3.0\% \pm 0.1\%$ ), Dixidae ( $1.8\% \pm 0.1\%$ ), and nine other Diptera families ( $21.5\% \pm 2.2\%$ ).

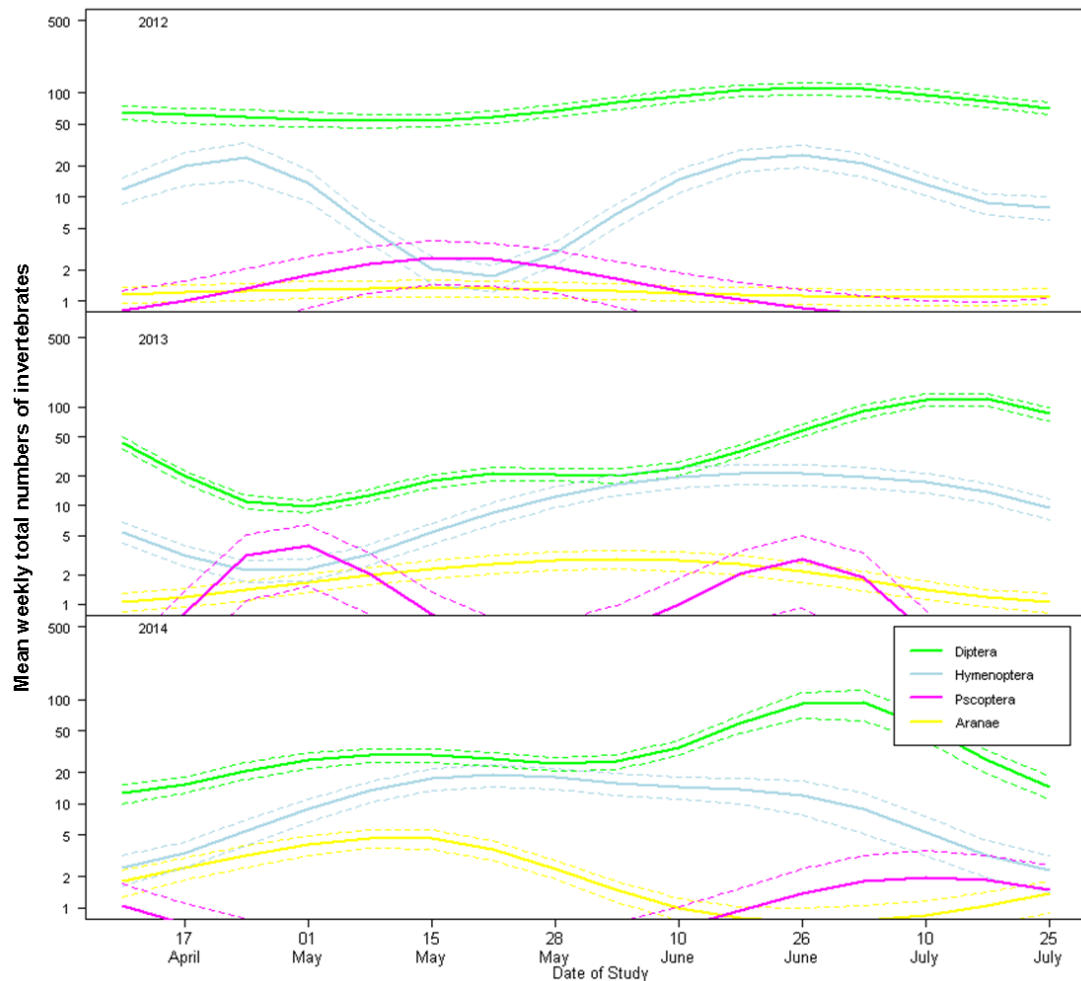


**Figure 2.1.** Stacked area plots of the invertebrate orders appearing in capture samples throughout the study period in Cardiff Bay Wetland Reserve 2011-2014, with the timing of typical reed warbler breeding events highlighted (based on data from Chapter 4).



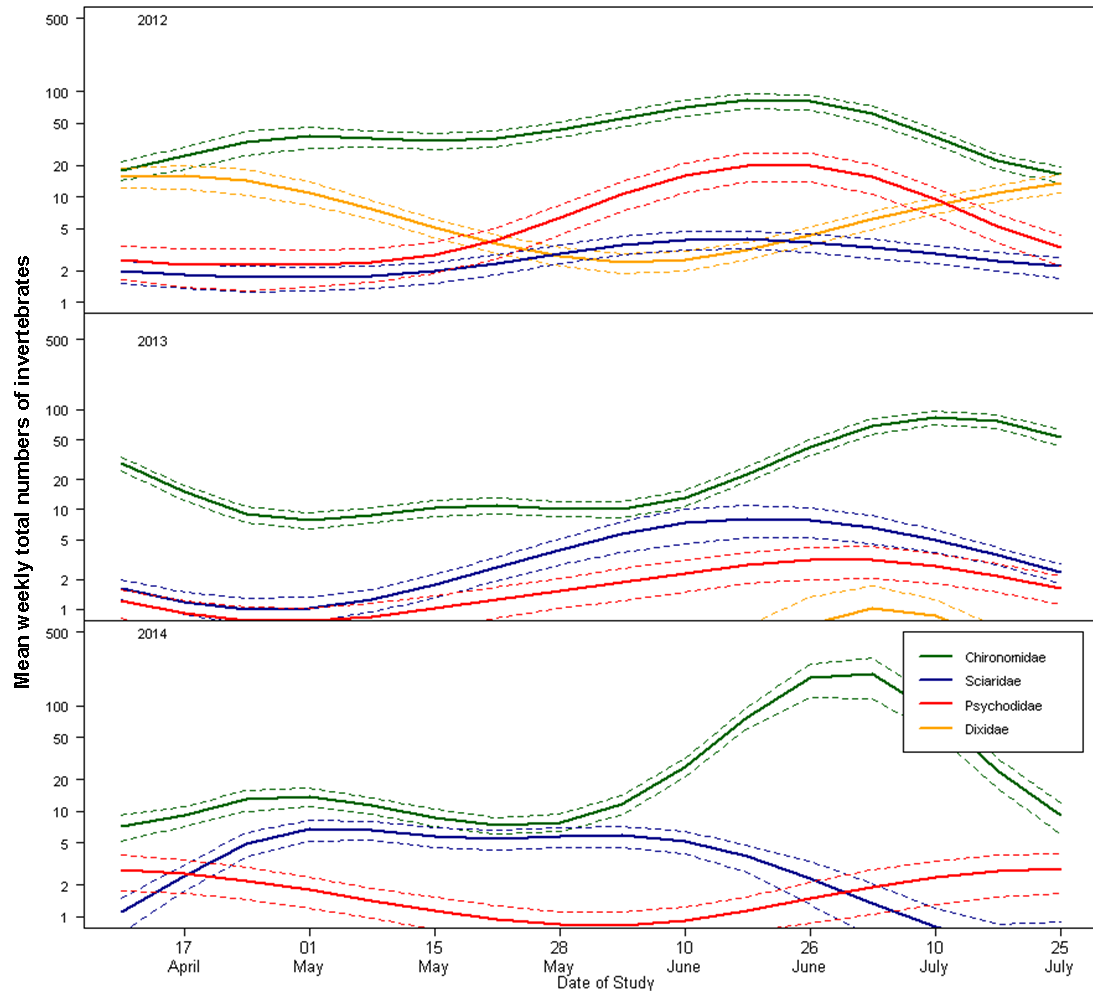
During the reed warbler breeding season (between April and July), Diptera maintain a relatively high and stable activity-density level from mid-April, reaching maxima between late June and July (Figure 2.2). The other more-abundant orders, Hymenoptera, Psocoptera and Aranea, show more variability in their activity-density between years.

**Figure 2.2.** Mean weekly numbers of the most abundant invertebrate orders (Diptera, Hymenoptera, Psocoptera and Aranea) featuring in invertebrate captures in Cardiff Bay Wetland Reserve in 2012-2014 during the main reed warbler breeding season (April-July). The dotted lines represent the standard errors of the means for each order.



Within Diptera, Chironomidae maintain the highest activity-density, reaching maxima in late June-July (Figure 2.3). With the exception of Dixidae, the other two abundant Dipteran families, Sciaridae and Psychodidae show a general pattern of increase between April and late June.

**Figure 2.3.** Mean weekly numbers of the most abundant families within Diptera (Chironomidae, Sciaridae, Psychodidae and Dixidae) featuring in invertebrate captures in Cardiff Bay Wetland Reserve in 2012-2014 during the main reed warbler breeding season (April-July). The dotted lines represent standard errors of the means for each family.

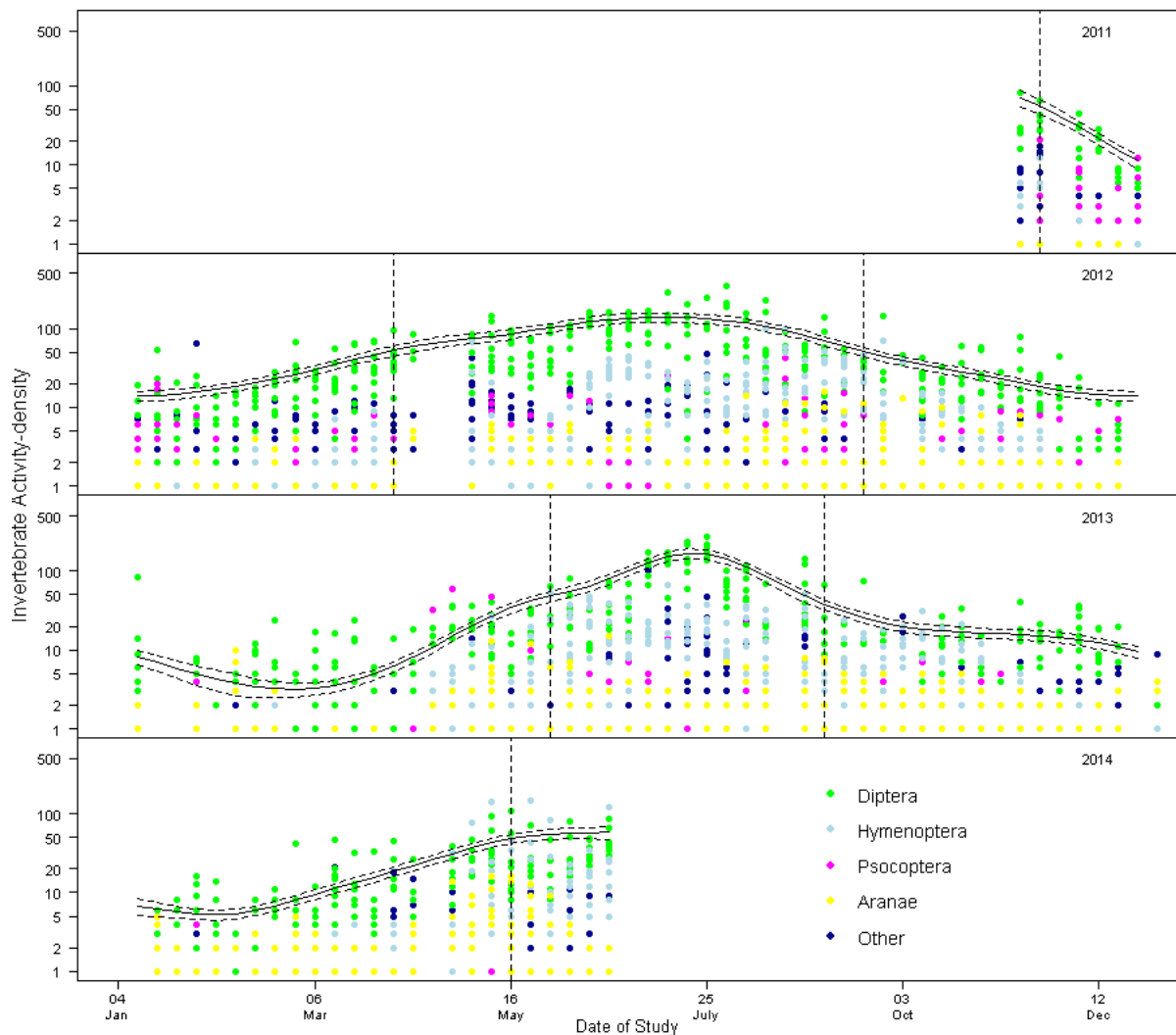


### 2.3.2 Seasonal and weather-related variation in invertebrate activity-density

There was a significant non-linear association between weekly activity-density and capture date in all years (GAMM: **2011**:  $F_{1,402,5}=1.359$   $P=0.009$ ; **2012**:  $F_{4,727,10}=10.106$   $P<0.0001$ ; **2013**:  $F_{7,215,10}=13.739$   $P<0.0001$ ; **2014**:  $F_{2,026,6}=2.525$   $P=0.0002$ ; Figure 2.4). In addition to this seasonal pattern, weekly mean air temperature, wind speed, rain and cumulative GDD values were all significant predictors of variation in activity-density (Table 2.1; Figure 2.5

and 2.6). Solar-radiation, water temperature and dew point did not improve the fit of the model and were excluded from the analysis.

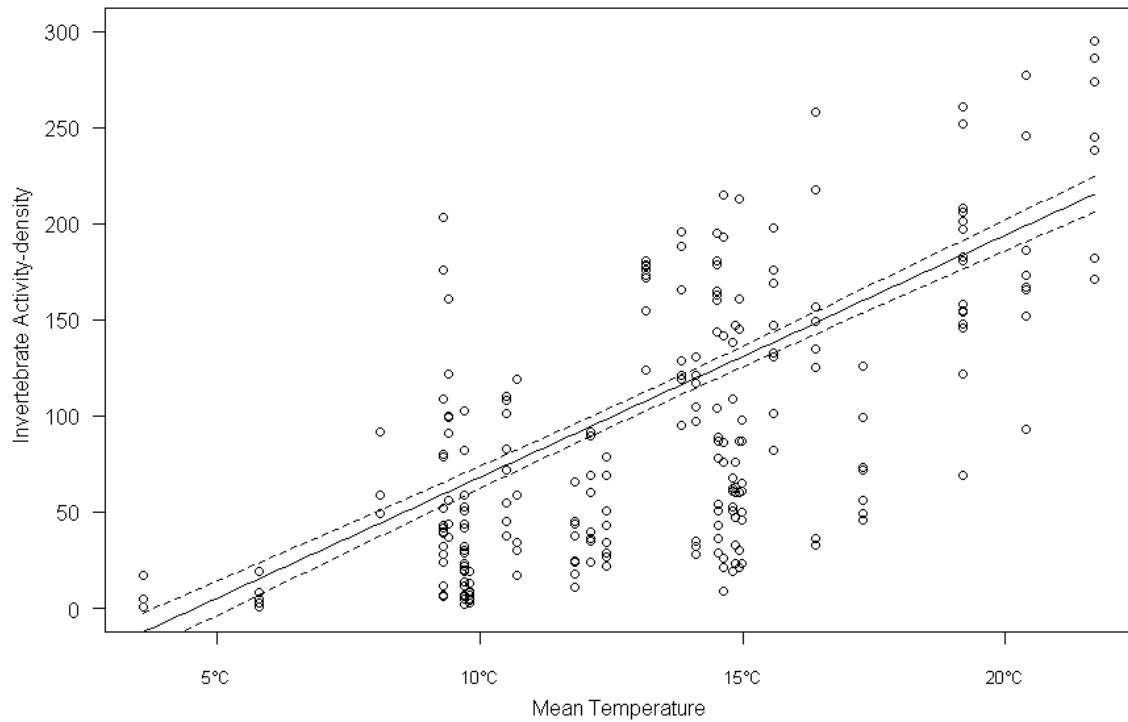
**Figure 2.4.** Intra- and inter-annual changes in mean total invertebrate numbers for 2011 to 2014 at Cardiff Bay Wetland Reserve. The individual points represent the total numbers of invertebrates in the main orders and dotted lines either side of the solid line represent the standard error of the total mean. The vertical lines indicate the period when the ‘minimum prey level’ required for breeding to begin (65.75 individuals per small-sized trap  $\pm 16.32$ ) was first and last recorded in each year.



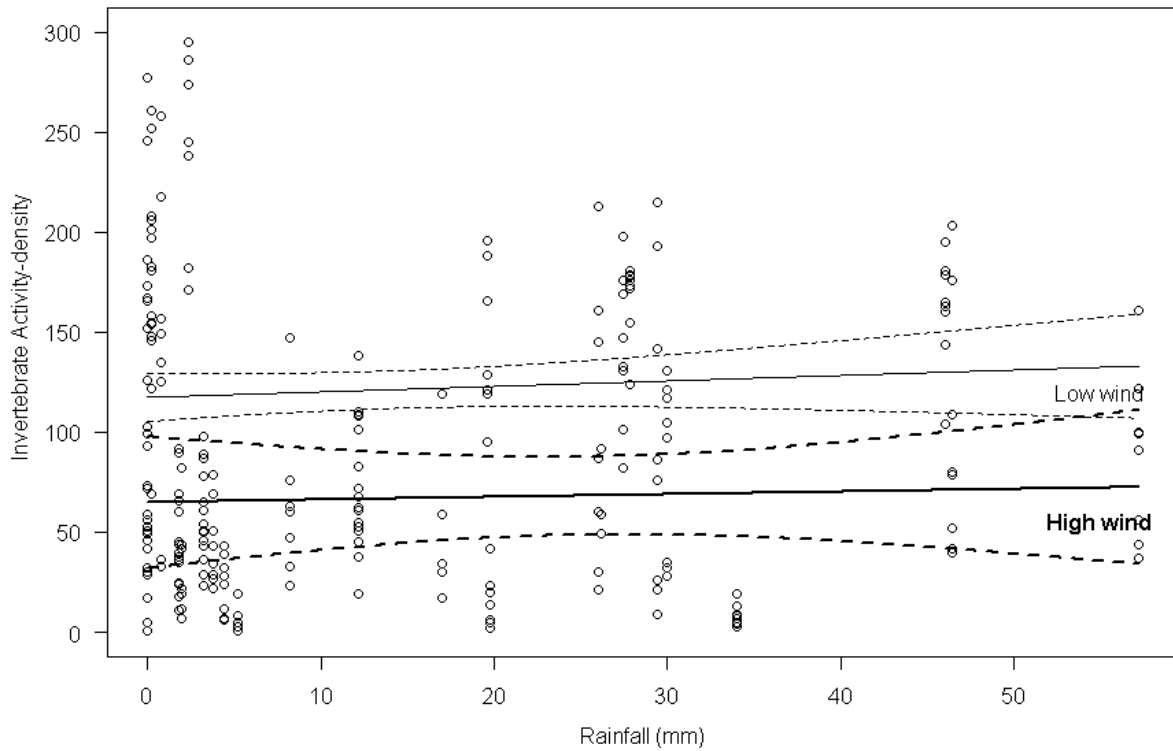
**Table 2.1.** GAMM analysis of invertebrate activity-density at CBWR 2011-2014 in relation to weekly weather measurements, controlling statistically for the seasonal pattern of activity-density (as a non-linear predictor: “Week”) and the effect of trap size. The intercept value is  $1.545 \pm 0.270$  and represents the predicted invertebrate activity-density measure when all independent variables have a value of zero.

Parameter	Estimate $\pm$ SE	<i>F</i>	<i>d.f.</i>	<i>P</i>
<b>Air temperature</b>	<b><math>0.129 \pm 0.017</math></b>	<b>58.383</b>	<b>876</b>	<b>&lt;0.001</b>
Wind speed	$-0.024 \pm 0.015$	2.394	876	0.122
<b>Rain</b>	<b><math>0.023 \pm 0.009</math></b>	<b>6.891</b>	<b>876</b>	<b>0.008</b>
<b>GDD</b>	<b><math>0.0001 \pm 0.001</math></b>	<b>4.191</b>	<b>876</b>	<b>0.041</b>
<b>Wind Speed: Rain</b>	<b><math>-0.002 \pm 0.001</math></b>	<b>13.732</b>	<b>876</b>	<b>&lt;0.001</b>
Air temp: Rain	$-0.0001 \pm 0.001$	0.061	876	0.804
Week	n.a.	14.46	6.724	<0.0001

**Figure 2.5.** The association of mean air temperature with weekly invertebrate activity-density for Cardiff Bay Wetland Reserve 2011-2014. The fitted line ( $\pm$  SE) was predicted using the GAMM in Table 2.1, controlling statistically for seasonal pattern (“Week”), trap size, wind speed and rainfall.



**Figure 2.6.** The interacting association between wind speed and rainfall with invertebrate activity-density, for Cardiff Bay Wetland Reserve 2011-2014. The fitted lines ( $\pm$  SE) for the rainfall effect on activity-density under observed high (18.6 mph) and low (4.48 mph) wind conditions were predicted using the GAMM in Table 2.1, controlling statistically for seasonal pattern (“Week”), trap size and air temperature.

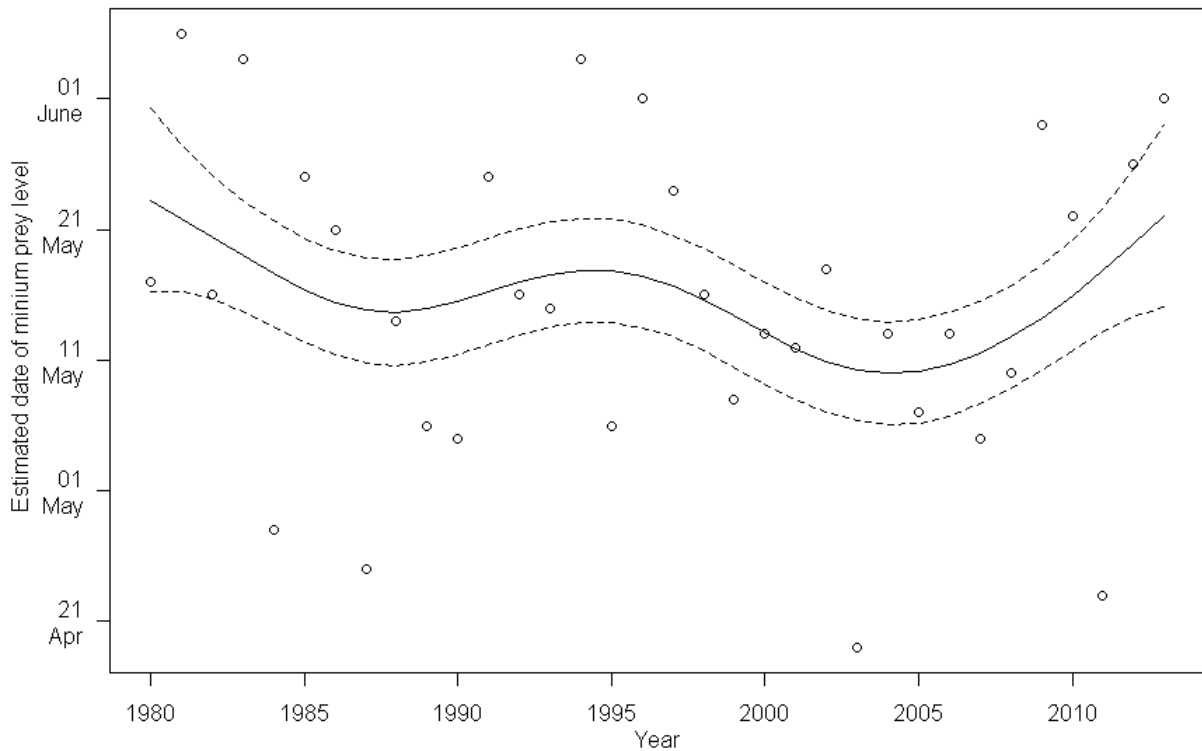


### 2.3.3 Hindcasting activity-density using historical weather data

For the years in which invertebrate availability was measured, the fitted values (“hindcasted” from the GAMM model) were correlated with the actual (observed) values (Pearson’s  $r$  correlations of +0.59 in 2012 and +0.64 in 2013). The ‘minimum prey level’ required for reed warbler breeding, generated from the mean prey activity-density recorded during the date of the first reed warbler egg during 2012 (8 May), 2013 (18 May) and 2014 (8 May), was  $65.75 \pm 16.32$  items per trap. The estimated dates of ‘minimum prey level’ were analysed in a GAM model using “Year” as a non-linear term ( $F_{3.774,6.761}=1.058$ ,  $P=0.399$ ;

Figure 2.7). The model was not improved by including the North Atlantic Oscillation NOA index.

**Figure 2.7.** Hindcasted dates of minimum invertebrate availability for breeding reed warblers for each year between 1980 and 2013 with GAM fitted line ( $\pm$  SE; the k-value chosen to minimise AIC).

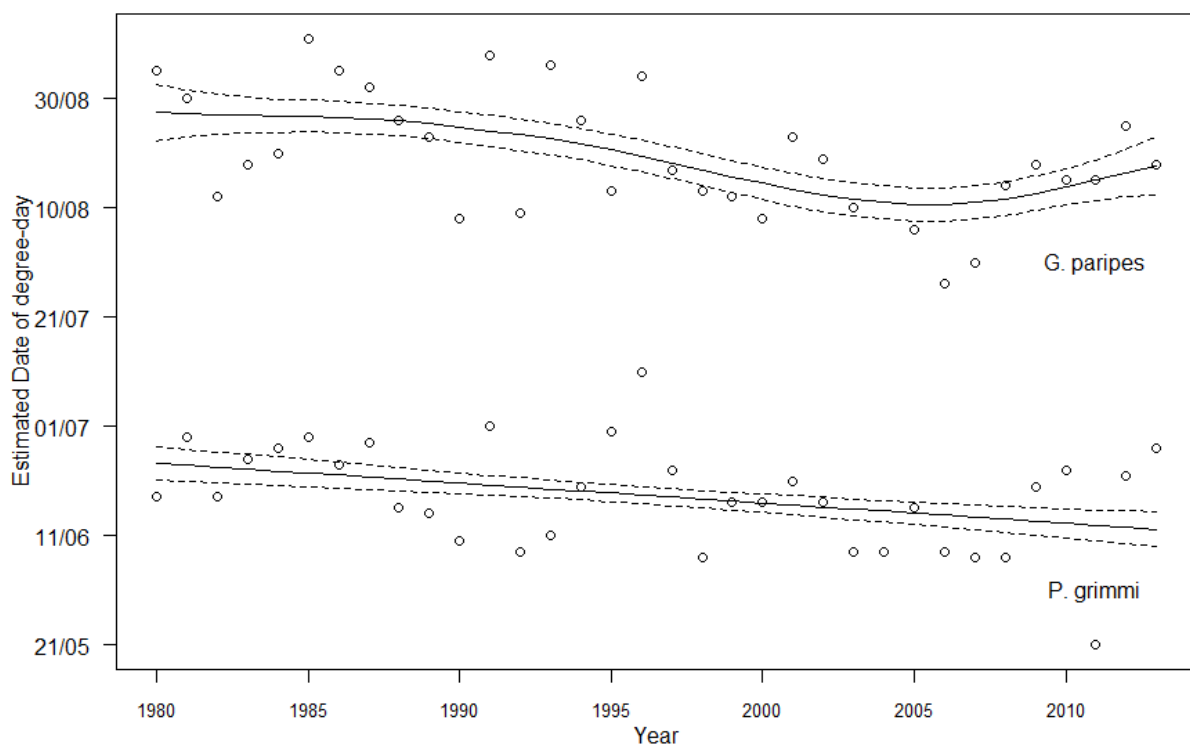


#### 2.3.4 Growing degree day

The modelled first emergence date of the two chironomid species *G. paripes* and *P. grimmi*, based on the known base temperatures and developmental degree day requirement, occurred significantly earlier by 0.554 days/year ( $\pm 0.171$ ,  $t_{33} = -3.241$ ,  $P = 0.003$ ) and 0.367 days/year ( $\pm 0.160$ ,  $t_{33} = -2.28$ ,  $P = 0.029$ ), respectively (Figure 2.8). The pattern of first emergence date

with year for *G. paripes* was best described as a generalised additive model GAM<sup>2</sup> ( $F_{3,261,4,049}=3.936$ ,  $P=0.0106$ ). Since the required GDD for *G. paripes* was so high, there were no instances of multiple generations. Although the estimated number of generations for *P. grimmii* showed a possible trend towards more generations over the study period (Figure 2.9), this was not significant (Poisson GLM;  $+0.007$  generations per year  $\pm 0.009$   $z_{33}=0.851$ ;  $P=0.395$ ).

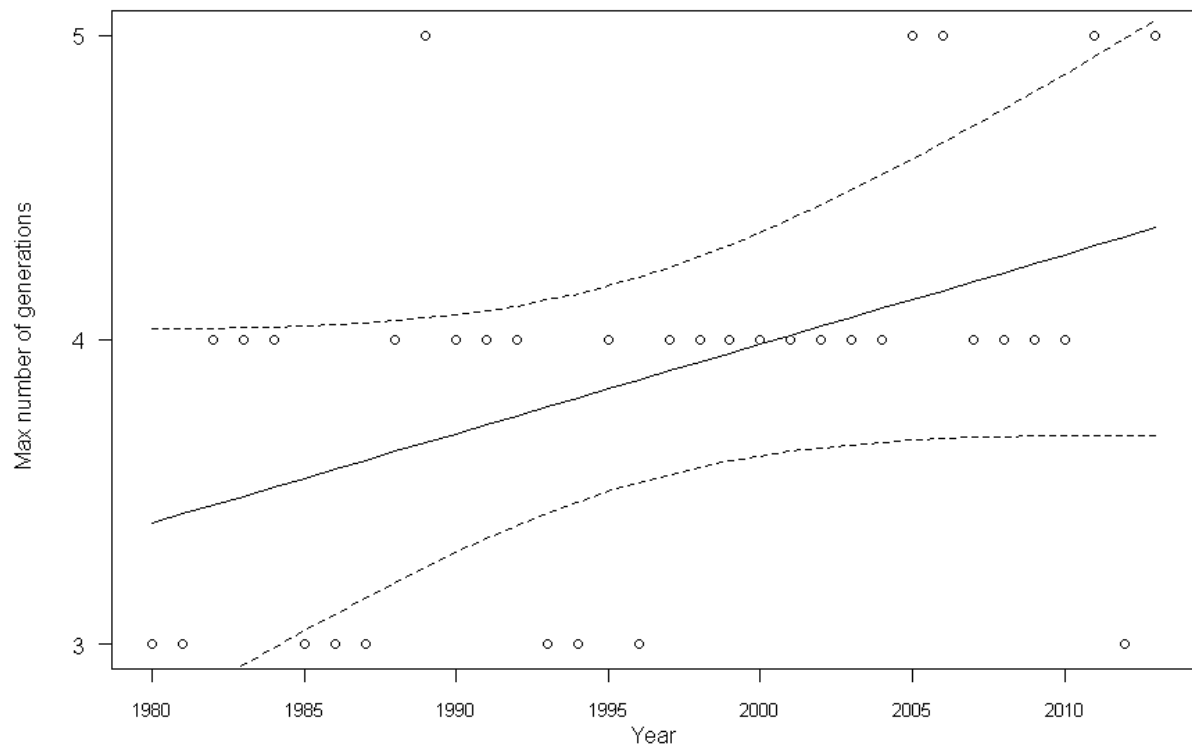
**Figure 2.8.** Extrapolated Growing Degree Day dates for chironomid species *P. grimmii* and *G. paripes* based on historical daily average temperatures between 1980- 2013 with GAM (*G. paripes*) and GLM (*P. grimmii*) fitted lines ( $\pm$  SE).



<sup>2</sup> By comparing the linear fit vs. non-linear fit



**Figure 2.9.** Extrapolated number of generations per year for *P. grimmii* based on estimated historical GDD values between 1980- 2013 with Poisson GLM fitted line ( $\pm$  SE).



## 2.4 Discussion

In this study, the total numbers of invertebrates, from many taxa, caught in sticky traps were used as a measure of food availability for reed warblers. The availability of invertebrate prey for breeding reed warblers was influenced by local weather variables, particularly air temperature (and the cumulative effect of temperature on invertebrate development), rainfall and wind speed. Of the 11 Orders considered in the present analysis, the Diptera, particularly Chironomidae, were most strongly affected by air temperature. This has particular relevance for reed warblers due to the importance of these taxa in their diet (Catchpole 1973; Chernetsov and Manukyan 1999). The effect of warming temperatures on activity of Diptera is well-established in both field and experimental studies (Taylor 1963; MacLean and Pitelka 1971; Briers *et al.* 2003; Goulson *et al.* 2005; Høye and Forchhammer 2008). The effect of temperature in advancing the timing of emergence, increasing hatching success and voltinism in Diptera is also well described (Singh and Harrison 1984; Gregory *et al.* 2000; Eggermont and Heiri 2012). The analysis revealed strong uni-modal seasonal availability curves, which represent the annual variation in invertebrate emergence and population density. These seasonal peaks in food availability are long-lasting (c3-5 months when food is abundant enough for reed warblers to initiate breeding attempts). The effect of the weather variables, particularly air temperature, explained significant proportions of the variation in activity-density around this overall seasonal pattern. The seasonal variation in the invertebrate captures was significant, indicating that the phenological processes driving seasonal changes in invertebrate availability have a large effect on the activity-density measure in combination with the short-term fluctuations in weather that influence the activity component of the composite activity-density measurement. Such findings are consistent with similar studies of Arctic arthropods (Høye and Forschhammer 2008; Tulp and Schekkerman 2008; Witter *et al.* 2012).

The date of minimum prey level required for reed warblers to initiate a breeding attempt between 2012 and 2014 differed by two to six weeks between successive years. This period of time may represent the difference between completing just one brood and having sufficient time to complete a second brood before food availability declines at the end of the summer. The high variation between years in spring temperatures suggests that there may be good years and bad years for initiating and completing second broods. The increasing reed warbler population trend may therefore be a result of higher frequencies of good years allowing the step-change to production of second broods, than bad years in which only one brood can be completed -rather than an incremental increase in breeding success in response to gradually increasing spring temperatures. The hindcasted activity-density values suggested that there has been a tendency for earlier dates for the 'minimum prey level' for reed warbler breeding onset which corresponds with a similar study conducted in the Arctic (e.g. four days in 30 years; Tulp and Schekkerman 2008). Although the precise consequences of earlier increases in invertebrate prey on the breeding performance of reed warblers is unknown, it has been suggested to be one of the drivers of earlier nesting in continental breeding populations of reed warblers, which facilitates higher rates of second-brooding (Halupka *et al.* 2008). An important consideration of this analysis is that the models used to hindcast invertebrate availability in the present study are based on just 147 weeks of invertebrate captures, which may not be sufficient to generate a model that adequately predicts invertebrate activity-density estimates from only three weather variables. The explanatory power of this model will be improved by extending the sampling period and by sampling at a higher temporal and taxonomic resolution. An important consideration in this study is that the yellow sticky traps may not reflect the true prey range available to reed warblers as they may also forage on ground dwelling taxa and those not attracted to yellow traps. Other sampling methods such as vacuum sampling may reflect a more reliable measure of invertebrate abundance but are likely to have a higher depletion effect on the local invertebrate population than sticky traps. It is possible that continuous trapping with

sticky traps may also result in localised depletion of the invertebrate population, although this was not apparent from the capture data.

The estimates of GDD for the two chironomid species based on historical temperature values reveal a significant advance in the date of emergence. Although this finding is based on an extrapolation from a statistical model, it provides support for the mechanism behind advances and increases in availability of invertebrate prey populations. Further work to isolate the precise effects of temperature using *in situ* canopies and constant temperature laboratories will enable a better understanding of the potential consequences of climate warming on prey availability, and will be the subject of the next study.

## **Chapter 3**

**Effects of temperature on the growth of common reed *Phragmites australis* and the wetland invertebrate community**

## Summary

Climate-driven changes to the phenology of wetland plant growth and emergence of invertebrate populations may have dramatic consequences for wetland birds that rely on these resources for nesting and foraging. To investigate these consequences, the growth rates of common reed *Phragmites australis* and the activity-density of invertebrate taxa were assessed in response to temperature in two experimental studies. In the first study, 48 replicate soil cores containing *Phragmites* rhizomes were grown in constant temperature (CT) laboratories at 10°C, 14°C, 16°C, 18°C, 20°C and 24°C. The second study monitored eight plots of *Phragmites in situ* within a reedbed habitat, with three of the plots enclosed within polytunnel canopies, which increased the ambient temperature by between 0.5 to 6°C. In both studies, the *Phragmites* shoot height and invertebrate activity-density were measured weekly. The constant temperature study revealed that, increasing treatment temperatures resulted in faster *Phragmites* shoot growth and earlier and larger peaks in arthropod emergence. The *Phragmites* grown in canopy treatment plots reached a height suitable for wetland warblers to begin nesting up to two weeks before control plots, and the phenology of invertebrate emergence was approximately two weeks earlier than in control plots. These results indicate that continued increases in spring temperatures will drive substantially earlier shifts in *Phragmites* emergence, increase reed growth rate and advance the window of high invertebrate prey abundance. This is predicted to have an impact on breeding migrant warblers by enabling earlier nesting and potentially facilitating more breeding attempts per year.

### 3.1 Introduction

Many insectivore birds are long-distance migrants that undertake migrations to temperate areas in spring to take advantage of the high invertebrate prey abundance in order to breed (Poulin *et al.* 2002; Zwarts *et al.* 2009; Newton 2010). Wetland breeding species such as the Eurasian reed warbler *Acrocephalus scirpaceus* (hereafter ‘reed warbler’) rely on both the peak emergence of invertebrates on which to feed and provision their young, and the growth of common reeds, *Phragmites australis* (hereafter ‘*Phragmites*’), in which they build their nests (Catchpole 1974; Hoi *et al.* 1995; Hawke and José 1996; Grim and Honza 1996; Chernetsov and Manukyan 1999). The relative timing of *Phragmites* growth, high invertebrate availability and the arrival of reed warblers at the breeding grounds has been shown to have important consequences for date of nesting, breeding success and productivity (Crick and Sparks 1999; Halupka *et al.* 2008). A potential source of disruption to the interlinked phenology of components of the reedbed ecosystem is the predicted increase in average surface temperatures for Europe as a result of climate change (Susan 2007); this may differentially alter the timing of *Phragmites* shoot emergence, rates of growth, invertebrate emergence and bird migration.

#### 3.1.1 *The importance of invertebrate prey availability for breeding reed warblers*

The timing of nesting in birds is adjusted so that nestling period coincides with seasonal increases in food resources (Lack 1950, Marshall 1951, Immelmann 1971, Drent 2006). Recent climate-driven changes in the timing of peak prey availability have led to a mismatch between peak food availability and the timing of breeding of some (but not all) species of insectivorous birds. This has been identified as a major cause of decline among trans-Saharan migrant bird species (e.g. European pied flycatchers *Ficedula hypoleuca*: Both *et al.* 2004, Both *et al.* 2006; Both *et al.* 2010). Such effects are, however, less well understood for

wetland habitats, where populations of reed warblers have remained stable or, in some cases, have increased (Gibbons *et al.* 1993; PECBMS 2012; Balmer *et al.* 2013). One potential cause of these population increases maybe the lengthening of the breeding season due to improved breeding conditions earlier in the spring (Crick and Sparks 1999). Reed warblers have been observed nesting up to three weeks earlier over a 36 year period, which has been attributed to earlier availability of suitable nesting habitat and prey availability as result of warmer spring temperatures (Halupka *et al.* 2008)

The analyses undertaken in Chapter 2 indicate that temperature is a key aspect of weather driving variation in invertebrate activity-density in temperate reedbed habitats. Predicting the response of invertebrate emergence phenology to climate warming under field conditions is challenging, not least because of the numerous potential abiotic effects of variable micro-climates, hydrology, shading and habitat management, but also due to the uncertain influence of variable predator, parasitoid and competitor community. Clearer insights to the direct effects of temperature on invertebrate communities, may be achieved under controlled and standardised temperature conditions (Lawton 1998).

### 3.1.2 *The importance of Phragmites growth for breeding reed warblers*

*Phragmites* stems are the favoured, primary vegetation substrate used by nesting reed warblers (Catchpole 1974). Although old *Phragmites* stems can provide important anchor points in nest construction, the dense cover and structure provided by new emergent stems is critical for screening the nest from predators (and brood parasites such as common cuckoo *Cuculus canorus*), as well as buffering and protecting the nest from the effects of wind, direct sunshine and rainfall (Burger 1985; Moskát and Honza 2000; Batary *et al.* 2004). Among reed warblers in the Cardiff Bay Wetland Reserve (CBWR) study area in South



Wales, the height at which *Phragmites* shoots are first used for nest building (i.e. 'suitable nesting height') is between 120 and 140 cm; a height typically reached around 25 April  $\pm$  10 days (Vafidis; unpublished data, 2006-2014;  $n = 337$ ). The timing of emergence of new *Phragmites* shoots is an important factor in nest initiation by reed warblers (Brown and Davies 1949). Typically, male reed warblers arrive in early April, before the females, in order to establish territories before the *Phragmites* have grown to sufficient nesting height (Brown and Davies 1949). Earlier and more rapid *Phragmites* growth has been shown to induce earlier nesting (Schaefer *et al.* 2006; Halupka *et al.* 2008; Dyrce and Halupka 2008) whereas slow growth of *Phragmites* can delay nesting and even cause reed warblers to select alternative nesting habitats such as dense scrub, which may carry an increased risk of predation (Catchpole 1974).

Several field and laboratory studies have demonstrated a strong relationship between temperature and *Phragmites* growth rate (Haslam 1974; Ostendorp 1991). Growth and seasonal productivity are strongly dependent on temperature during the start of the growing season (Kühl and Kohl 1992; Zemlin *et al.* 2000). As with other field-based investigations, the difficulty in forming clear conclusions about environmental effects is in separating the influence of temperature from other factors such as hydrology, nutrient regime and interspecific competition. Water depth is identified as an important limiting factor for *Phragmites* growth (Haslam 1970; Clevering 1998). Weisner and Ekstam (1993) and Armstrong *et al.* (1999) found negative associations between water depth and aspects of life history such as shoot emergence date, and final shoot height. Another important consideration is the provenance of the *Phragmites* genotypes used in each study, since different genotypes may respond differently to environmental changes. Many of these studies neglect to examine the genotype used in their investigations. Daniels (1991) demonstrated, under standardised conditions, significant differences in the temperature-dependent growth responses of *Phragmites* grown from seeds and rhizomes from sites with

different climatic and soil conditions. Further work confirms that growth and structural characteristics (e.g. node interval) depend both on environment and genotype (Koppitz *et al.* 1997; Kühl and Zemlin 2000; Clevering *et al.* 2001; Bastlová *et al.* 2004; Hansen *et al.* 2007). Since each *Phragmites* reed swamp typically contains several genotypes (Clevering *et al.* 2001; Bastalova *et al.* 2006), predicting the growth response is, however, often limited to the population-level unless the single genotypes are isolated (Brix 1999; Clevering and Lissner 1999; Kühl *et al.* 1999; Rolletschek *et al.* 1999; Hansen 2007).

In the present study, the ecological effects of temperature-rise were investigated in order to assess the extent to which temperature-induced changes in *Phragmites* and invertebrate emergence phenology in wetlands may affect important events, such as nesting and chick-provisioning, in the reed warbler breeding season. Specifically, we test whether the observed advances in reed warbler nesting phenology (e.g. three weeks; Halupka *et al.* 2008) can be explained by changes in *Phragmites* growth and invertebrate availability driven by small increases in temperature.

Replicated plots of a natural *Phragmites* reedbed and their invertebrate communities were monitored in response to experimental warming under differing temperature treatments; (i) in a constant temperature (CT) study, and (ii) in an *in situ* ‘canopy’ field study.

The first hypothesis is that temperature will have a reducing effect on the period taken to reach ‘suitable nesting height’ ( $\geq 120\text{cm}$ ) which may be reduced by at least three weeks. This was tested by comparing the growth of *Phragmites* between temperature treatments in both studies. The second hypothesis that ‘increases in temperature will advance the timing of high activity-density of invertebrates’ by at least three weeks, was tested by monitoring

weekly measures of invertebrate activity-density in each temperature treatment and comparing the period taken to reach their maxima (in the CT experiment) or a measure comparable with peak reed warbler nesting activities (in the *in situ* canopy experiment).

## 3.2 Methods

### 3.2.1 Constant Temperature study

The CT study was conducted between 20 February 2013 and 18 June 2013, and between 21 February 2014 and 10 July 2014. *Phragmites* rhizome soil cores (with shoots yet to emerge) were collected from a reedbed in Cardiff Bay Wetland Reserve, Wales, UK (CBWR; 51° 27' 32'' N, 3° 10' 11'' W) on 11 February 2013 and 21 February 2014. All samples were selected from areas with similar density of dry *Phragmites* stems (approximately 40-60 stems per m<sup>2</sup>) and minimal standing-water (<10cm) above ground. A total of 48 soil core samples (approximately 0.135m<sup>2</sup>) were placed within 50 litre-capacity flexible plastic buckets, topped up with water from the marsh and transported to the laboratory within 2h. Eight soil cores were transferred to each of six constant temperature laboratories at 10°C, 14°C, 16°C, 18°C, 20°C and 24°C, all with a 12:12h light:dark cycle. CBWR has a mean growing season temperature of 14.8°C, a diurnal mean temperature of 15.3°C, and a mean maximum of 25.9°C (April-July 2007-2014, weather data from Cardiff Harbour Authority). Buckets were enclosed within a fine nylon mesh (1mm) tube extending 2m towards the ceiling to allow for new *Phragmites* growth, while enclosing the invertebrate community (Figure 3.1). Temperatures in the laboratories were controlled using recirculation heating and cooling units (2x ACS Ltd VIP 396; 1x Porka M Ltd). The water levels within the buckets were maintained throughout the experiment by topping up weekly with rainwater as necessary, to maintain a water level (approx. 5cm) below the top of the bucket. *Phragmites* growth was measured every week by measuring the height of 10 labelled shoots in each

bucket from the top of the bucket. The abundance of the natural populations of invertebrates emerged from the substrate was measured every week by gently sweeping the sample enclosure with a small D-frame sweep net (1mm mesh, 250cm diameter) maintaining a constant effort of four sweeps for each sample. Each sweep net catch was transferred to a counting jar, contents recorded (see 3.2.3 *Invertebrate identification*) and all invertebrates returned to the sample enclosure. The experiment continued until the invertebrate numbers in each weekly sample dropped to zero.

Figure 3.1 Constant temperature buckets and nylon sleeves (prior to *Phragmites* growth)



### 3.2.2 *In Situ study*

The *in situ* study was conducted within a four hectare reedbed system in Cadoxton Ponds in Barry, South Wales (CPB; 51° 24' 35'' N, 3° 14' 49'' W). This site was used instead of CBWR for practical reasons such as site security and continuity and homogeneity of *Phragmites* habitat suitable for replicated enclosures. Eight *in situ* (3 x 2m) plots of *Phragmites* were monitored during experimental manipulation treatments at CPB between 15 February 2013 and 06 June 2013. Four of the eight plots were enclosed by vented polytunnels (3 x 2m square, 2m high, Figure 3.2) to elevate temperatures above ambient. On Week 5 of the experiment (commencing 10 May 2013), one canopy was destroyed by high winds, so this plot was removed from the experiment, leaving three treatment plots. The other four plots continued to be monitored as un-manipulated control plots, subject to ambient temperatures. All plots were subject to the same (un-manipulated) waterlogged conditions throughout the sample period, during which standing surface water depth varied between 30 and 80 cm above the substrate level. Water depth was monitored using barometer data loggers (Solinst Level logger Model 3001). The temperatures within treatment plots were measured using air (Lascar EL-USB-1) and water (Solinst Level logger Model 3001) temperature data loggers, recording every hour. Air and water temperatures in the treatment plots were elevated, but variable and not adjustable.

Figure 3.2. *In situ* canopy enclosure (prior to *Phragmites* growth).



The invertebrate community was sampled with a 1-mm mesh D-frame sweep-net once a week, by sweeping the vegetation from the bottom up with the net frame at an angle of 45° a total of five times on each half of each plot (producing two replicate samples per plot). Samples were transferred into counting jars and sorted live in the field before being returned to the original plots. This approach, as well as not depleting the arthropod community, has been shown to represent up to 98% of the taxa preyed upon by reed warblers and other insectivorous passerines (Poulin and Lefebvre 1997; Poulin *et al.* 2002). Reedbed warbler diets comprise a wide range of arthropod taxa (Kerbirou *et al.* 2011) and studies using faecal analysis, stomach flushing and retrieved prey from neck ligatures have shown that arthropod sampling methods in the upper vegetation, such as those used in this study, provide a useful index of reed warbler prey (Bibby and Thomas 1985; Chernetsov and Manukyan 1999; Grim 2006). A mean invertebrate activity-density value representing the local prey availability during the typical reed warbler hatching period was derived from the mean activity-density of invertebrates in the control plots between 10 and 29 June 2013. The length of time taken to reach this value was compared between treatment plots.

### 3.2.3 *Invertebrate identification*

Invertebrates were inspected using a 10x hand lens where necessary. The following taxa were identified to Order level: Araneae (spiders), Coleoptera (beetles), Dermaptera (earwigs), Hemiptera (bugs), Hymenoptera (sawflies and wasps), Lepidoptera (moths and butterflies), Megaloptera (alderflies), Odonata (dragon- and damselflies) and Psocoptera (barklice). As the most abundant prey group, Diptera were identified to Family level including Chironomidae, Culicidae, Dixidae, Mycetophilidae, Psychodidae, Sciaridae, Tipulidae, Trichoceridae, Muscidae and Tachinidae using Tilling (1987), Unwin (1981) and Watson and Dallwitz (2003).

### 3.2.4 *Data analysis*

Differences in *Phragmites* growth periods, invertebrate emergence periods, peak abundance and net abundance were compared between CT treatments using a general linear model (GLM) in R, version 3.01. Generalized additive mixed-effects models (GAMMs) with ‘negative binomial’ distribution of errors and ‘log’ link functions, were used to account for repeated measures from *in situ* study plots, by including ‘replicate’ or ‘plot identity’ as random intercept effects to control for spatial pseudo-replication. The degree of smoothing (non-linearity) in the model (6 “knots”) was selected to maximise explanatory power whilst minimising over-fitting of the data (Hastie and Tibshirani 1990). Each analysis was initiated with a full model including all main effects and all two-way interaction terms between date, site and environmental variables. Reduced models were compared with the full model using Akaike’s Information Criterion, adjusted for small samples (AIC<sub>c</sub>; Burnham and Anderson 2004). The R packages ‘mgcv’ (Wood 2011) and ‘nlme’ (Pinheiro *et al.* 2013) were used to generate mixed-effects models. Residual diagnostic plots from the models were used to

verify the assumptions of normality and homogeneity of model residuals, and to test for unduly influential observations (Zuur *et al.* 2010). In the CT study, the 24°C treatment failed to produce data for the *Phragmites* growth-period analysis, as plants died before reaching the ‘suitable nesting height’ due to heat stress, so was excluded from the analysis.

### 3.3 Results

#### 3.3.1 CT study: duration of the *Phragmites* growth period

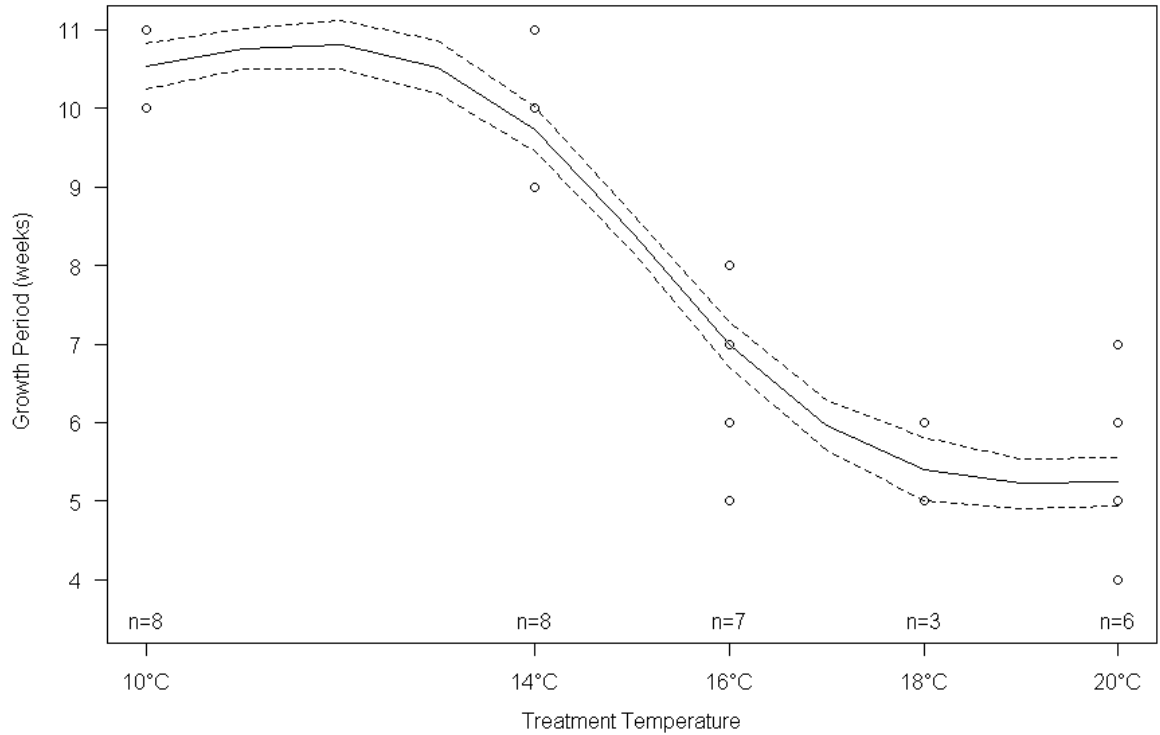
Temperature treatment affected the length of the growth-period of *Phragmites* stems, with higher temperature treatments shortening the growth period. The *Phragmites* heights in the 24°C treatment were more variable than in the other treatments, ranging between 66 and 106 cm in height (all shorter than the ‘suitable nesting height’ value of 120 cm) so were omitted from analysis. The fastest growth was observed in the 18°C and 20°C treatments which reached ‘suitable nesting height’ five weeks earlier than the 10°C treatment (Table 3.1; Figure 3.3). The overall effect of temperature on the growth period was a shortening effect of  $-0.581 (\pm 0.005)$  weeks per 1°C increase (GLM  $t = -10.51$ ,  $df = 32$ ,  $P < 0.0001$ ).

**Table 3.1.** GLM parameter estimates for the effect of CT treatments on the growth period of *Phragmites* up to ‘suitable nesting height’ (120cm). The growth period estimates are relative to reference treatment of 10°C with an intercept value of 10.5 weeks  $\pm$  0.5.

Parameter	Estimate $\pm$ SE	<i>t</i> -value	<i>d.f.</i>	<i>P</i>
Temp 14°C	-0.625 $\pm$ 0.421	-1.485	42	0.149
Temp 16°C	-3.643 $\pm$ 0.435	-8.364	42	<0.0001
Temp 18°C	-5.167 $\pm$ 0.570	-9.069	42	<0.0001
Temp 20°C	-5.214 $\pm$ 0.435	-11.973	42	<0.0001



**Figure 3.3.** Growth periods of *Phragmites* up to ‘suitable nesting height’ (120cm) in weeks with fitted line ( $\pm$  SE). The variable sample sizes between treatments represent the numbers that reached the ‘suitable nesting height’ out of the eight samples.



### 3.3.2 CT study: invertebrate emergence

The invertebrate community across all treatments was dominated by Diptera ( $97.0 \pm 1.3\%$ ) with Thysanoptera ( $1.9 \pm 0.6\%$ ), Hymenoptera ( $0.6 \pm 0.11\%$ ), Lepidoptera ( $0.2 \pm 0.1\%$ ) and Coleoptera ( $0.2 \pm 0.1\%$ ). Diptera consisted of Chironomidae ( $68.0 \pm 9.8\%$ ), Sciaridae ( $9.2 \pm 3.4\%$ ), Dixidae ( $5.3 \pm 2.7\%$ ), Psychodidae ( $2.1 \pm 0.9\%$ ), Culicidae ( $0.9 \pm 0.1\%$ ), Tipulidae ( $0.6 \pm 0.3\%$ ), Syrphidae ( $0.6 \pm 0.1\%$ ), seven other families representing  $<0.5\%$  of the total catch and an unknown Diptera group ( $3.8 \pm 0.4\%$ ).

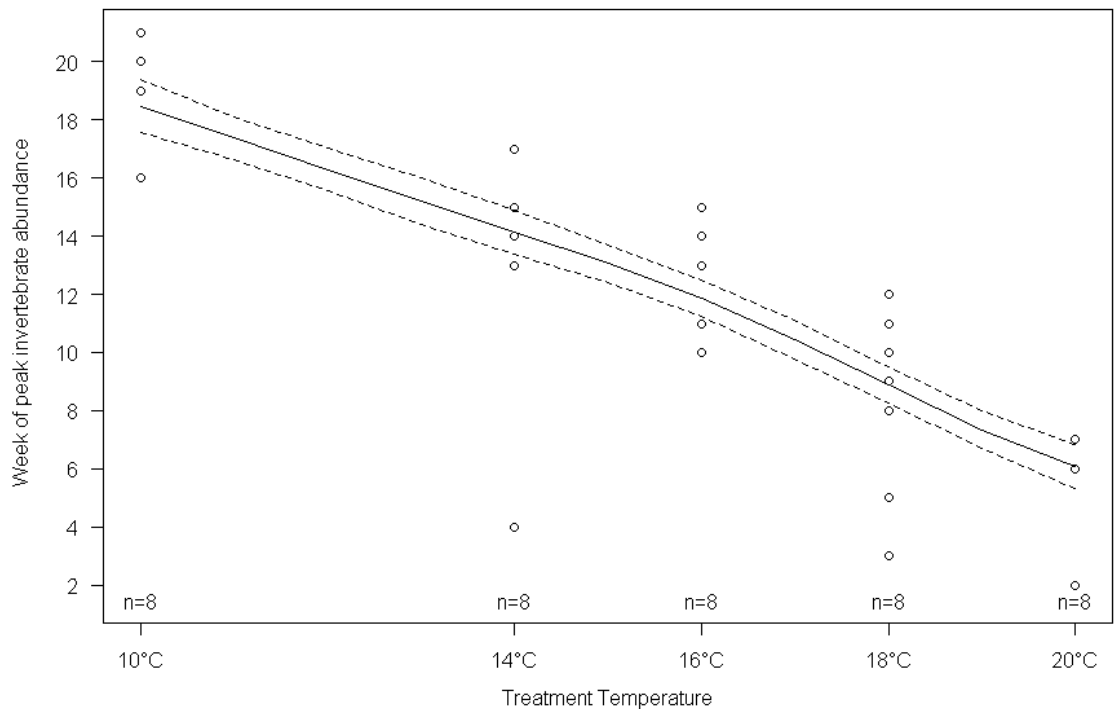
The period prior to the peak in invertebrate abundance varied significantly between temperature treatments, with these periods getting shorter with higher temperatures. The

greatest advance was observed in the 24°C treatment which reached a peak in abundance 13 weeks before the 10°C temperature treatment (Table 3.2; Figure 3.4). The effect of temperature shortened the time period taken to reach the abundance maximum by 1.025 ( $\pm$  0.091) weeks per 1°C increase (GLM  $t=-11.26$ ,  $df= 47$ ,  $P<0.0001$ ).

**Table 3.2.** GLM parameter estimates for the effect of CT treatments on length of period taken to reach peak of invertebrate abundance. The abundance estimates are relative to an intercept value of 18.5 weeks  $\pm$  1.34, representing a reference treatment of 10°C.

Parameter	Estimate $\pm$ SE	<i>t</i>	<i>d.f.</i>	<i>P</i>
Temp 14°C	-4.750 $\pm$ 1.310	-3.626	42	<0.0010
Temp 16°C	-5.875 $\pm$ 1.120	-4.485	42	<0.0001
Temp 18°C	-9.750 $\pm$ 0.912	-7.443	42	<0.0001
Temp 20°C	-12.875 $\pm$ 1.420	-9.829	42	<0.0001
Temp 24°C	-13.250 $\pm$ 1.130	-10.115	42	<0.0001

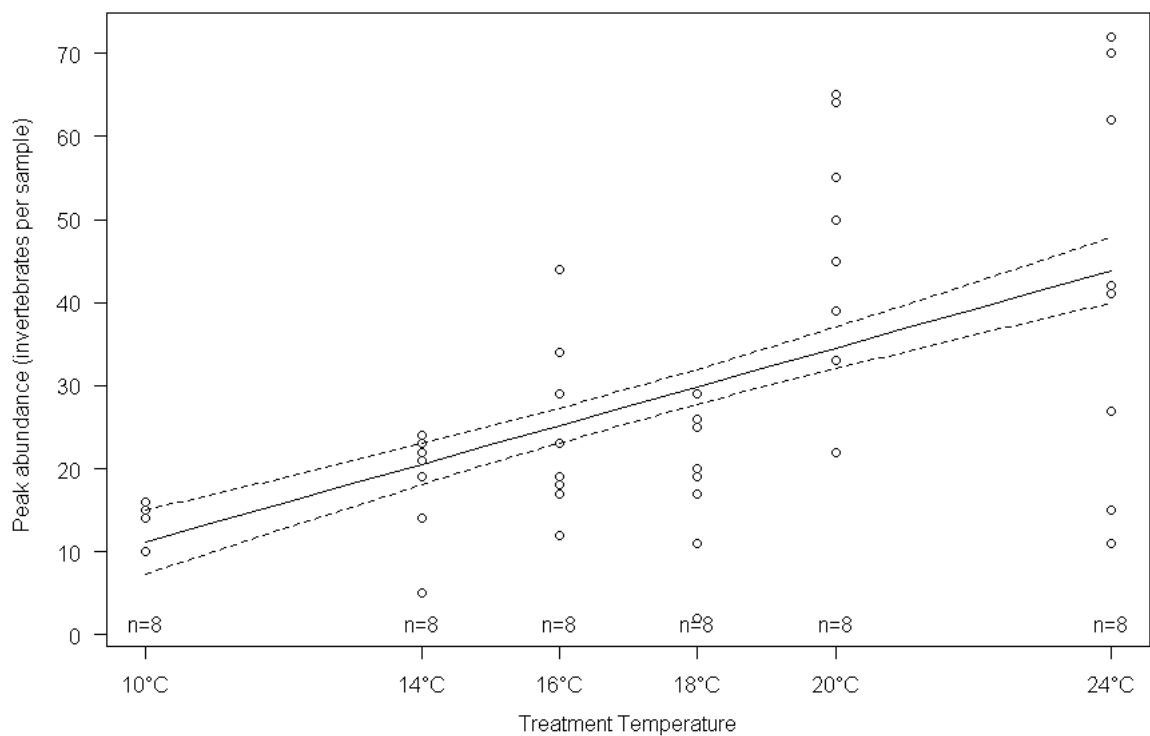
**Figure 3.4.** Period taken to reach the peak in invertebrate abundance in weeks with fitted line ( $\pm$  SE) for each CT treatment.



### 3.3.3 CT study: size of emergence peak

The maximum number of invertebrates recorded during the sample peak varied significantly between temperature treatments, with numbers increasing with higher temperatures. The greatest effect was observed between the 10°C and 20°C temperature treatments, which differed by a mean of 32.4 individuals per sample; Figure 3.5; Table 3.3). The overall effect of temperature on the peak abundance was an increase by  $2.3 (\pm 0.5)$  invertebrates per 1°C increase (GLM  $t = 4.999$ ,  $df = 47$ ,  $P < 0.0001$ ).

**Figure 3.5.** Invertebrate peak abundance values for each CT treatment with fitted line ( $\pm$  SE).



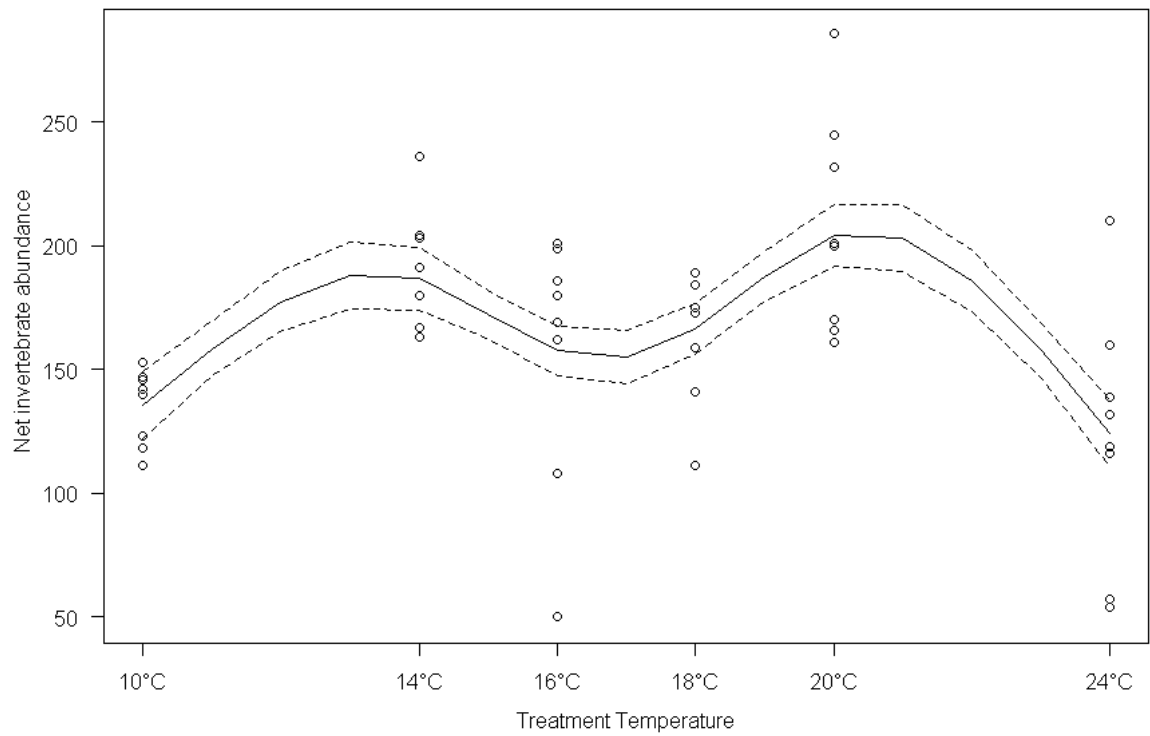
**Table 3.3.** GLM parameter estimates for the effect of CT treatments on the size of the peak in invertebrate abundance. The abundance estimates are relative to an intercept value of  $14.250 \pm 4.627$ , representing a treatment of 10°C.

Parameter	Estimate $\pm$ SE	<i>t</i>	<i>d.f.</i>	<i>P</i>
Temp 14°C	$4.375 \pm 3.133$	0.669	42	0.5074
Temp 16°C	$10.250 \pm 4.241$	1.566	42	0.1247
Temp 18°C	$4.375 \pm 3.351$	0.669	42	0.5074
Temp 20°C	$32.375 \pm 6.543$	4.948	42	<0.0001
Temp 24°C	$28.250 \pm 5.891$	4.317	42	<0.0001

#### 3.3.4 CT study: net invertebrate abundance

Increases in temperature did not have a consistent effect on net invertebrate abundance with significant differences between the lowest treatment temperature 10°C and two other treatments at 14°C and 20°C, which differed by a mean of 53.4 and 72.6 individuals per sample, respectively (Table 3.4; Figure 3.6). The overall effect of temperature on net abundance was not significant (GLM;  $t=-0.096$   $df=47$ ,  $P=0.924$ ).

**Figure 3.6.** Invertebrate net abundance values ( $\pm$  SE) for each CT treatment with fitted line.



**Table 3.4.** GLM parameter net invertebrate abundance estimates for the effect of CT treatments. The net abundance estimates are relative to an intercept value of  $135.000 \pm 13.580$  mean number of individuals in a temperature treatment of 10°C.

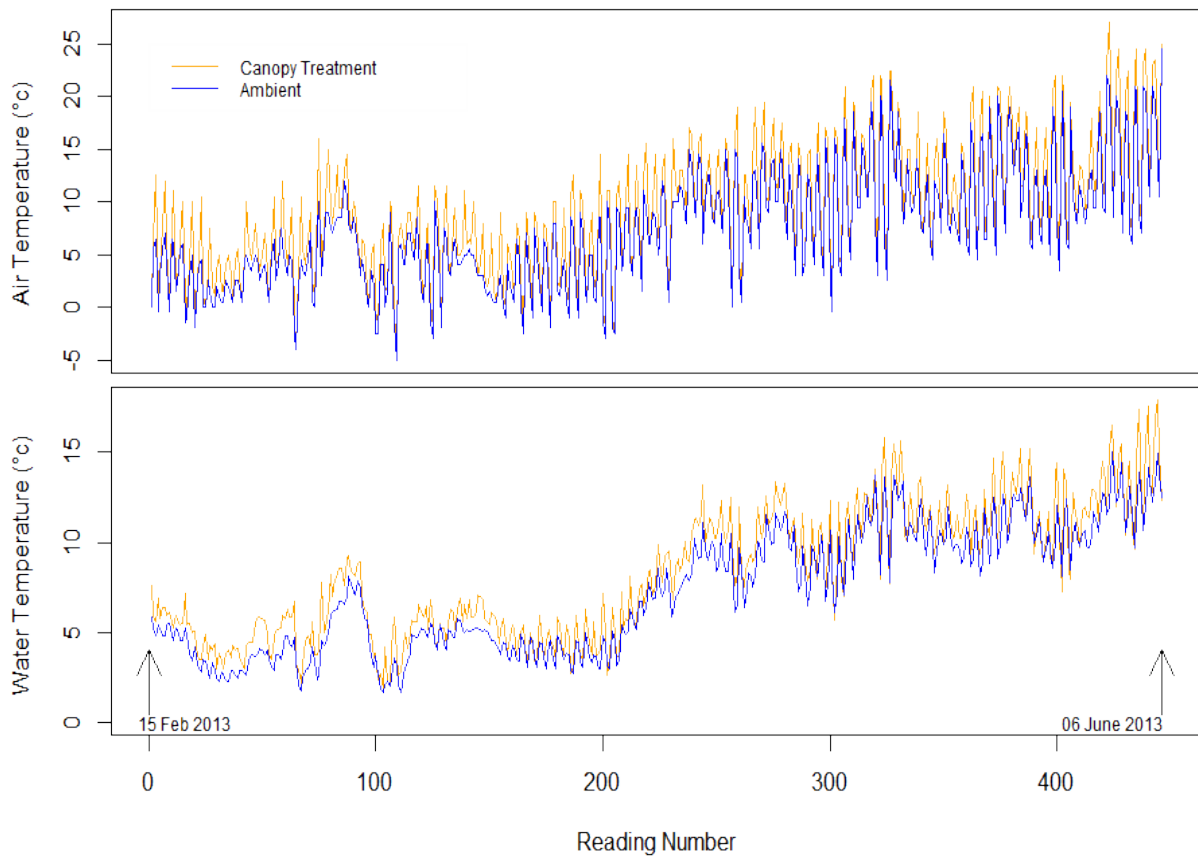
Parameter	Estimate $\pm$ SE	<i>t</i>	<i>d.f.</i>	<i>P</i>
Temp 14°C	53.380 $\pm$ 19.211	2.779	42	0.0081
Temp 16°C	21.870 $\pm$ 9.161	1.139	42	0.2612
Temp 18°C	28.120 $\pm$ 10.540	1.464	42	0.1506
Temp 20°C	72.620 $\pm$ 11.214	3.781	42	0.0005
Temp 24°C	-11.630 $\pm$ 8.210	-0.605	42	0.5483

### 3.3.5 *In Situ study: effect of experimental treatment on microclimate*

The difference in diurnal mean air temperature between control and canopy treatments was highly significant (control mean =  $13.23^{\circ}\text{C} \pm 3.63^{\circ}\text{C}$ , canopy mean =  $17.41^{\circ}\text{C} \pm 5.0^{\circ}\text{C}$ ,  $t_{896} = 4.47$ ,  $P < 0.001$ ) and represented by a mean difference of  $4.22^{\circ}\text{C} \pm 2.68^{\circ}\text{C}$ ; Figure 3.7). The

minimum air temperatures were not significantly different between the control and canopy plots (control min= -5.00°C, canopy min = -4.85°C,  $t_{896} = 0.31$ ,  $P < 0.840$ ). The difference in water temperature was also not significant (control mean = 7.56°C, canopy mean= 8.93°C,  $t_{887.971} = 0.83$ ,  $P < 0.3114$ ).

**Figure 3.7.** Air and water temperature regime across canopy and ambient treatments throughout the study period.

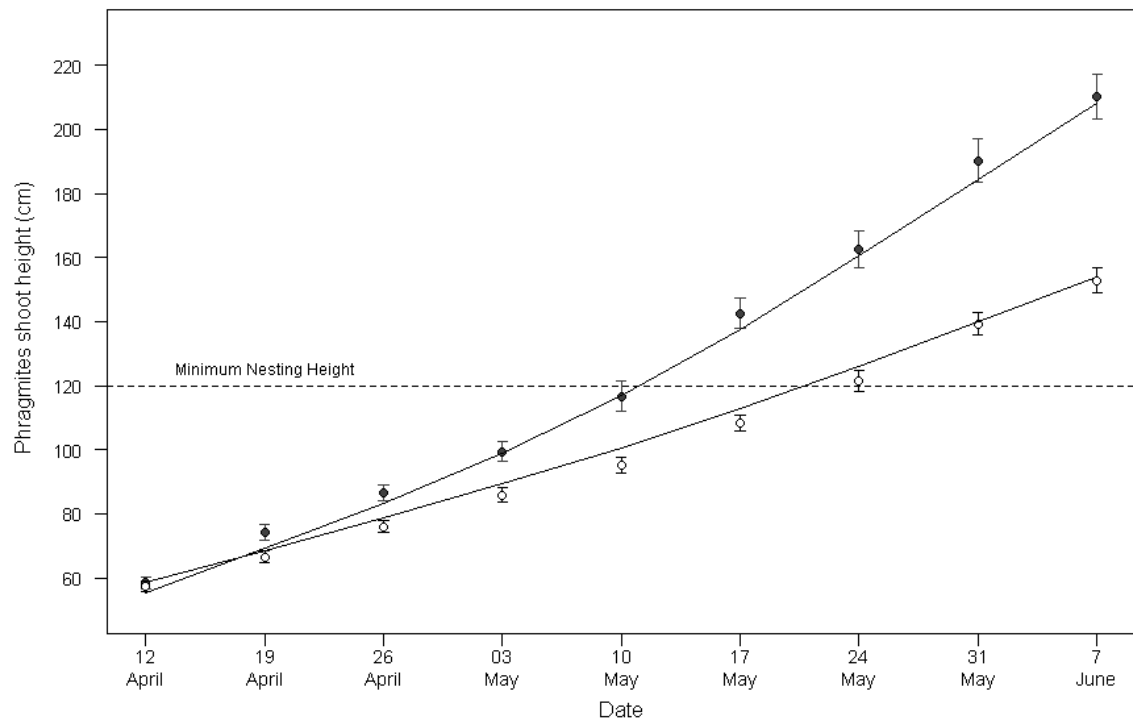


### 3.3.6 *In Situ study: duration of reed growth period*

A significantly higher *Phragmites* growth rate was recorded in the canopy plots than in the control plots (GAMM parameter estimate; growth rate was  $6.354 \pm 0.74$  cm/week higher,  $t = -8.567$ ,  $P < 0.0001$ ). While the *Phragmites* stems in control plots reached a height suitable

for reed warblers to nest on 24 May, this height was attained at least one week earlier between 10 and 17 May in canopy plots (GLM  $t = -4.8$ ;  $df=35$ ,  $P < 0.0001$ ; Figure 3.8).

**Figure 3.8.** Mean *Phragmites* height ( $\pm$  SE) in control (white-filled circles) and canopy (black-filled circles) plots between 12 April and 7 June 2013 with fitted lines.

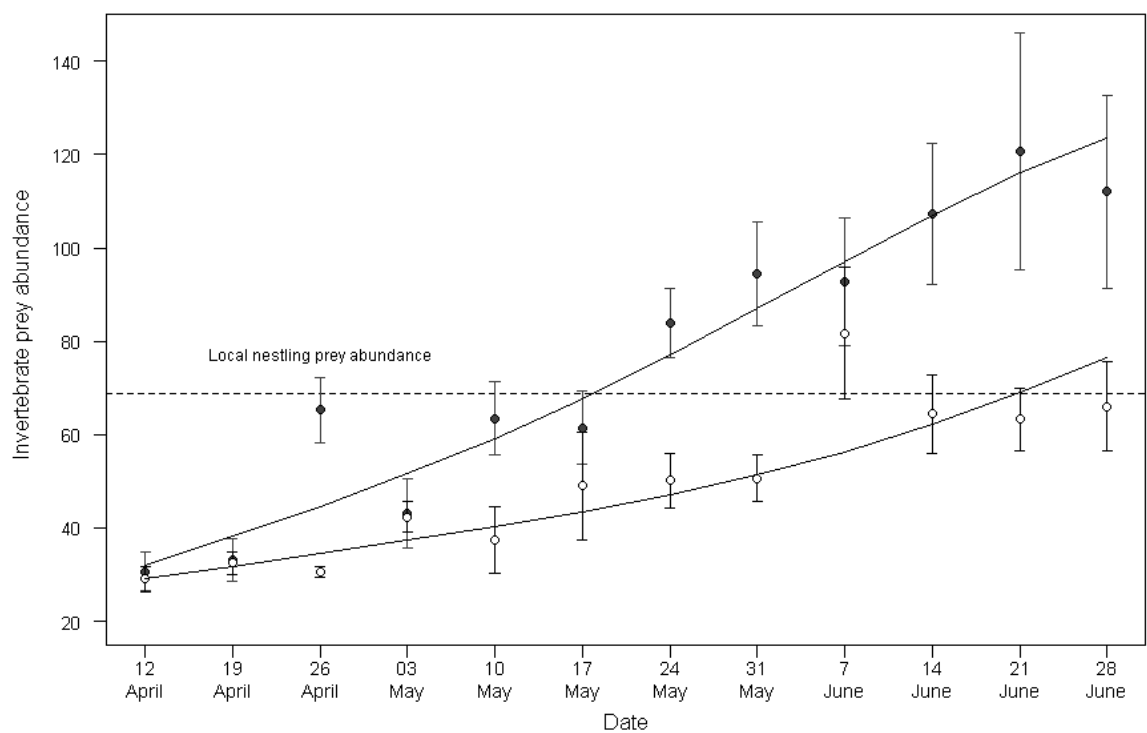


### 3.3.7 *In Situ study: invertebrate emergence*

A significantly higher invertebrate abundance was recorded in the canopy plots than in the control plots (GAMM estimate:  $+0.263 (\pm 0.133)$ ,  $t=1.967$ ,  $P= 0.0499$ ). The GAMM model using date, air temperature and treatment explained 45% of the deviance in invertebrate abundance. The mean invertebrate prey abundance in the control plots at the start of the reed warbler nestling period (between 10 and 29 June) was  $68.84 (\pm 14.86)$  mean total captures of invertebrates per plot. The date on which the control mean abundance exceeded this value

was 7 June, while in canopy plots it was two weeks prior on 24 May ( $t_{12} = -2.79$ ;  $P = 0.016$ ; Figure 3.9).

**Figure 3.9.** Mean prey abundance ( $\pm$  SE) in control (white-filled circles) and canopy (black-filled circles) plots between 12 April and 28 June 2013 with fitted lines. Local nestling abundance value of 68.84 invertebrates per trap is derived from mean control plot abundance during the local reed warbler nestling period (10-29 June 2013) in the surrounding habitat.





### 3.4 Discussion

*Phragmites* growing under elevated temperatures grew to a suitable height for nesting reed warblers sooner than those growing under lower temperature conditions. The maximum temperature-driven advance in the period taken to suitable nesting height in the constant temperature study was 5.2 weeks, while in the canopy study this was just over one week. This finding provides strong support for the effect of temperature in driving earlier nesting conditions and suggests that continued increases in early spring temperatures will enable reed warblers to nest earlier. The greater rate of reed growth at higher temperature treatments was consistent with the majority of studies investigating the effect of temperature on primary productivity in *Phragmites* (Haslam 1974; Ostendorp 1991), particularly that growth is strongly dependent on temperature at the start of the growing season (Kühl and Kohl 1992; Kühl and Zemlin 2000). Although not presented, the *Phragmites* grown in the 16°C treatment reached the greatest overall height ( $134.75 \pm 5.68$  cm), which also most closely represents the diurnal mean air temperature of 15.3°C at CBWR during the main growing season (01 April to 31 July 2007-2014). The unnatural conditions of the CT treatments, particularly the absence of diurnal-nocturnal temperature fluctuations and the lack of difference between air and substrate temperature, limit the applicability of the effect sizes of different temperature treatments. Equally, such conditions are likely to have adverse consequences such as the foliage desiccation which occurred shortly after week five in the 24°C treatment. The *in situ* study provided a way of incorporating more natural conditions, allowing diurnal-nocturnal temperature fluctuations and more standardised substrate conditions. The main result from this study was that *Phragmites* grown in an environment with a mean temperature 4.2°C warmer than ambient, reached a height suitable for nesting reed warblers almost two weeks before the control treatment plants. However, a major consideration in this study is that as well as providing a warmer environment for *Phragmites* to grow, the canopies are shielding the plants from the effects of wind and rain experienced by the control treatment plants. Consistent strong winds can have a stunting effect on plants

and, in stormy weather with high gusts and heavy rain, can collapse the structure (Biddington 1986). Wind can also strengthen and rigidify plant stems providing stronger support (Mitchell and Myers 1995).

The invertebrate populations emerging under elevated temperature conditions reached their peak abundance (in the CT study) and levels of high abundance (in the *in situ* study) sooner than those in lower temperature treatments. In the CT study, an advance in the period taken to reach invertebrate abundance peak of 13.2 weeks was observed, while in the canopy study it was two weeks. This provides support for the effect of rising temperature driving earlier peaks in invertebrate prey for nesting birds and indicates that the continued increases in early spring temperatures expected under climate change (IPCC 2013) may continue to provide a higher availability of invertebrate prey for breeding reed warblers earlier in the season. The peak invertebrate abundance was greatest in the 20°C treatment and lowest in the 10°C treatment with a mean invertebrate count of 46.6 and 14.2 individuals, respectively. The greater numbers of invertebrates recorded during the higher temperatures may be attributed to higher rates of activity, an increase in the rate of emergence, lower rates of mortality, or a combination of such changes. Similarly, in the colder treatments, invertebrates may take longer to emerge and are more likely to retreat into the litter layer or stem sheaths where they are less exposed, and consequently less likely to be sampled. The smaller differences in emergence dates and peak abundance between similar temperatures are consistent with other experimental warming studies (Gendron and Laville 1992; Pinder *et al.* 1993).

The non-linear differences in net invertebrate abundance with increasing temperature and non-significance of overall temperature effect on net invertebrate abundance suggest that either temperature has a variable effect on voltinism, or there may be large differences in the population sizes or invertebrate groups collected between the soil core samples. Responses

to temperature are likely to differ between invertebrate groups depending on their life-cycle strategies. High sensitivity in development and emergence to temperature might be expected in multi-voltine taxa such as Nematocera (Pollard and Yates 1994; Bale *et al.* 2002). The close association of invertebrate activity-density with temperature have been observed in other similar studies of multi-voltine species (MacLean and Pitelka 1971; Goulson *et al.* 2005; Tulp and Schekkerman 2008). Both CT and canopy studies provide general support for the positive direct effect of temperature on both invertebrate emergence phenology and activity-density within a specific temperature range. By contrast, the lower representation of seasonal and obligate long life-cycle groups such as Tipulidae, Odonata and Trichoptera in the elevated-temperature samples suggests a lower effect of temperature on these groups.

The present study confirms that plant growth and emergence phenology are responsive to temperature and that advances in emergence peaks can be expected with warming ambient temperatures. While this study confirms many of the findings of other temperature manipulation studies on *Phragmites* and invertebrate populations, it builds on this work by using natural extracted soil cores with actual densities of rhizomes rather than germinating seeds under controlled conditions (Haslam 1970; 1974; Ostendorp 1991; Kuhl and Kohl 1992; Zemlin *et al.* 2000). This has the advantage of representing actual reed warbler habitat, which provides the context for the study on *Phragmites* growth, for which no published study currently exists. Similarly, while there are several studies investigating the effect of temperature changes on the development, metabolism and activity of Diptera and other relevant prey taxa (Ward and Stanford 1977; P'ery and Garric 2006; Danks 2007; Eggermont and Heiri 2012), there are no studies which explicitly test the effect of temperature on natural densities of emerging wetland invertebrates in the context of food for breeding warblers. Studies are now needed to determine the response of breeding reed warblers to experimental increases in early spring invertebrate abundance. This will be the subject of Chapter 4.

## **Chapter 4**

**The effect of food availability on breeding  
performance and mass regulation in Eurasian reed  
warblers *Acrocephalus scirpaceus***

## Summary

The effects of climate change on the phenology and abundance of invertebrate prey populations may have important consequences for the breeding performance of insectivorous migratory birds, particularly during the early part of the season, when food is relatively scarce. The response of birds to food supplementation can reveal the extent of energy limitation on breeding performance and body reserves. The impact of experimentally supplemented food was tested on the breeding behaviour, productivity and body mass of a long distance migrant, the Eurasian reed warbler *Acrocephalus scirpaceus* over three breeding seasons (2012-2014). Food-supplementation advanced the laying date, reduced the periods between egg laying, shortened the incubation duration and increased the rate of nestling growth. These effects potentially enable earlier fledging of the first brood, increasing the opportunity for a second breeding attempt within the window of high invertebrate prey abundance. In addition, shorter periods of incubation and faster nestling growth reduce the period of vulnerability for eggs and nestlings to predation. Food supplementation did not affect clutch size or hatching success, suggesting that not all aspects of breeding biology are food limited. Adults responded to supplemental food by increasing their mass during the prelaying/laying, incubation and nestling phases, suggesting local prey availability may be limiting during the early stages of the breeding season. These results suggest the effects of higher prey availability earlier in the breeding season will improve body condition of adults, accelerate the production of a better quality first brood, and enable the possibility of higher success rate for second breeding attempts.

## 4.1 Introduction

Climate change is causing advances in the timing of availability of temperate invertebrates so that food availability for breeding insectivorous songbirds is becoming higher earlier in the breeding season (Dell *et al.* 2005; Studds and Marra 2005; Both *et al.* 2006; Thackeray *et al.* 2010). As income breeders, whose breeding productivity depends on current resources, songbirds require large quantities of food to support the energetically costly activities of egg production, incubation and nestling provisioning. It is therefore a period when birds are likely to be strongly responsive to changes in food availability. Many breeding birds are strongly affected by these changes in the timing of food availability and have shown significant advances in mean laying date in response (Crick *et al.* 1997; McCleery and Perrins 1998; Crick and Sparks 1999; Dunn 2004; Dunn and Winkler 2010). Some species have also shown higher rates of success completing second-broods in conditions where food availability allows a longer breeding season (Crick *et al.* 1993; Halupka *et al.* 2008; Wright *et al.* 2009; Dunn *et al.* 2011).

Earlier laying dates are associated with larger clutch sizes (Klomp 1970), as shown in pied flycatcher *Ficedula hypoleuca* (Jarvinen 1989), tree swallow *Tachycineta bicolor* (Winkler and Allen 1996) and great tits *Parus major* (Winkel and Hudde 1997). However, increasing the energetic investment in the first brood may have a delaying effect on the date of first brood completion, which could jeopardise the chances of success of completing a second brood. Birds attempting to double brood have a better chance of success if they complete their first brood quickly. This can be achieved by maintaining typical clutch sizes, reducing the incubation period, and hastening nestling growth. An experimental food supplementation study in wheatears *Oenanthe oenanthe* showed that supplemented birds were able to increase productivity by breeding earlier without increasing clutch size, with faster nestling

growth and higher success in second breeding attempts (Seward et al. 2014). Although the productivity of double-brooding exceeds that of maximising the first brood, the strategy carries a higher risk of poorly synchronising both broods with the food peak as the nestling period occurs too early and too late for first and second broods respectively (Pearce-Higgins and Green 2014). This is reflected in the decline in the number of recruits produced from second clutches, implying that females should switch to a single-brood strategy in order to optimise their breeding output with lower risk of failure.

Phenological mismatch between the period of peak prey availability and the birds' peak food requirement has caused declines in some long-distance migrant populations that have been unable to adjust their arrival dates to the changing conditions (Berthold 1996, Sanz 2003). Birds breeding in wetland habitats are considered less likely to suffer mismatch with the peaks in their prey populations on account of the continuous emergence of aquatic invertebrates which provides a protracted period of abundant prey across the summer season with no discernible peak (Both et al. 2010). In reedbeds, there is also a relatively long time lag between the arrival of birds on the breeding grounds and period of suitability when the growth of the common reed *Phragmites australis* reaches a stage when it can support nests. European populations of Eurasian reed warblers *Acrocephalus scirpaceus* (hereafter 'reed warbler') have shown increasing trends seemingly in response to advances in both food availability and the advancing stage of suitability in *Phragmites* growth, resulting in a lengthening in the breeding season. Reed warblers are double-brooding species but have been reported with larger clutch sizes in association with earlier laying dates (Schaefer et al. 2006) as well as higher success rates in second broods (Halupka et al. 2008). The trade-off associated with maximising productivity between larger first-brood clutch sizes and early completion of the first brood may be more favourable for prioritising second broods in wetlands than in other more seasonal habitats.

The direct consequences of changes to food availability on energetic reserves (stored as body fat and muscle mass) may serve as an important predictor of adult body condition. While most breeding birds, particularly females, show an increase in mass during the laying period, due to the accumulation of energy reserves (fat and muscle), gonadal tissue development (oviduct) and egg production, there is a marked decline in body mass across the incubation period and the nestling stage (Moreno 1989; Cichon 2001; Blem and Blem 2006). The causes and consequences of this phenomenon of mass loss over the breeding season have been the subject of long standing debates among biologists over the last three decades (Ricklefs and Hussell 1984; Hillström 1995, Cavitt and Thompson 1997, Woodburn and Perrins 1997, Neto and Gosler 2010). Such mass loss is either attributed to the expenditure of energy reserves during breeding (the ‘energetic stress hypothesis’; Ricklefs 1974, Moreno 1989, Johnson *et al.* 1990, Martins and Wright 1993; Suarez *et al.* 2005) or part of a strategy to actively reduce the wing-loading costs during the nestling feeding stage when parents are most active (the ‘flight efficiency hypothesis’; Freed 1981, Norberg 1981, Jones 1994, Curlee and Beissinger 1995, Gebhardt-Henrich *et al.* 1998; Blem and Blem 2006). Because of the influence of body condition on various aspects of breeding (Lifjeld and Slagsvold 1986; Bolton *et al.* 1992; Svensson and Nilsson 1995; Sanz 1996; Ramsay and Houston 1997; Eikenaar *et al.* 2003; Illera and Diaz 2006; Preston and Rotenberry, 2006; Banbura *et al.* 2011), the extent to which mass loss is determined by food limitation or energetic stress may be an important consideration for the effects of future changes in food availability on adult breeding condition, and the knock-on effect this may have on nesting activities and breeding productivity.

In this study, the response to earlier food availability on breeding date, clutch size and first brood completion are investigated in reed warblers using experimental food



supplementation. This species has an increasing European population and a northwest-advancing geographic distribution, which have been attributed to warmer spring temperatures and improved habitat management on their breeding grounds (Crick and Sparks 1999; Burfield *et al.* 2004; Thaxter *et al.* 2006; Halupka *et al.* 2008). By supplementing food resources in a population across three breeding seasons, the sensitivity of different aspects of breeding performance to changes in food availability were tested and used to predict whether reed warblers are adapted to increase first clutch productivity or strive to complete the first brood early for increased productive benefits of double-brooding. We predict that reed warblers, as adapted to an environment with less intense seasonality, will prioritise the opportunity for double brooding over maximising productivity in the first brood. Specifically we expect birds in supplementary treatments to advance the date of first brood completion by advancing their laying date, maintaining low clutch sizes, reducing the incubation period and increasing nestling growth rates. These mechanisms, linking environmental change to reed warbler breeding behaviour, may represent a key difference between migrant songbirds breeding in highly seasonal habitats currently in decline as a result of climate change.

It is hypothesised that increasing prey availability through supplementary feeding will affect breeding in reed warblers by advancing the completion of the first brood by advancing laying date, shortening incubation duration, and increasing nestling growth rates. The second hypothesis is that increasing prey availability through supplementary feeding will increase adult body mass through the nesting stage.

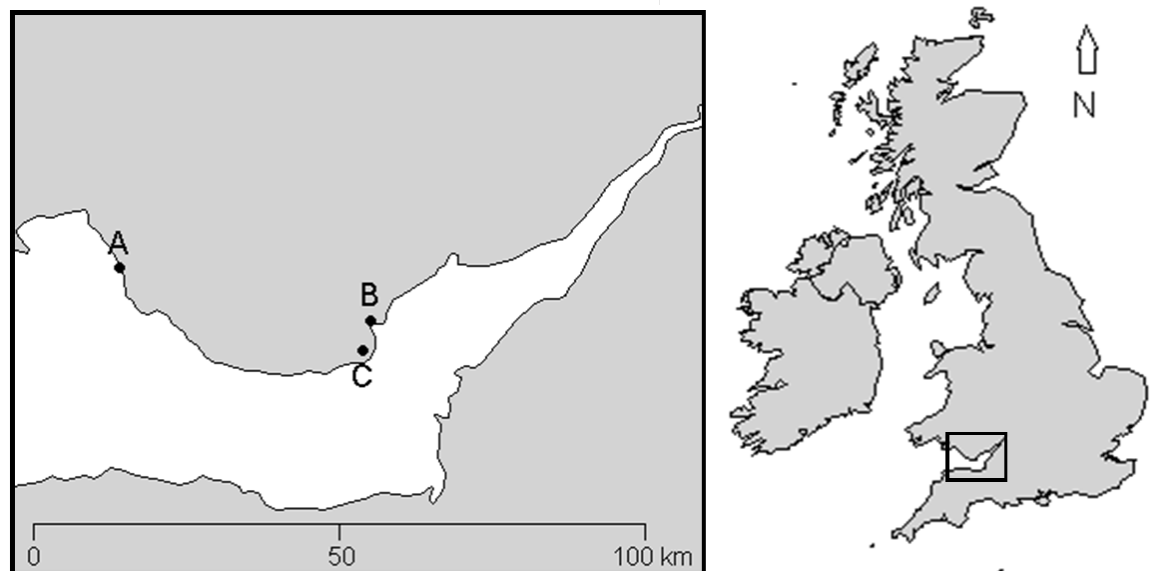
Reed warblers are long-distance insectivorous migrants that breed in temperate wetlands of Northern Eurasia (Cramp 1992; Procházka *et al.* 2007) and feed opportunistically on a wide range of invertebrate prey groups (Cramp 1998). Breeding adults are typically socially monogamous, with both sexes incubating, feeding and brooding the young (Davies and Green 1976; Snow and Perrins 1998). Reed warblers lay between three and five eggs in a clutch but four eggs is most common (Davies and Green 1976; Snow and Perrins 1998; Schaefer *et al.* 2006). The lengths of the incubation and nestling periods are generally 12 and nine days, respectively (Davies and Green 1976; Snow and Perrins 1998). Breeding pairs typically raise a single brood per year, but an increasing proportion (currently < 35%) of the population is able to successfully raise a second brood (Schulze-Hagen 1991, Cramp 1992, Borowiec 1994; Halupka *et al.* 2008). Breeding males maintain small song-territories (20-100 m<sup>2</sup>) in the breeding season but both adults will travel up to 150 m from the territory to collect food for their young (Cramp *et al.* 1998). Sexes are similar in size and weight, but can be distinguished by the presence of a vascularised brood patch (females) or a 'cloacal protuberance' (male; Bensch and Neilsen 1999; Redfern and Clarke 2001). The breeding weights of females can vary significantly over the breeding season (10.1-14.0 g), with egg weight accounting for up to 1.8 g of female body mass per egg prior to laying (BTO 2005).

## 4.2 Methods

### 4.2.1 Study sites

Three wetland locations in South Wales were used for the current study (Figure 4.1). Cardiff Bay Wetland Reserve (CBWR; 51° 27' 32'' N, 3° 10' 11'' W) is a four hectare wetland consisting of mixed scrub habitat, open pools and large areas of *Phragmites australis* reedbed (*see* Supporting information S4.1). Cosmeston Lakes Country Park (CLCP, 51° 24' 53'' N 3° 6' 0'' W) supports two adjacent small reedbed sites (with total area of approximately 1.5 hectares) separated by 200 m of freshwater lake habitat (*see* Supporting information S4.2). Kenfig National Nature Reserve (KNNR; 51° 32' 16'' N, 3° 45' 47'' W) is a large (six hectare) natural established reed swamp (*see* Supporting information S4.3). All three sites are publicly owned and access was arranged through the local authority.

**Figure 4.1.** Wetland study sites in South Wales, UK: A) Kenfig National Nature Reserve KNNR; B) Cardiff Bay Wetland Reserve CBWR; C) Cosmeston Lakes Country Park CLCP.



#### 4.2.2 *Bird biometric data*

Bird biometric data were collected during the course of 72 ringing sessions between April 2012 and August 2014. During each session, between 72 and 108 m of mist net (Ecotone polyester 14 x 14 mm mesh; [www.ecotone.com.pl](http://www.ecotone.com.pl)) were erected in suitable habitat. Nets were checked every 20 minutes. Captured birds were taken in cotton bags to a processing station nearby (10-200 m away) where species, sex (when possible) and age were determined using plumage and other features. Birds were aged as either fledged in the current year (immature) or fledged before the current year (adult; Svensson 1992). A measure of structural size of each bird was derived from measurements taken of wing length (maximum wing chord to 1 mm), tarsus (tarsal joint to top of flattened foot to 0.1 mm), and total head and bill length (to 0.1 mm). All birds were weighed on an electronic balance (Satrue SA-500; accurate to 0.1 g). The size of the pectoral muscle was scored following Bairlein (1995) on a four-class scale (0 = emaciated to 3 = large muscle mass) and fat score was estimated visually following Kaiser (1993) on a nine-class scale (0 = no fat, 8 = whole belly covered in fat). 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.

#### 4.2.3 *Nest monitoring*

Reed warbler nests were located by systematic searching of suitable nesting habitat (dense, tall stands of *Phragmites*) and by visually tracking adults back to the nest. Once an active nest was located, the status of the nest and the mean total height of the *Phragmites* stems supporting the nest were recorded. In order to obtain a relative measure of the status of *Phragmites* growth at the time of nesting, the heights of the stems supporting the nests were transformed into positive or negative differences of the overall mean height of all measured stems (i.e. '*Phragmites* height index'). The status of each nest was checked every two days

until the first egg was laid, then they were checked twice a day (at ~10:00 and ~16:00 BST) until fledging. In order to generate an index of 'earliness' in the analysis of laying phenology, the dates of the first egg from the first ten nests in each supplementary food treatment (see 4.2.4 *Food supplementation*) each year were transformed into deviates of the mean 'first egg' laying date. The incubation period was defined as the time between the last egg and the day of hatching. Eggs (on laying day) and nestlings (at day four and day six after hatching (day 0 = hatching day)) were weighed to 0.1 g using an electronic balance (Satrue SA-500). On day six of the nestling stage, each nestling was fitted with a unique combination of three plastic colour rings and a numbered metal ring to enable individual identification in the field.

#### 4.2.4 *Food supplementation*

Prey availability for reed warblers was experimentally increased in selected territories at all study sites upon territory establishment in April<sup>3</sup>, by providing live and dried mealworms *Tenebrio molitor* larvae (Coleoptera) in circular containers (2 litre-capacity) resting on wooden bird-tables at 1.5 m height. The food supplementation and unfed treatment groups will be referred to as 'fed' or 'control' treatments respectively, hereafter. These feeding stations were supplied with at least 200 mealworms (mean weight  $\pm$  SD of mealworms =  $0.112 \pm 0.026$  g,  $n = 100$ ) and refilled on at least 3 of every 7 days, until the departure on autumn migration of all the fed adults and their offspring (late August). Feeding bowls were enclosed in a wire mesh cage (an adapted 'potter trap', measuring approximately 300 x 200 x 200 mm of 10 x 10 mm wire mesh) to prevent the mealworms being taken by carrion crows *Corvus corvus* and black-billed magpies *Pica pica*, but permitting access to reed warblers. Other small passerines including European robins *Erithacus rubecula*, common

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<sup>3</sup> When adult males begin to sing consistently.

reed buntings *Emberiza schoeniclus* and Eurasian blue tits *Cyanistes caeruleus* occasionally gained access to the mealworms, but mealworms were always available for reed warblers using the feeders. All adults nesting within 50 m of the feeding stations discovered the mealworms within two to five days and fed daily from containers from the laying period until the end of the breeding season. Fed and control sites were located at least 100 m apart, to minimise the likelihood of accidental supplementary feeding of control birds visiting fed areas. All nests in both treatment groups were filmed for up to two hours, on at least three occasions during the nestling period, to confirm whether or not nestlings were being provisioned with mealworm larvae as well as other invertebrate taxa. The positions of feeding stations were moved between successive breeding seasons to allow the treatment state of site-faithful individuals to change between years, in order to measure the response to treatment at an individual level (*see* Supporting information S4.1-3 for positions of feeding stations in each year).

Adult mass was monitored throughout the breeding cycle and obtained by one of two methods. First, birds attending feeding stations were weighed remotely when they landed on perches in front of the food containers which were temporarily attached to electronic weighing balances (My Weigh iBalance 500, <http://myweigh.com>) and recorded with small video cameras (Sony Handycam DCR-SR32, Sony Corporation, <http://sony.co.uk>) or infrared-triggered trail cameras (Bushnell HD, <http://Bushnell.co.uk>). When adults could not be confidently identified as a specific individual, or if they were not on the perches long enough for the scale to stabilize, no mass value was recorded. Videos were recorded between 06:00 and 18:00 BST every two days throughout the breeding cycle. The second method for obtaining mass was capturing birds in mist nets and weighing them using electronic scales (as described in 4.2.2 *Bird biometrics*). To check that mass estimates taken from mist nets were similar to mass estimates obtained from video methods, mass data on a subset of 30 fed birds were collected using both methods (matched by date and time) and no significant

difference between methods was found (paired t-test,  $t_{29} = 0.324$ ,  $P = 0.748$ ). Weights obtained from both methods were therefore included together in the analysis of body mass.

#### 4.2.5 *Invertebrate monitoring*

A measure of invertebrate prey availability was determined at each site using double-sided yellow (dry-stick) invertebrate traps (Oecos, UK; <http://www.oecos.co.uk/dry%20stick.htm>). This is a standard technique for studying and monitoring activity-density of Diptera (Black and Krafur 1985; Hogsette *et al.* 1993; Goulson *et al.* 2005), the primary prey taxon of Eurasian reed warbler in Europe (see Supporting information S2.1). The availability of wetland invertebrate prey resources were monitored on a weekly basis for the duration of the study (see Chapter 2) using eight traps set in the same locations at a height of 50-120 cm. Total weekly captures of Diptera, Aranea, Hymenoptera and Hemiptera, as well as other less-frequently encountered taxa (<1%) such as Coleoptera and Lepidoptera were recorded for each trap.

#### 4.2.6 *Weather variables*

Air temperature, wind speed and rainfall data were collected every 15 minutes by an automated weather station (Davis Instruments Vantage Pro 2, Hayward CA), located 750 m from the study site for the duration of the study. Temperature measurements were summarised for the analysis to include mean April temperature (mean of all air temperature measurements taken in April), mean laying temperature (the mean of air temperature measurements taken in the five days leading up to the production of the first egg for each nest), mean incubation temperature (the mean of air temperature measurements during the incubation period for each nest) and mean nestling temperature (the mean of air temperature measurements upto six days after hatching). Total rainfall (in mm) was the total measure of

all the rainfall measurements taken during the laying, incubation or nestling periods (as specified for mean temperature) for each nest. Likewise, wind speed (m/sec) was the mean windspeed value for the laying, incubation or nestling periods in each nest.

#### 4.2.7 *Permits*

Licences for the trapping, ringing and colour ringing of birds were obtained from the British Trust for Ornithology. An assent from Natural Resources Wales was required to use KNNR as it is designated Special Area of Conservation and Site of Special Scientific Interest.

#### 4.2.8 *Statistical analysis*

This study tested the effects of food treatment on reed warbler laying date, clutch size, incubation duration, rates of nestling growth, adult mass, fat score and muscle score. As well as the availability of food, these reproductive parameters may also be affected by factors such as adult body size (wing length), time of day, date, local weather conditions and other unmeasurable constraints which may vary by year (e.g. competitive pressure, predator density). Other parameters of interest included laying interval, egg mass, hatching success and nest predation. These effects were investigated using the statistical package R, version 3.1.2 (R Development Core Team, 2014) fitting generalised linear mixed-effects models (GLMMs) using the R package ‘lme4’ (Bates *et al.* 2013). Where appropriate, the identity of the female parent (i.e. their BTO ring number) was used as a random effect in mixed-effects models to account for repeated measures (e.g. repeated egg or nestling measurements from the same nest). All models included year (e.g. 2012, 2013 or 2014) and site (e.g. CBWR, CLCP or KNNR) as random effects to account for year and site-related variances. The final models were selected using the dredge function of the R package ‘MuMIn’ (Barton 2014), which compares candidate models from global models including all relevant variables



(Table 4.1) on the basis of the Akaike's Information Criterion, corrected for small sample size (AICc; Burnham and Anderson 2004).

**Table 4.1** GLMMs of breeding performance parameters monitored in the study

Model	Family/link function	Random Effect	Variables	Interactions
<b>Laying phenology</b>	Guassian/identity	Year Site	Treatment (fed/control) Local invertebrate availability Weather data <i>Phragmites</i> height index	Treatment x Local inverts Treatment x Weather data Treatment x height index Weather data x Weather data
<b>Clutch size</b>	Poisson/log	Year Site	Treatment Local invertebrate availability Weather data Laying date Female wing length	Treatment x Local inverts Treatment x Weather data Treatment x Laying date Treatment x F wing length Weather data x Weather data
<b>Incubation duration</b>	Guassian/identity	Year Site	Treatment Local invertebrate availability Weather data Clutch size hatch date Female wing length	Treatment x Weather data Treatment x Clutch size Treatment x Laying date Treatment x F wing length Clutch size x hatch date
<b>Nestling growth</b>	Guassian/identity	Female ID Year Site	Treatment Local invertebrate availability Weather data Nestling age Brood size Laying date Incubation duration	Treatment x Weather data Treatment x Laying date Treatment x Nestling age Weather data x Weather data Brood size x Weather data
<b>Laying interval</b>	Poisson/log	Year Site	Treatment Local invertebrate availability Weather data Laying date Female wing length	Treatment x Weather data Treatment x Laying date Treatment x F wing length
<b>Egg mass</b>	Guassian/identity	Female ID Year Site	Treatment Local invertebrate availability Weather data Laying date Laying order Clutch size Female wing length	Treatment x Weather data Treatment x Laying date Treatment x F wing length Weather data x Weather data Clutch size x weather data
<b>Hatching success</b>	Binomial/ logit	Female ID Year Site	Treatment Local invertebrate availability Weather data Laying date Laying order Clutch size Female wing length	Treatment x Weather data Treatment x Laying date Treatment x F wing length Weather data x Weather data Clutch size x weather data

**Table 4.2** GLMMs of mass, fat and muscle of breeding adult reed warblers

Model	Family/link function	Random effect	Variables		Interactions
<b>Mass GLMM</b>	Guassian/identity	Individual ID Year Site	✓	Treatment (fed/control)	All two-way interactions
			✓	Local invertebrate availability	
			✓	Weather data	
			✓	Time of measurement	
			✓	Wing length	
			✓	Sex	
			✓	Date (within breeding cycle)	
<b>Fat GLMM</b>	Guassian/identity	Individual ID Year Site	✓	Treatment	All two-way interactions
			✓	Local invertebrate availability	
			✓	Weather data	
			✓	Time of measurement	
			✓	Sex	
			✓	Date	
			✓		
<b>Muscle GLMM</b>	Poisson/log	Individual ID Year Site	✓	Treatment	All two-way interactions
			✓	Local invertebrate availability	
			✓	Weather data	
			✓	Time of measurement	
			✓	Sex	
			✓	Date	

### 4.3 Results

Between 2012 and 2014, 91 breeding adult reed warblers, 165 nests, 496 eggs and 428 nestlings were monitored in CBWR, CLCP and KNNR. The following results examine how food availability and weather variables influence reproductive performance and mass regulation over the breeding season.

#### 4.3.1 Laying Phenology

Laying date was analysed for 120 nests. The most parsimonious model (i.e. with the lowest AIC<sub>c</sub> value) of first-egg laying date included treatment, invertebrate availability, mean April temperature, the mean temperature, total rainfall and mean wind speed, year and the interaction of treatment with April temperature (Table 4.3). Treatment was a significant predictor of the earliness of laying, with fed birds laying earlier ( $13.357 \pm 3.54$  days,

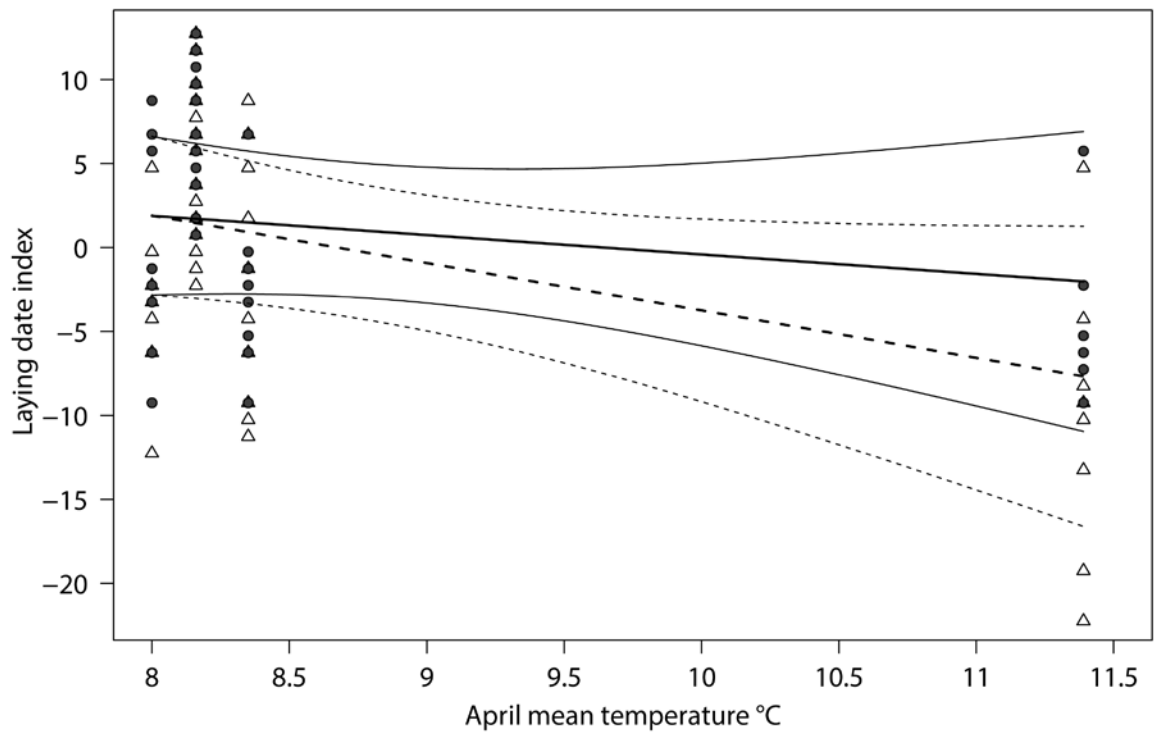
$t_{87.47}=3.766$ ,  $P=0.0003$ ). The interaction with April temperature shows a significant advance in laying date in the higher spring temperatures by up to  $1.67 \pm 0.399$  days ( $t_{87.47}=-4.181$ ,  $P<0.0001$ ; Figure 4.2).

**Table 4.3.** GLMM analysis of breeding Eurasian reed warbler first-egg laying date. ‘Year’ and ‘Site’ are included as random effects to account for non-independence of data from the same year or site conditions. The estimated effects are relative to an intercept value of -67.288, representing the ‘laying date index’ value of a control treatment and ‘zero’ values for the other measured parameters. Positive estimates represent effects that cause later laying while negative estimates represent effects that cause earlier laying.

Parameter	Estimate $\pm$ SE	df	t	P
Treatment (Fed)	-13.357 $\pm$ 3.547	87.47	3.766	0.0003
Invertebrate availability	0.805 $\pm$ 0.072	61.58	11.179	<0.0001
April temp	-0.029 $\pm$ 0.072	2.57	-0.012	0.9914
Mean pre-laying temperature	0.946 $\pm$ 0.177	88.58	5.331	<0.0001
Mean pre-laying Wind	0.460 $\pm$ 0.188	88.23	2.446	0.0164
Total pre-laying Rain	-0.009 $\pm$ 0.003	89.43	-2.825	0.0058
Treatment (Fed) x April temp	-1.670 $\pm$ 0.399	87.47	-4.181	<0.0001

Treatment was a significant predictor of the earliness of laying with fed birds laying earlier. The interaction with April temperature shows a significant advance in laying date in the higher spring temperatures in 2014 by up to  $6.115 (\pm 0.415)$  days (Figure 4.2).

**Figure 4.2.** The effect of mean April temperature on laying index value, showing the interaction with treatment. A zero 'laying date index' value represents the mean laying date, while positive and negative values represent later and earlier laying dates respectively. Fed treatment index values are represented by triangles (and a thicker regression line) while control nests are circles (and a thinner regression line).



#### 4.3.2 Egg mass

The mean egg mass was  $1.76 (\pm 0.07)$  g. Clutch size was the only fixed term in the selected model representing an effect of  $-0.048 (\pm 0.016)$  g per additional egg in the clutch ( $t_{87.21} = -2.894$ ,  $P = 0.0048$ ), with lower weight eggs associated with larger clutches. The inclusion of treatment was not supported in the best model suggesting no significant effect on egg mass.

#### 4.3.3 Clutch size

Of the 165 nests monitored as part of the study, only 99 completed their clutch, the other 66 were predated, abandoned or destroyed by bad weather. Although most nests (89) produced a total of four eggs, nine nests produced five eggs and one nest produced three eggs. The

null model (i.e. containing no fixed terms) was best supported, indicating no significant effects of treatment, local invertebrate activity-density, laying date, weather variables or female size on clutch size.

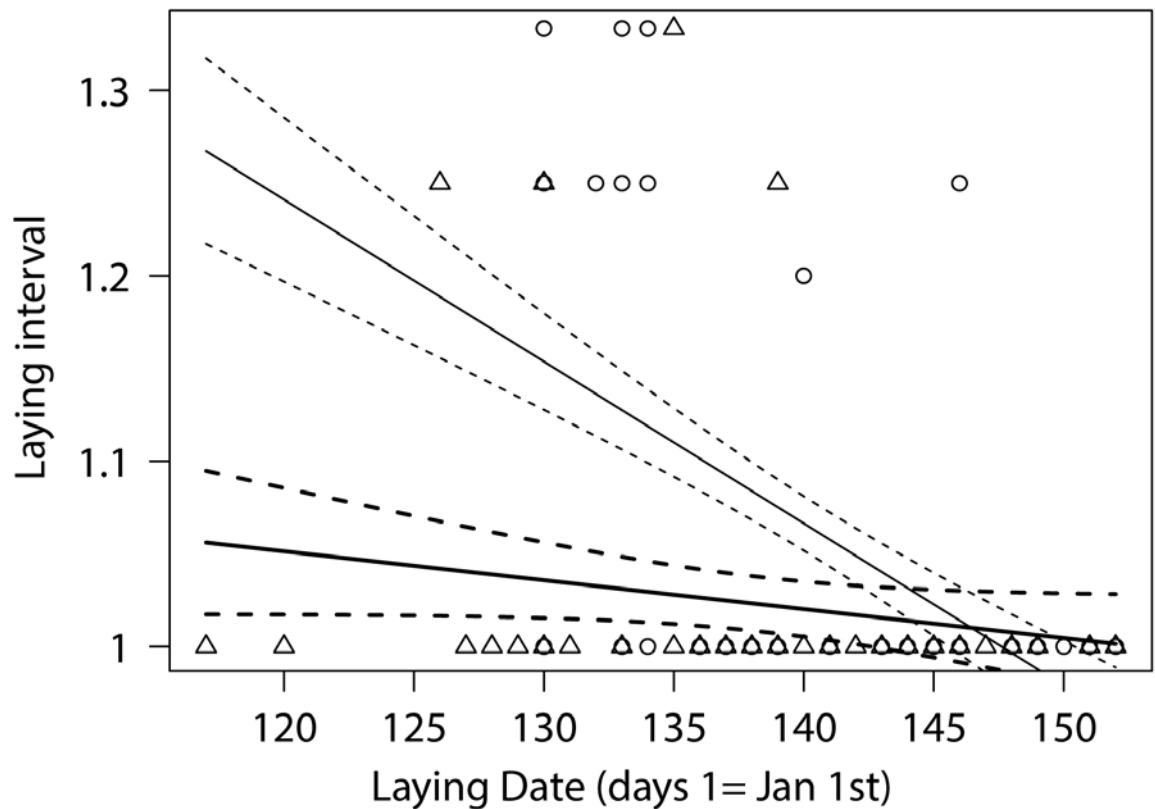
#### 4.3.4 *Laying interval*

The rate of egg laying in reed warblers was generally one egg per 24 hours after the first egg (i.e. an interval of one day), although in 15 out of 99 nests there were intervals of two days or more between eggs. Only one out of these 15 cases occurred in a fed treatment nest. The best model identified treatment and laying date as having a significant reducing effect on laying interval (Table 4.4). Treatment was a significant predictor of shorter laying intervals and the interaction with laying date indicates that fed females are more likely to lay at intervals of one day, regardless of date while control females are more likely to lay at longer intervals earlier in the season (Figure 4.3).

**Table 4.4.** GLMM analysis of reed warbler laying interval. The estimated effects are relative to an intercept value of 2.225, representing a hypothetical laying interval in a control treatment at zero value for laying date.

Parameter	Estimate $\pm$ SE	<i>d.f.</i>	<i>t</i>	<i>P</i>
Treatment (Fed)	-1.058 $\pm$ 0.345	94.21	-3.071	0.0028
Laying date	-0.008 $\pm$ 0.002	54.31	-3.812	0.0003
Treatment x Laying date	0.007 $\pm$ 0.002	94.14	2.943	0.0041

**Figure 4.3.** The effect of treatment interaction with laying date on laying interval. Fed treatment interval values are represented by triangles (and a thicker regression line and dashed upper SE lines) while control interval values are circles (and a thinner regression line and dashed upper SE lines).



#### 4.3.5 Incubation duration

The incubation period varied between nine and 13 days. The model included treatment, mean April temperature, mean incubation temperature and clutch size (Table 4.5) and indicates that supplementary feeding treatment and mean incubation temperature reduced the incubation period (Figure 4.4). Clutch size was an important predictor in this model, increasing the incubation period by  $1.668 (\pm 0.301)$  days for each additional egg.

#### 4.3.6 Hatching success

Out of the 165 nests monitored across the three breeding seasons, 99 nests resulted in hatching success. Of these successful nests, 14 contained unhatched eggs, resulting in a total of 390 hatched eggs. The inclusion of treatment was not supported by the best model suggesting no significant effect on hatching success. The best model revealed mean April temperature, mean incubation temperature invertebrate availability and laying date to be significantly positively associated with hatching success, while mean incubation wind speed to be negatively associated (Table 4.5, Figure 4.4). There was a significant effect of treatment on egg predation with control nests suffering 25 predation events out of 85 nests and fed nests suffering eight predation events out of 50 nests (Fishers exact test; odds ratio= 0.442,  $P=0.0480$ ).

**Table 4.5.** Binomial GLMM analysis of reed warbler hatching success. The estimated effects are relative to an intercept value of -75.657.

Parameter	Estimate $\pm$ SE	$z$	$P$
April temperature	2.735 $\pm$ 1.182	2.313	0.0207
Mean incubation temperature	0.942 $\pm$ 0.225	4.176	<0.0001
Mean incubation wind speed	-0.358 $\pm$ 0.071	-5.025	<0.0001
Date of laying	0.334 $\pm$ 0.039	8.486	<0.0001

Figure 1 is a scatter plot with a fitted logistic curve and confidence interval. The x-axis is labeled 'Laying Date (days 1 = Jan 1st)' and ranges from 115 to 155. The y-axis is labeled 'Hatching success' and ranges from 0.0 to 1.0. The data points are open circles. A solid line represents the fitted logistic curve, and two dashed lines represent the confidence interval. The data shows a sharp increase in hatching success as the laying date increases, starting near 0.0 at day 115 and reaching near 1.0 by day 145.

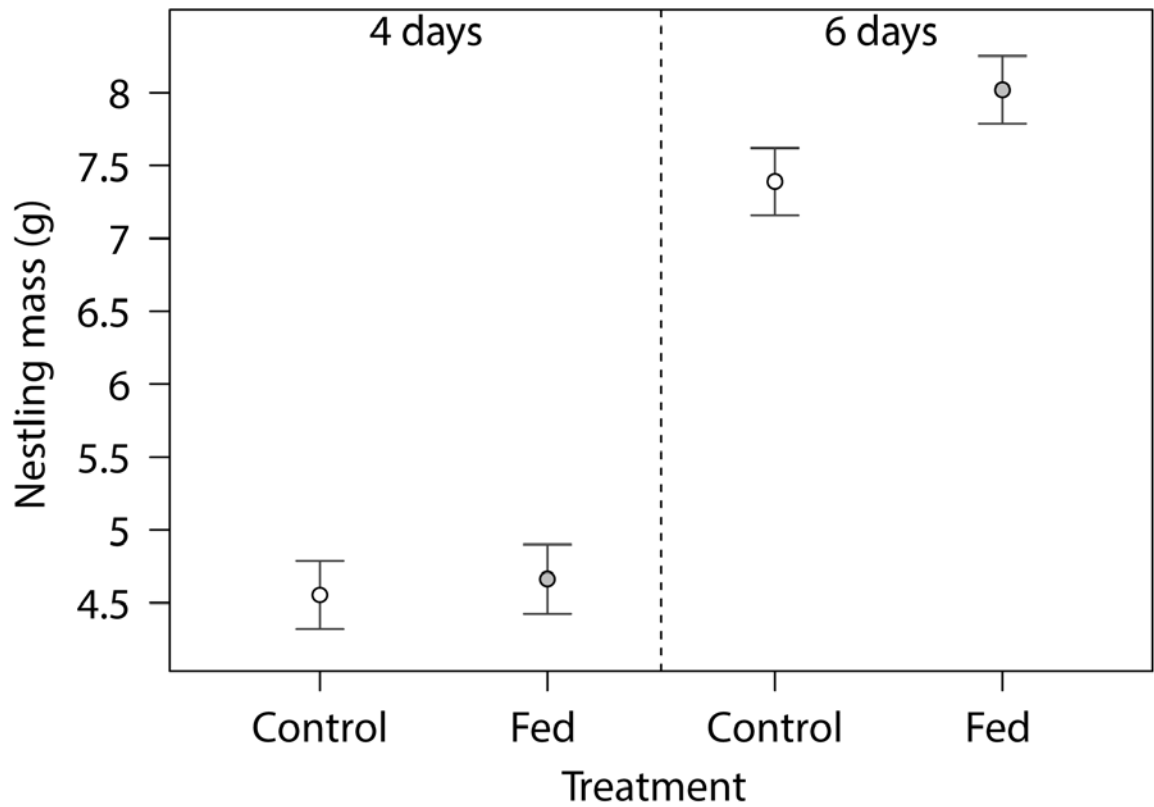
The nestling growth model identified the mean difference in nestling mass between day four and day six as  $1.417 \pm 0.034$  g. Nestling mass was significantly greater in the fed treatment group than control group (Table 4.6; Figure 4.5). Brood size was also significantly associated with nestling mass, with lighter nestlings associated with larger brood sizes. Higher values of wind and rain were also associated with lower nestling mass.



**Table 4.6.** GLMM analysis of reed warbler nestling mass. The estimated effects are relative to an intercept value of 15.076 representing a control bird at age 4 with hypothetical zero values for invertebrate availability, mean temperature and siblings.

<b>Parameter</b>	<b>Estimate <math>\pm</math> SE</b>	<b><i>df</i></b>	<b><i>t</i></b>	<b><i>P</i></b>
Treatment (Fed)	-0.929 $\pm$ 0.289	627.9	-3.209	0.0014
Mean temperature	-0.847 $\pm$ 0.335	92.2	-2.530	0.0131
Total rain	-0.086 $\pm$ 0.019	109.4	-4.578	<0.0001
Mean wind	-0.612 $\pm$ 0.246	101.1	-2.485	0.0146
Brood size	-3.041 $\pm$ 1.192	90.6	-2.550	0.0124
Age (day 6)	1.417 $\pm$ 0.034	593.4	41.357	<0.0001
Mean temperature x Brood size	0.169 $\pm$ 0.080	91.8	2.116	0.0371
Mean temperature x Mean wind	0.030 $\pm$ 0.015	96.7	2.035	0.0446
Total rain x Mean wind	0.008 $\pm$ 0.002	103.3	4.519	<0.0001
Treatment (Fed) x Age (day 6)	0.260 $\pm$ 0.052	629.6	5.007	<0.0001

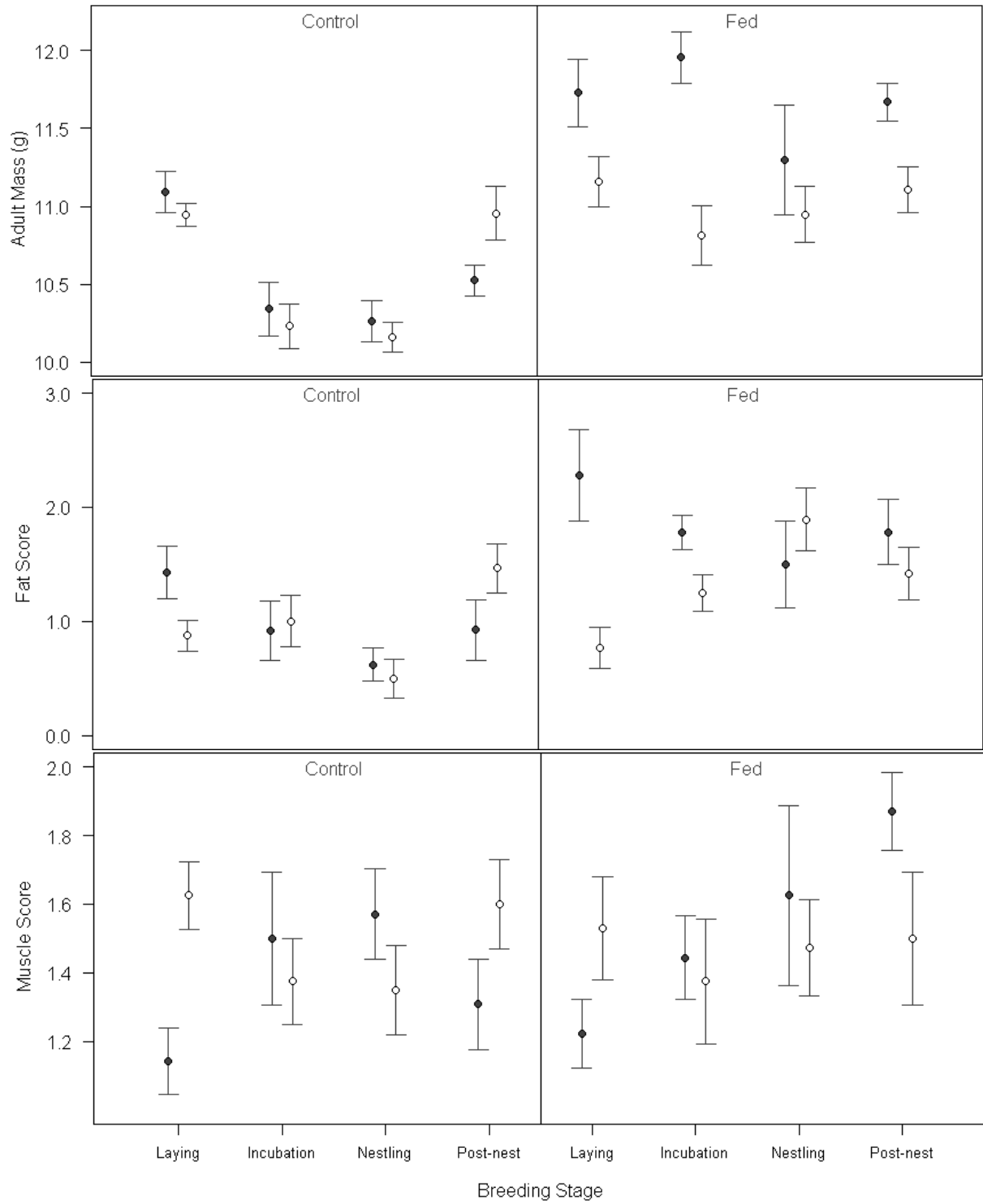
**Figure 4.5.** Reed warbler nestling mass in relation to age and treatment. Predicted mean nestling mass values represented by circles (Control: white-filled; Fed: black-filled) with standard error bars, accounting for brood size, invertebrate activity-density, temperature and year effects.



#### 4.3.8 Adult mass, fat and muscle

The body masses of 58 unfed adult birds (35 males and 23 females) and 46 fed adult birds (21 males and 25 females) were measured over the course of three breeding seasons. The best model explaining the overall variation in body mass revealed that breeding stage was an important predictor, with mass lowest during the nestling period (Figure 4.6; Table 4.7).

**Figure 4.6.** Body mass, fat score and muscle score of female (black-filled points) and male (white-filled points) reed warblers in control and fed treatments during periods of the breeding season. Filled points represent means with  $\pm$  standard error bars.



**Table 4.7.** GLMM analyses of overall breeding Eurasian reed warbler mass. The effects of time of day were controlled for by including them as covariates. The estimated effects are relative to an intercept value of 5.123, representing male control treatment mass in the laying stage and hypothetical zero value for date, time and wing size.

<b>Parameter</b>	<b>Effect <math>\pm</math> SE</b>	<b>df</b>	<b><i>t</i></b>	<b><i>P</i></b>
Time of day	-0.03 $\pm$ 0.024	231.77	-1.258	0.2098
Wing size (mm)	0.058 $\pm$ 0.036	69.68	1.603	0.1135
Treatment (Fed)	-1.147 $\pm$ 0.699	249.96	-1.640	0.1022
Date	0.015 $\pm$ 0.006	186.18	2.457	0.0149
Stage (incubation)	-0.551 $\pm$ 0.129	247.19	-4.274	<0.0001
Stage (nestling)	-1.033 $\pm$ 0.178	226.91	-5.787	<0.0001
Stage (fledging)	-0.996 $\pm$ 0.248	198.79	-4.021	0.0001
Sex (F)	0.157 $\pm$ 0.158	70.45	0.992	0.3246
Treatment (Fed) x Sex (F)	0.626 $\pm$ 0.180	113.130	3.484	0.0007
Treatment (Fed) x Date	0.010 $\pm$ 0.004	242.84	2.320	0.0212

Treatment was identified as a significant predictor of mass interacting with date (i.e. the mass increase over time was larger in fed treatments) and sex (females showed a larger mass increase in fed treatments than males).

The pattern of mass change is matched most closely by fat score (Table 4.8; Figure 4.6). The best model for fat score did not include date as predictors. The model indicated that fat score was only significantly lower during the nestling stage. Treatment had a significant positive effect in interaction with sex (higher fat in fed females) and with breeding stage (higher fat in fed birds in the nestling stage).

**Table 4.8.** GLMM analyses of overall breeding Eurasian reed warbler fat score. The estimated effects are relative to an intercept value of 1.031, which represents the fat score of male reed warbler in the control treatment during the laying stage of the breeding season.

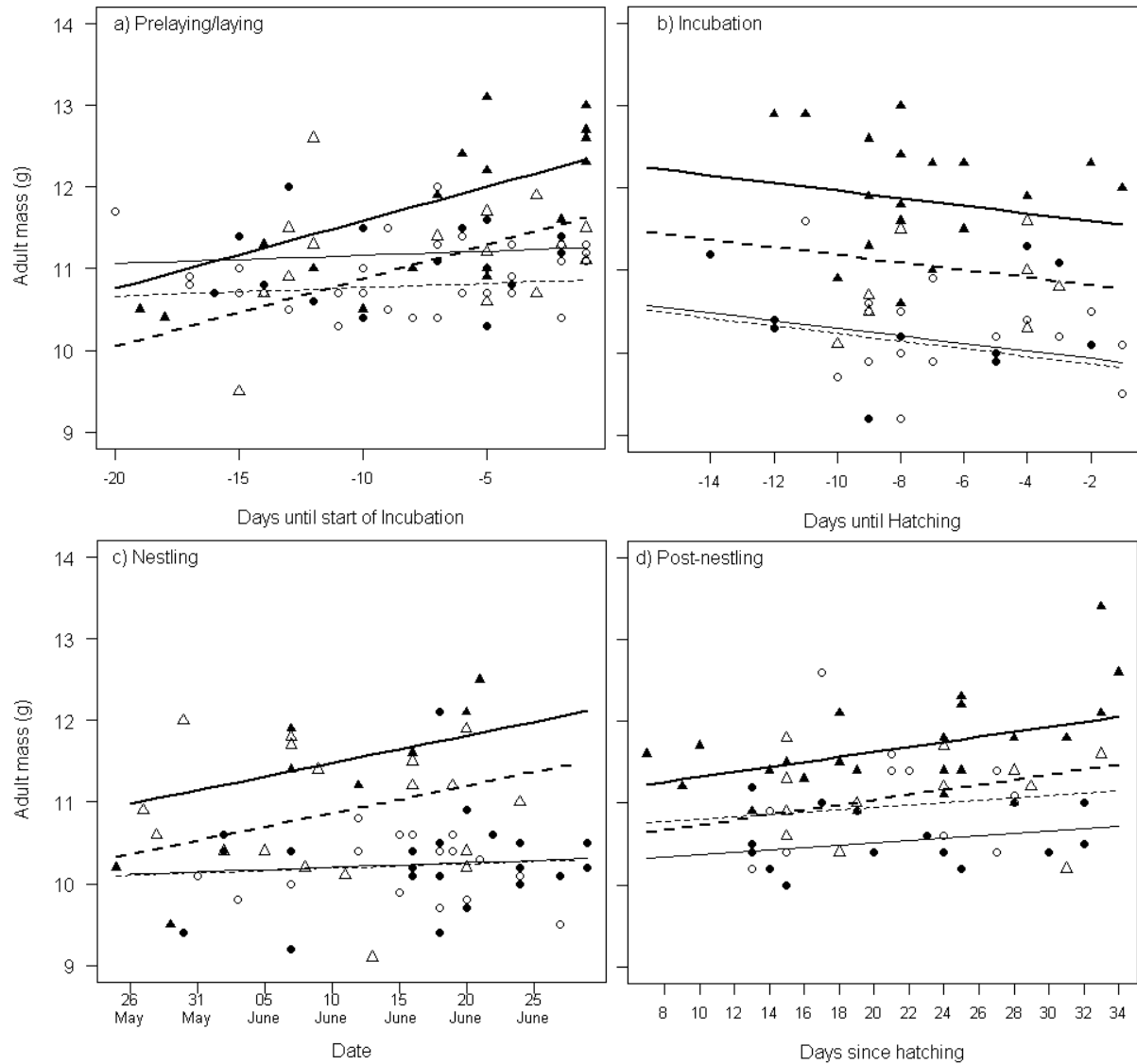
Parameter	Effect $\pm$ SE	df	t	P
Treatment (Fed)	0.182 $\pm$ 0.258	232.09	1.839	0.4805
Stage (incubation)	-0.022 $\pm$ 0.235	247.02	1.636	0.9257
Stage (nestling)	-0.475 $\pm$ 0.213	247.63	3.421	0.0270
Stage (fledging)	0.163 $\pm$ 0.234	238.69	1.651	0.4863
Sex (F)	0.011 $\pm$ 0.190	111.91	1.115	0.9542
Treatment (Fed) x Sex (F)	0.587 $\pm$ 0.278	152.34	5.113	0.0362
Treatment (Fed) x Stage (incubation)	0.021 $\pm$ 0.347	245.15	0.981	0.9520
Treatment (Fed) x Stage (nestling)	0.916 $\pm$ 0.333	248.92	6.919	0.0064
Treatment (Fed) x Stage (fledgling)	-0.075 $\pm$ 0.332	241.29	1.112	0.8207

The best model for variation in muscle score across the breeding season did not include breeding stage but included date. Muscle score showed a slight but significant increase with date (GLMM estimate  $0.006 \pm 0.002$  (relative to an intercept of 0.636),  $t_{250.52}=11.379$ ,  $P=0.0066$ ).

#### 4.3.9 Mass and fat change within breeding stages

Mass change within breeding stages was significant with particularly strong treatment effects in the prelaying/laying, incubation and nestling periods (Figure 4.7; Table 4.9).

**Figure 4.7.** Body mass of control (circles) and fed (triangles) female (black-filled) and male (white-filled) reed warblers during **a)** the prelaying/laying **b)** incubation **c)** nestling and **d)** post-nestling period of the breeding season. Regression lines (Females: solid lines; Males: dashed lines; Control: thin lines; Fed: thick lines) represent estimated changes in mass.



**Table 4.9.** GLMM analyses of breeding Eurasian reed warbler mass during the a) Prelaying/laying stage; (intercept value of 5.251) b) Incubation stage; (intercept value of 9.139) c) Nestling stage; (intercept value of 4.931) d) Post-nestling stage; (intercept value of 6.10).

Parameter	Effect $\pm$ SE	<i>df</i>	<i>F</i>	<i>P</i>
<b>a) Prelaying/Laying</b>				
Treatment (Fed)	0.755 $\pm$ 0.243	71.00	20.016	0.0028
Days prior to incubation (DPI)	0.010 $\pm$ 0.015	59.00	18.366	0.4832
Sex (F)	0.317 $\pm$ 0.228	56.88	6.464	0.1689
Treatment (Fed): Sex (F)	0.363 $\pm$ 0.263	64.10	1.909	0.1719
Treatment (Fed): DPI	0.069 $\pm$ 0.021	58.58	11.072	0.0015
<b>b) Incubation</b>				
Treatment (Fed)	0.955 $\pm$ 0.226	46.03	54.646	<0.0001
Days prior to hatching	-0.046 $\pm$ 0.018	16.09	6.734	0.0195
Sex (F)	0.064 $\pm$ 0.246	40.17	4.630	0.0375
Clutch size	0.282 $\pm$ 0.193	24.50	2.138	0.1563
Treatment (Fed) x Sex (F)	0.717 $\pm$ 0.337	46.91	4.524	0.0387
<b>c) Nestling</b>				
Treatment (Fed)	0.969 $\pm$ 0.173	62.99	20.016	<0.0001
Date	0.034 $\pm$ 0.014	62.57	18.366	0.0170
Treatment (Fed) x Sex (F)	0.601 $\pm$ 0.360	60.37	2.784	0.10036
Treatment (Fed) x Date	0.028 $\pm$ 0.02	61.98	1.901	0.17296
<b>d) Post-nestling</b>				
Treatment (Fed)	0.275 $\pm$ 0.139	55.99	29.913	0.1688
Date	0.028 $\pm$ 0.009	55.99	10.270	0.0022
Sex (F)	-0.366 $\pm$ 0.191	55.99	0.307	0.5964
Treatment (Fed) x Sex (F)	0.875 $\pm$ 0.267	55.99	10.710	0.0018

In the prelaying/laying period, fed birds of both sexes increased mass at a greater rate than control birds. During the incubation period, all birds lost mass at a similar rate although fed females carried highest mass, followed by fed males. Clutch size was not a significant predictor of mass. During the nesting stage, the fed birds increased mass while control birds did not change. The pattern of mass loss over time in this stage was best described using the ordinal date rather than the 'period since hatching'. In the post-nesting stage, all birds

increased mass with fed females carrying highest mass and control females carrying the least mass. Fat score varied significantly between sexes in the prelaying/laying stage and between fed and control birds during the prelaying/laying, incubation and nestling stages over the course of breeding stages (Table 4.10).

**Table 4.10.** GLMM analyses of breeding Eurasian reed warbler fat during the a) Prelaying/laying stage; (intercept value of 0.771) b) Incubation stage; (intercept value of 1.165) c) Nestling stage; (intercept value of 0.561) d) Post-nestling stage (intercept value of 1.601).

<b>Parameter</b>	<b>Effect <math>\pm</math> SE</b>	<b>df</b>	<b>F</b>	<b>P</b>
<b>a) Prelaying/laying</b>				
Treatment (Fed)	0.554 $\pm$ 0.447	72.99	6.077	0.0160
Days prior to incubation (DPI)	0.002 $\pm$ 0.030	72.99	5.135	0.0264
Sex (F)	0.478 $\pm$ 0.321	72.99	15.145	0.0002
Treatment (Fed): Sex (F)	0.867 $\pm$ 0.466	72.99	3.464	0.0667
Treatment (Fed): DPI	0.089 $\pm$ 0.042	72.99	4.636	0.3460
<b>b) Incubation</b>				
Treatment (Fed)	-6.662 $\pm$ 3.262	40.71	4.171	0.0476
Clutch size	-0.417 $\pm$ 0.346	46.75	1.407	0.2337
Treatment (Fed) x Clutch size	1.914 $\pm$ 0.803	40.51	5.096	0.0294
<b>c) Nestling</b>				
Treatment (Fed)	1.217 $\pm$ 0.226	65.99	5.390	<0.0001
<b>d) Post-nestling</b>				
Treatment (Fed)	0.490 $\pm$ 0.456	52.91	20.016	0.0877
Date	-0.020 $\pm$ 0.020	59.66	18.366	0.3256



## 4.4 Discussion

This study used supplementary feeding to investigate the degree to which changes in food availability may impact on the reed warbler's behaviour, mass regulation across different parts of the breeding cycle and overall breeding performance. Supplemental food advanced the laying date, reduced the laying interval and incubation period, and increased nestling growth rates. The size of these effects on laying date and laying interval were dependent on spring temperature and date respectively. Specifically, during the warmer spring temperatures in 2014 (but not during the cooler springs of 2012 and 2013), food supplementation advanced the mean laying date by 6.1 days ( $\pm 0.4$ ). Food supplementation reduced the laying interval most strongly at the start of the breeding season, reducing the mean period between eggs by 0.2 days ( $\pm 0.2$ ). The mean incubation period was reduced in fed treatments by 0.5 days ( $\pm 0.2$ ), whilst nestlings of food-supplemented parents weighed 0.7 g ( $\pm 0.01$ ) more at day six; which could represent more rapid growth, larger nestlings or heavier stomach contents. Food supplementation did not measurably influence hatching success or clutch size.

### 4.4.1 *Laying phenology*

This study shows that laying date has strong associations with temperature and invertebrate activity-density. The significant interaction between treatment and mean April temperature indicated that food supplementation caused a more substantial advance in laying date during the warmer of the three years. These results are consistent with observational studies of reed warblers (Schaefer *et al.* 2006; Halupka *et al.* 2008), where earlier breeding was associated with warmer May to July temperatures and advanced *Phragmites* growth. Continental European populations of reed warbler have been reported laying 18 days earlier over the last 33 years, as well as increasing the proportion of second broods from 0-10% in the 1970s and

1980s to 15-30% between 1994 and 2006 (Halupka and Wroblewski 1998; Halupka *et al.* 2008). It has hitherto been unclear if the primary driver behind earlier laying is the faster growth of *Phragmites* reed as nesting vegetation, or the earlier rise in availability of invertebrate prey, but the significant food supplementation effect on laying phenology in our study suggests that laying date is constrained by food availability as both treatments had the same *Phragmites* conditions. Consistent with our findings, experimental increases in food availability are associated with earlier breeding dates in other passerines including common starling *Sturnus vulgaris* (Kallander and Karlsson 1993); Eurasian blue tit (Svensson and Nilsson 1995), European blackbirds *Turdus merula* (Desrochers 1992) and great tits *Parus major* (Kallander 1974). Many of these species rely on highly seasonal prey resources (e.g. caterpillars) and therefore have a risk of mismatch between supply and demand if they nest late, which could translate into a decrease in productivity (Visser *et al.* 1998, Both and Visser 2001, Thomas *et al.* 2001). This is less likely to be the case for reed warblers, which feed their young on a diverse range of invertebrate prey populations which emerge sequentially throughout the summer, resulting in a prolonged period of high abundance without any clear peak (Dyrce 1979, Bibby and Thomas 1985, Schulze-Hagen 1991; Dyrce and Zdunek 1996, see Chapter 2). Male reed warblers arrive on the breeding grounds weeks before laying begins, and thus, the onset of breeding is unlikely to be constrained by the timing of arrival on the breeding grounds, as has been suggested for European pied flycatchers *Ficedula hypoleuca* (Both and Visser 2001). Therefore, if earlier nesting is possible (i.e. through sufficient *Phragmites* growth and if weather conditions permit (Dyrce 1981, Borowiec 1994, Halupka and Wroblewski 1998)), the benefit for doing so is greater hatching success, a higher survival rate of early first brood fledglings (Daan *et al.* 1988; Price *et al.* 1988; Moller 1994) and increased recruitment across the whole breeding season from potentially raising a second brood. Such results suggest that reed warblers will advance their laying date in the future in response to warming temperatures. However, constraints on the advancement of the arrival time of adult females on the breeding grounds may ultimately

restrict the extent to which laying date can advance (Borowiec 1992, Witkowski *et al.* 1995; Halupka *et al.* 2008).

#### 4.4.2 *Clutch size*

Although clutch size has been related to laying date for a range of species (Jarvinen 1989; Winkler and Allen 1996; Winkel and Hudde 1997), including reed warblers (Schaefer *et al.* 2006), this study did not reveal a significant ‘calendar effect’, nor was there a significant effect of food supplementation on clutch size. There was also no evidence to suggest that egg quality (measured as egg weight) was higher in fed treatments. Clutch size and egg quality in reed warblers appear to have very little variance compared to many other passerines (Christians 2002) and this may represent the optimum investment effort based on a trade-off between current reproductive effort and future reproduction and survival (Nilsson and Svensson 1996).

#### 4.4.3 *Laying interval*

An important finding was the effect of supplemental food on laying interval, particularly in interaction with laying date, which indicates that egg laying rate is directly food limited in the early stages of the breeding season when food is less abundant. Shorter laying intervals have been reported in blue tits *Cyanistes caeruleus* (Nilsson and Svensson 1993) and European Kestrels *Falco tinnunculus* (Aparicio 1994) provisioned with supplementary food but not in Australian reed warblers *A. australis* (Eikenaar *et al.* 2003). The benefit of shorter laying intervals is the earlier onset of incubation, which reduces the period of vulnerability to egg predation (Clarke and Wilson 1981). There may be strong selection for shorter laying intervals in reed warblers as they are prone to high rates of nest predation (Honza *et al.* 1998).

#### 4.4.4 Incubation duration

The fed treatment effect was estimated to shorten the incubation period by almost half a day, a substantial effect size in the context of the typical 12-day incubation period. Such an effect suggests that fed birds are incubating the clutch more consistently or intensively than control birds, perhaps as they are able to forage for shorter periods if food is readily available during foraging bouts, or if they already carry sufficient reserves. Birds in better condition may also be less likely to leave the nest to forage during the colder periods at dusk and dawn, so eggs may be kept closer to optimal temperatures throughout the incubation period. Significantly shorter incubation periods in response to supplementary feeding have been found in a range of passerine species; including the Australian reed warbler (Eikenaar *et al.* 2003), as well as blue tits (*Cyanistes caeruleus*; Nilsson and Smith 1988), northern wheatears (*Oenanthe oenanthe*; Moreno 1989) and pied flycatchers (Sanz 1996).

By reducing the requirement to leave the nest, it is possible that lower rates of nest predation would occur, since the frequency and duration of eggs being uncovered (and undefended) by the well-camouflaged parent would be lower (Skutch 1962; Eikenaar *et al.* 2003). Indeed, nest predation occurred more frequently in control nests than supplementary fed nests. Similar patterns have been found in mourning doves *Zenaida macroura* (Westmoreland and Best 1986), common eiders *Somateria mollissima* (Swennen *et al.* 1993) and common pheasants *Phasianus colchicus* (Persson and Goransson 1999) and are at least partly attributed to reduced periods of nest vulnerability.

#### 4.4.5 Nestling growth

The supplementary food effect in our study resulted in an increased rate of nestling growth, measured by nestling weight at day six. Such effects have been shown in food limitation

experiments which limit the growth rates in other passerines (Rodenhous and Holmes 1992). The body condition of female pied flycatchers during incubation is an important predictor of fledgling mass; heavier, food-supplemented females produced heavier fledglings (Lifjeld and Slagsfold 1986). Similarly, offspring of supplementary fed great tits grew faster than control nestlings (Banbura *et al.* 2011). Greater prey availability for parents and nestlings is therefore likely to be beneficial for nestling growth rates, which could accelerate fledging and thus reduce the period of vulnerability to predation and adverse weather conditions. Nestling reed warblers fledge at 10-11 days but are able to jump from the nest to evade predators from day seven (Leisler *et al.* 2011). Given the high rates of predation in wetlands, adaptations to reduce the period of nestling vulnerability will be strongly favoured by selection. Increases in food abundance, parental investment and predation have all been shown to modify nestling growth rate in acrocephalids (Ricklefs 1969; Duckworth 1991; Kleindorfer *et al.* 1997).

#### 4.4.6 *Mass and fat change*

Through experimental supplementary feeding, this study has revealed patterns of mass change in breeding reed warblers consistent with the energetic stress hypothesis as found in other species (Johnston 1993), particularly those studied at natural breeding densities (Cucco and Malacarne 1997; Nagy *et al.* 2007; Neto and Gosler 2010). The size of the effect of supplemental food on adult body mass was greatest during the incubation stage, when access to local invertebrate prey is at its lowest. The statistical models of body mass had better explanatory power (goodness of fit) by relating mass to corresponding (first egg) laying dates or hatching dates for each individual, rather than the ordinal date. Since the (first egg) laying dates and hatching dates in this study varied by 16-28 days, this suggests that mass change was strongly associated with nesting activities rather than seasonal changes in the environment and any associated changes in food availability. During the pre-laying/laying

period, fed birds were heavier compared with those in control treatments. In control treatments, both sexes showed only a minor increase in mass, with females on average 0.317g heavier than males. This difference may be attributable to the development of the oviduct, vascularisation of the brood patch and assimilation of the constituents of egg production (Ricklefs and Hussell, 1984; Moreno 1989; Gosler, 1991; Houston *et al.* 1995; Woodburn and Perrins 1997; Redfern 2010) as well as the accumulation of fat. The higher fat reserves in fed birds correspond with more consistent laying rates (i.e. every 24 hours) than in control females, which had higher incidences of egg laying interruptions (i.e. a 48-hour gap between laying successive eggs). In passerines in particular, it is apparent that egg production is constrained by immediate foraging intake (Lack 1968, Winkler and Walters 1983), therefore additional fat reserves during this period may enable birds to prioritise foraging for specific nutrient components of egg production (e.g. calcium-rich prey) rather than for energy intake.

The mass change observed in males during prelaying/laying is attributed to fat or muscle accumulation since the equivalent development of testes has not been shown to have significant influence on body mass (Redfern 2010). The seasonal pattern of mass change was exhibited (albeit to different extents) by both males and females in each treatment group, as expected of species that share incubation (e.g. house sparrow *Passer domesticus*; Schifferli, 1976, European starling Ricklefs and Hussell 1984 and Eurasian blackcap *Sylvia atricapilla* Redfern 2010). The highly significant difference between the two sexes in fat levels during the pre-laying/ laying stage suggests that, while males are preparing for incubation, they may be strongly limiting their rate of fat accumulation as a strategy to limit their body mass in order to reduce mass-dependent costs of engaging in territorial and courtship activities (Norberg 1981; Lima 1986; Moreno 1989). This sex difference in mass regulation lends support to the flight efficiency hypothesis. However, the significant increase in mass among supplementary fed males during this stage also provides evidence for a

strong influence of food limitation within this period. Overall, these findings indicate that, early in the breeding cycle when food resources are at their lowest, birds are (to an extent) food limited and will deposit energy reserves in preparation for the subsequent activities of egg production and incubation when possible, despite the apparent compromises to flight efficiency and predation.

During the nestling stage, significant declines in body mass of parents were observed over time and between treatment groups. Birds with larger broods were significantly lighter than those with smaller broods, as found in similar studies that conclude energetic stress was the primary determinant of mass levels at this stage in the breeding cycle (Askenmo 1977, Bryant 1979, Ricklefs and Hussell 1984, Merilä and Wiggins 1997). Supplemented female black-throated blue warblers *Dendroica caerulescens* spent less time foraging and more time at the nest than control females (Nagy *et al.* 2007). One of the benefits of this might be increased brooding activity which may result in faster nestling development, which was observed in fed nests in Nagy's study, as in the present study on reed warblers.

A limitation of the present supplementation experiment was that individual breeding pairs could not be provisioned with an additional amount of food predicted to occur under a particular climate projection. This was because multiple birds (and species) used the same feeding station and precisely regulating the amount of food for each pair was not feasible. Thus, the study should not be viewed as an attempt to simulate future food availability. Rather, by supplementing food across whole breeding seasons, aspects of reed warbler performance that are currently limited by food availability have been identified. The most important of these traits were clutch initiation, incubation duration, nestling development (this Chapter) and annual survival (Chapter 6). These are therefore the factors that are most likely to be affected by climate-linked changes in food availability. Similarly, the measure of

local invertebrate activity-density was based on weekly measures (as described in Chapter 2), but is insufficient to represent differences in availability between days, which may be the timescale on which reed warblers respond to changes in food availability.

The different methods of recording mass in control and fed treatment birds may also represent a source of bias since control birds were always caught in mist nets to weigh them, while fed birds may have been recorded on the remote weighing stations. Other than the previously-described bias toward catching more males than females in mist nets during the early stages of the breeding cycle, there is also the issue of the potential effects of repeated capture and handling stress on long term weight and possibly breeding performance (Schwilch and Jenni 2001). Inter-annual weather variation is another important consideration for this study. The 2012 season was a bad year for breeding birds because of the storms and heavy rainfall during the main incubation period (Whitehouse *et al.* 2013), leading to the abandonment of many reed warbler nesting attempts. Similarly, the 2013 season commenced later than 2012 and 2014 as a result of cold temperatures throughout late March and early April. Consequently, *Phragmites* growth was delayed, which may have caused some reed warblers to build nests in adjacent alternative habitats, which were missed by nest finding efforts focussed in the reedbeds. It is possible that the intensive nest monitoring in this study may influence the success of the nesting attempt with such high rates of disturbance potentially leading to parental abandonment or increased rates of predation, particularly during more stressful years. It is unknown whether this is the case, but since the success rates of the nests ( $\sim 0.45 \pm 0.15$ ) was higher than the national average ( $0.35 \pm 0.11$ ; Baillie *et al.* 2012), there is little support for this.

Another limitation of the study design is that it is unknown whether the extra energy from food supplementation increased fecundity by enabling reed warblers to initiate second



broods. Maximising lifetime reproductive success is assumed to be a strategy of short-lived species given unlimited resources (Hillström 1995, Potti and Morino 1997, Cichon 2001, Holt *et al.* 2002). Future investigations would repeat this experiment to generate larger sample sizes and follow individuals through second broods and between seasons, to consider the diverse energetic demands and the balance between investments for maximizing lifetime reproductive success. This may shed further light on why parent birds, particularly females, lose mass during the breeding season.

This study focussed on the responses of birds to changes in environmental conditions and tested how phenotypic plasticity at the population-level can adjust behaviour and physiological processes to optimise breeding performance and survival. However, there was individual variability in the level of responsiveness to these changes, in particular whether parent reed warblers took advantage of supplementary food or not. Whether this trait actually improves breeding performance in the long term (i.e. lifetime fitness) is beyond the scope of the present study, but is the focus of current research efforts. Further work in this field would assess the heritability of these traits in subsequent generations in order to gain an understanding of possible long-term evolutionary consequences of changes in food availability.

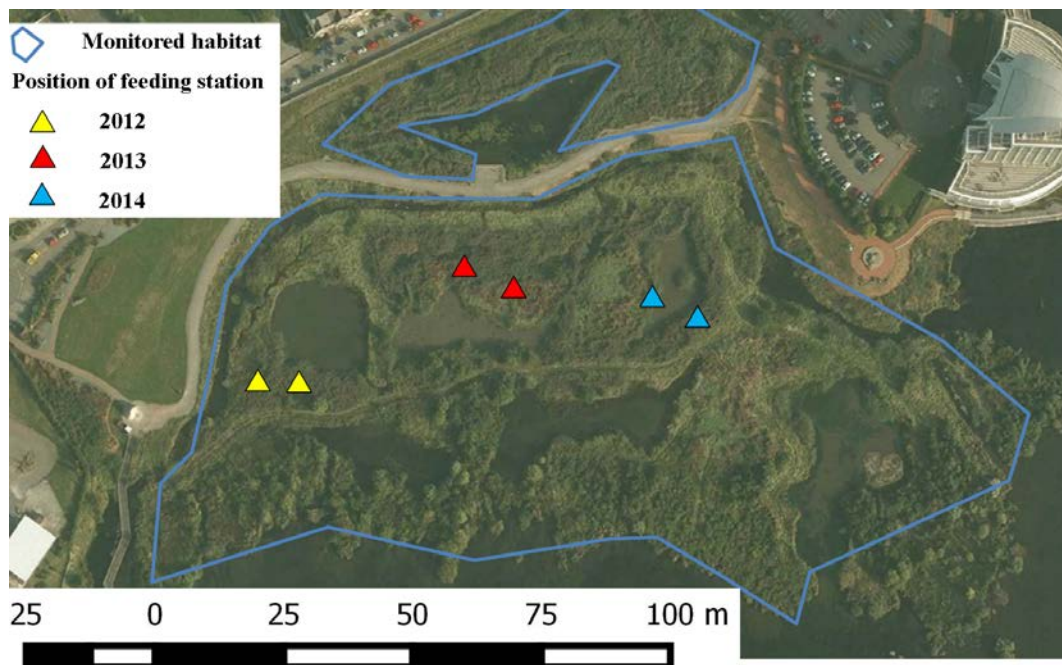
#### 4.4.7 *Conclusions*

While European wetlands currently provide seemingly abundant prey resources for breeding wetland migrants, it is predicted that climate warming over the coming decades will increase overall prey abundance, and higher abundances of prey will become available earlier in the breeding season. This study has shown that increased food availability, particularly early in the breeding season, has the potential to increase the fitness of reed warblers by allowing

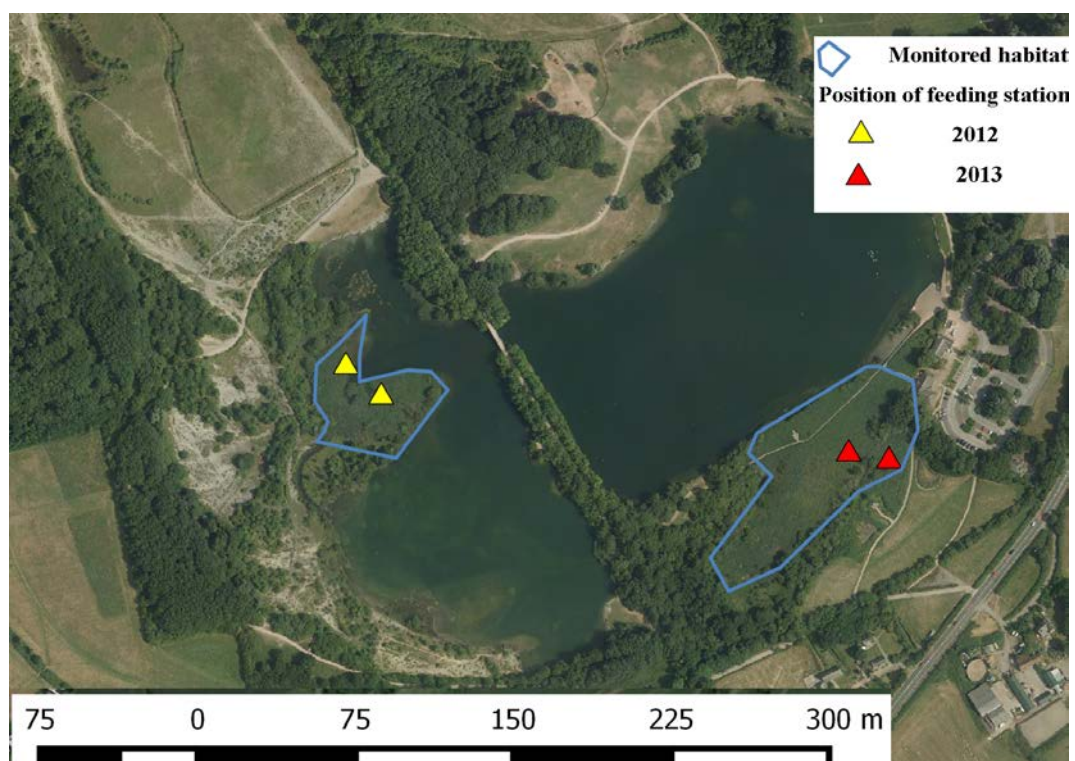
earlier breeding and shorter nesting durations which, in theory, may allow second broods to be completed within the time-window of sufficient invertebrate prey availability. Although hatching success and productivity were not affected by additional food, the faster growth rates in fed nestlings may represent a greater rate of offspring survival by reducing the period of nestling vulnerability. Earlier fledging is also associated with higher rates of fledgling survival and subsequent recruitment, which is a key factor driving population change (Roper *et al.* 2010; Etterson *et al.* 2011; Oppel *et al.* 2013). This study suggests that breeding reed warblers will respond to higher availability of food by increasing their pre-laying/laying mass, which may in turn facilitate reduced egg laying intervals, shorter incubation durations and earlier hatching dates. The responses to food availability measured in the form of breeding parameters and mass regulation reveal the extent to which individuals can respond to environmental change. Such phenotypic plasticity in breeding parameters, in response to climate-driven changes in food availability, may be behind the increasing population size of reed warblers in the UK over recent decades, coinciding with regional climate warming in NW Europe.

## Supporting Information

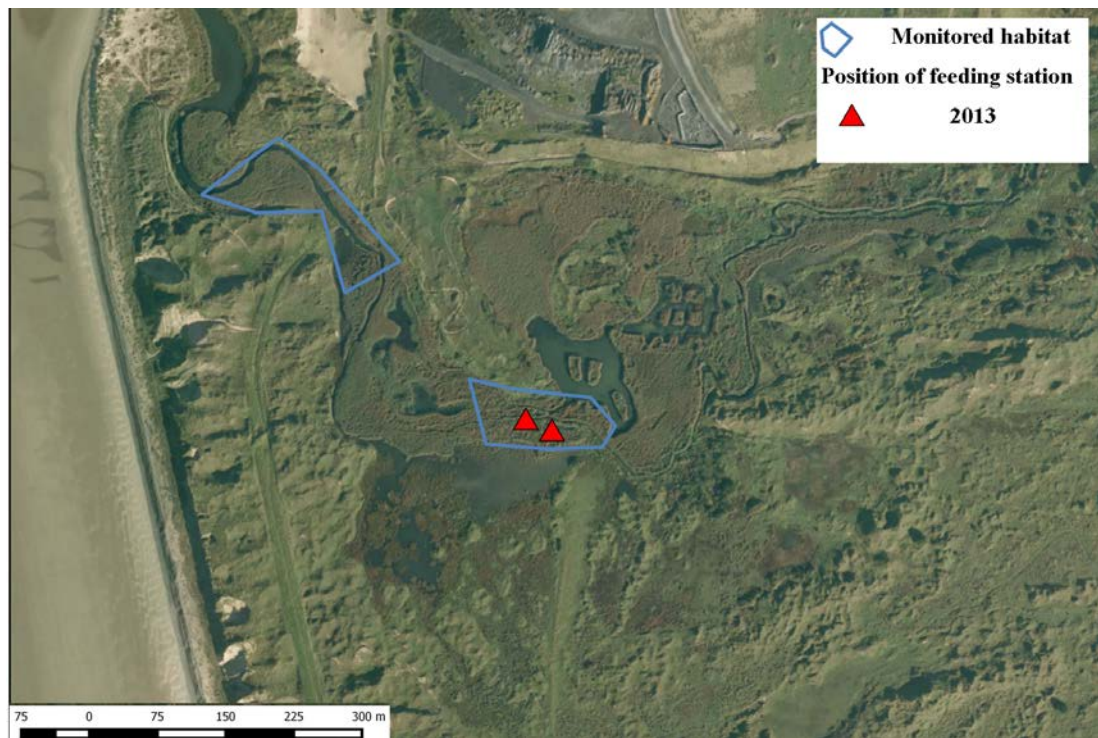
### S4.1 *Position of feeding stations in Cardiff Bay Wetland Reserve CBWR 2012-2014*



### S4.2 *Position of feeding stations in Cosmeston Lakes Country Park CLCP 2012-2013*



S4.3 *Position of feeding stations in Kenfig National Nature Reserve KNNR 2013*



## **Chapter 5**

### **Habitat use and body mass regulation among warblers in the Sahel region during the non-breeding season**

## Summary

Migratory birds face significant challenges across their annual cycle, including occupying an appropriate non-breeding home range with sufficient foraging resources. This can affect demographic processes such as over-winter survival, migration mortality and subsequent breeding success. In the Sahel region of Africa, where millions of migratory songbirds attempt to survive the winter, some species of insectivorous warblers occupy both wetland and dry-scrubland habitats, whereas other species are wetland or dry-scrubland specialists. In this study we examine evidence for strategic regulation of body reserves and competition-driven habitat selection, by comparing invertebrate prey activity-density, warbler body mass, body size and extent of fat and pectoral muscle deposits, in each habitat type during the non-breeding season. Invertebrate activity-density was substantially higher in wetland habitats than in dry-scrubland. Eurasian reed warblers *Acrocephalus scirpaceus* occupying wetland habitats maintained lower body reserves than conspecifics occupying dry-scrub habitats, consistent with buffering of reserves against starvation in food-poor habitat. A similar, but smaller, difference in body reserves between wet and dry habitat was found among subalpine warblers *Sylvia cantillans* but not in chiffchaffs *Phylloscopus collybita* inhabiting dry-scrub and scrub fringing wetlands. Body reserves were relatively low among habitat specialist species; resident African reed warbler *A. baeticatus* and migratory sedge warbler *A. schoenobaenus* exclusively occupying wetland habitats, and Western olivaceous warblers *Iduna opaca* exclusively occupying dry habitats. These results suggest that specialists in preferred habitats and generalists occupying prey-rich habitats can reduce body reserves, whereas generalists occupying prey-poor habitats carry an increased level of body reserves as a strategic buffer against starvation.

## 5.1 Introduction

Migratory birds face the challenge of finding sufficient food resources on their wintering grounds to avoid starvation during the non-breeding season and to prepare themselves for the return migration to their breeding grounds. To do this, they must select suitable wintering habitat, in competition with other migrant and resident species (Hutto 1985; Leisler 1992; Jones *et al.* 1996). The causes and consequences of habitat choices made by migratory birds outside the breeding season are widely studied and much debated (Hinde 1956; Rogers 2005; Fernández and Lank 2006; Zwarts *et al.* 2009). Although it is well established that competition affects the distribution of individuals on their temperate breeding grounds (Newton 1998; Dhondt 2011), it has been suggested that competition may be less important on the wintering grounds where migrant birds may have lower energetic requirements (Greenberg 1986; Salewski *et al.* 2003; Salewski and Jones 2006). Migratory birds arriving *en masse* in the wintering areas must, however, select between habitats that may differ in foraging quality, the density of resident and migrant competitors, and other factors such as predation pressure (Lima and Dill 1990; Sutherland 1996). The strength of these factors is likely to be affected by variations in climate. Indeed, overwinter survival of some long-distance migrant birds is closely linked to climate-driven measures of broad-scale environmental conditions on their wintering grounds, such as El Niño Southern Oscillation, Sahel Precipitation Index and Normalised Difference Vegetation Index (Hutto 1980; Den Held 1981; Peach *et al.* 1991; Sillett *et al.* 2000; Johnson *et al.* 2006; Norman and Peach 2013). Such correlations imply that survival of some, or many, migrant species may be limited by overwinter foraging conditions.

In a competition-driven system, residents and dominant or early-arriving migrants may be able to secure territories in primary (higher quality) habitat while subordinate or late-arriving individuals may be competitively excluded into secondary habitats: the competitive

exclusion hypothesis (Hutto 1980; Levey and Stiles 1992; Herremans 1997). Compelling evidence for the role of inter-specific competitive exclusion in the shaping of migrant and resident communities in the wintering grounds is lacking (Leisler 1992; Greenberg 1986; Salewski and Jones 2006). However, evidence for such competitive exclusion in an intra-specific context was provided by Perez-Tris and Telleria (2002), who showed that resident blackcaps *Sylvia atricapilla* breeding in southern Spain maintained their breeding territories in primary forest habitats into the non-breeding season, while migrant blackcaps arriving at the start of the wintering season ‘leap-frogged’ into the secondary (lower quality) scrub habitats not occupied by residents.

An alternative to the competitive exclusion hypothesis (though not necessarily mutually exclusive with it) is that migrants are “eurytopic” (i.e. adaptable) and have less restrictive habitat requirements during the non-breeding season, allowing them to use a wider range of winter habitat types than ecologically similar but more specialised resident species (Leisler 1992; Levey and Stiles 1992; Salewski *et al.* 2002). Such adaptability and breadth of foraging strategies has been shown in wintering golden orioles *Oriolus oriolus*, which were, by virtue of their wider range of foraging tactics, able to survive in lower quality microhabitats than were preferred by resident species (Baumann 2001). Migrants may therefore be able to exploit lower quality habitats with lower densities of resident competitors (Cox 1968; MacArthur 1972; Karr 1976; Cox 1985), even though they may be markedly different from the habitat types used on their temperate breeding grounds (Strong and Sherry 2000; Marra and Holmes 2001; Salewski *et al.* 2002; Salewski and Jones 2006). Furthermore, migrants may be able to occupy habitats which residents may find unsuitable, either due to vegetation structure or insufficient food availability to sustain future breeding attempts (i.e. habitats of ‘low breeding currency’; Greenberg 1995; Johnson *et al.* 2005).



It is well-established by both theoretical and empirical studies that the level of body reserves carried by small birds reflects a trade-off between starvation and mass-dependent costs of body reserves (McNamara and Houston 1990; Verboven and Visser 1998). These mass-dependent costs include increased predation risk, flight costs and increased foraging requirements (Blem 1975; Witter and Cuthill 1993; Thomas 2000; Gosler *et al.* 2002). Balanced against these mass-dependent costs are the benefits of the stored body reserves acting as a strategic buffer against starvation in situations where food is scarce or unpredictable. This hypothesis of ‘adaptive mass-regulation’ or ‘strategic buffering against starvation’ is supported by experimental studies on north-temperate wintering birds such as greenfinches *Carduelis chloris* (Ekman and Hake 1990), European starlings *Sturnus vulgaris* Witter *et al.* 1995; Witter and Swaddle 1997) and great tits *Parus major* (Bednekoff and Krebs 1995). These species responded to food limitation by accumulating mass (in comparison to controls) and to food supplementation by decreasing mass. Strategic buffering has been implicated in the observed fattening of wintering brambling *Fringilla montifringilla* (Jenni and Jennieiermann 1987), great tits (Gosler 1996) and Siberian Jays *Perisoreus infaustus* (Ratikainen and Wright 2013) in response to declining food availability or the risk of prolonged periods of food limitation. While the influence of predation pressure and competition are important determinants of energy reserves carried by birds (Gosler *et al.* 2002; Witter and Swaddle 1995), it is clear that the overall availability of food in a habitat is a major influence of bird foraging and mass regulation strategies. Despite these examples, however, little is known about the mass regulation strategies used by European migrants wintering in Africa.

Wetlands in the western Sahel, mostly within the Inner Niger Delta and Senegal Delta, represent the main overwintering area for many Western Palearctic-African migrant bird species (Grimmett 1987). The area and quality of these wetlands is dependent on the extent of summer rainfall across West Africa. These gradually declined through much of the 20<sup>th</sup>

Century (Zwarts *et al.* 2009), reducing their carrying capacity for wintering songbirds (Peach *et al.* 1991; Norman and Peach 2013). In addition to climate impacts, habitat loss and degradation from agriculture and irrigation have led to further reduction of available wetland habitat in the Sahel (Zwarts *et al.* 2009). Many of the areas surrounding the wetlands comprise dry scrub habitats, which are also occupied by migrants. The invertebrate-rich wetlands support a mixed community of insectivorous ‘Old World’ warblers (superfamily *Sylvoidea*), including the resident species, the African reed warbler *Acrocephalus baeticatus* and greater swamp warbler *A. rufescens*, as well as migrant species including sedge warbler *A. schoenobaenus* and Eurasian reed warbler *A. scirpaceus* (Moreau 1972; Aidley and Wilkinson 1987; Sauvage *et al.* 1998; Leisler *et al.* 2011). The dry scrub supports dry-habitat breeding migrant warblers, such as subalpine warbler *Sylvia cantillans*, western olivaceous warbler *Iduna opaca* and common chiffchaff *Phylloscopus collybita* (henceforth “chiffchaff” (Brown and Demey 2001). Most of these species are restricted to either wetland or scrub habitats, but three are relative habitat generalists: Eurasian reed warbler regularly occupies dry scrub, while subalpine warbler and chiffchaff often forage in the ecotone between scrub and wetland habitats. Such use of multiple winter habitat types by warbler species is well known (Rabøl 1987; Leisler 1992; Salewski *et al.* 2002). Furthermore, there appears to be significant intra-specific variation in the body reserves (in the form of fat and pectoral muscle) of birds wintering in West Africa (Aidley and Wilkinson 1987a; Loske 1990), although the reasons for such variation are unknown. However, while several studies have shown intraspecific responses of wintering migrant birds to habitat quality gradients in Neotropical ecosystems (Sherry and Holmes 1996; Johnson *et al.* 2006; Smith *et al.* 2010), no study has attempted to investigate mass regulation strategies among warbler species occupying the two major types of wintering habitats in the Sahel; wetland and dry-scrub.

In the present study, we investigated the distribution, structural size and extent of body reserves (in the form of fat and pectoral muscle) of insectivorous songbirds in a wintering

area in Senegal, West Africa, during three successive non-breeding seasons. The aims of the study were to: 1) assess the relative abundance of invertebrate prey resources in wetland and dry scrub habitats, providing a measure of habitat quality; 2) identify habitat preferences of five migratory warbler species and one resident, comprising two wetland specialists, one dry scrub specialist and three habitat generalists; and 3) compare the body mass, fat, pectoral muscle and size of individuals in wet and dry habitats, to test the hypothesis that habitat usage and body condition are driven by strategic responses to the availability of food in the different habitats. We tested predictions about the level of body reserves (in the form of fat and pectoral muscle) expected under conditions of direct food limitation compared to strategic regulation of body reserves, in both wetland and dry-scrub habitats. Specifically, if warblers are strategically regulating their body reserves as a buffer against starvation, we predict that individuals inhabiting dry scrub habitat where food availability is lower (and thus starvation risk is greater), carry higher levels of energy reserves than in habitats where food is more abundant. If, however, warbler body reserves are directly limited by food availability, we predict body reserves to be lower in the habitat with lowest food availability. By including the 'habitat specialist' species African reed warbler, sedge warbler and western olivaceous warbler in this study, we test whether this pattern extends across species among habitat specialist and habitat generalist species differing in their migratory tendency and timing of arrival on the wintering grounds.

## 5.2 Methods

### 5.2.1 Study Area

The ‘Parc National des Oiseaux du Djoudj’ (16° 21’ 59’’ N, 16° 16’ 26’’ W) is located in the semi-arid zone in Senegal, West Africa and covers an area of 16,000 ha of seasonally flooded waterways. Its landscape is *Acacia-Commiphora* grassland and *Tamarix senegalensis* scrub savannah interspersed with a range of *Phragmites* and *Typha*-dominated wetland habitats. The study area supports wintering populations of a range of warbler species including Eurasian reed warbler, sedge warbler, chiffchaff, subalpine warbler, western olivaceous warbler and African reed warbler (Table 5.1). Fieldwork was conducted near the village of ‘Diadiem 3’ (16° 21’ 7’’ N, 16° 16’ 34’’ W), in the south west of the national park in wetland and dry scrub habitats near Marigot du Khar. Permission to undertake fieldwork was obtained from the national park authority.

**Table 5.1.** Study species status and winter habitat preferences.

Study Species	Status	Winter Habitat
<i>Eurasian reed warbler</i>	migrant	generalist
<i>common chiffchaff</i>	migrant	generalist
<i>subalpine warbler</i>	migrant	generalist
<i>sedge warbler</i>	migrant	wetland
<i>African reed warbler</i>	resident	wetland
<i>western olivaceous warbler</i>	migrant	dry scrub

Mist nets (Ecotone polyester 14 x 14 mm mesh; [www.ecotone.com.pl](http://www.ecotone.com.pl)) were used to sample the community of warblers occupying four locations within an approximately 40 hectare section of wetland (centred at 16° 22' 25" N, 16° 16' 12" W) over three winter seasons (January 2012, 2013 and 2014) and six locations within an approximate 400 hectare section of dry scrub habitat (centred at 16° 21' 44" N, 16° 15' 49" W) in the surrounding area in two winter seasons (January 2013 and 2014). Wetland study sites were located 260-1550 m apart. Dry scrub study sites were located 100-2000 m apart. The minimum distance between wetland and dry study sites was 775 m. Although individual birds were occasionally caught in sites adjacent to those in which they were originally ringed, no individuals ringed in wetland sites were recorded in dry scrub sites, or vice-versa. Bird biometric data were collected during 24 morning or evening ringing sessions across the three years, during a period when birds were not migrating (between 17 and 29 January in each year). Each habitat type was subject to the same netting effort per ringing session, over the course of the study (66 m per session, approximately 36 hr/m). Nets were checked at least every 20 minutes.

### 5.2.2 *Bird biometric data*

Captured birds were taken in cotton bags to a nearby processing station where species and age (where possible) were recorded following Svensson (1992). The following biometric measurements taken: wing length (maximum wing chord to 1 mm), tarsus length (tarsal joint to top of flattened foot to 0.1 mm), total head length (back of skull to distal tip of bill, to 0.1 mm) and mass using an electronic balance (to 0.1 g) with time of weighing recorded. The measurement techniques followed the methods described by Svensson. The size of the pectoral muscle was scored following Kaiser (1993; 0 = emaciated to 3 = large muscle mass) and subcutaneous fat deposits were estimated following Bairlein (1995: fat score; 0 = no visible subcutaneous fat, 8 = whole belly covered in fat). To eliminate among-observer

variability, all measurements were either made or checked by one person (JV). The recording period occurred after the typical winter moulting period for Eurasian reed and sedge warblers, so age was generally not determinable. Each bird was fitted with a British Trust for Ornithology (BTO) issued metal ring.

### 5.2.3 *Invertebrate Monitoring*

A measure of invertebrate prey availability was determined using sticky traps (yellow, double sided, effective area 100 cm<sup>2</sup>, Oecos, Hertfordshire, UK). These traps are highly effective for sampling the activity-density of Diptera (Black and Krafur 1985; Hogsette *et al.* 1993; Goulson *et al.* 2005), the primary prey taxon of Eurasian reed warbler in Europe (Cramp 1992). To assess stability of wetland invertebrate prey resources over the dry season we monitored the invertebrates on a weekly basis for a period of three months between 16 January and 20 March 2012. Seven traps were set in each of the four sites used for bird monitoring, attached to a mixture of scrub and *Phragmites* vegetation at heights of between 0.5-1.2 m and at least 10 m away from mist net positions and any regular pathways used by mammals (including humans). These wetland sites and four dry scrub habitats were also monitored using seven traps in each site over the course of one week in 2013 and 2014 (with traps set in the same positions in wetlands as in 2012) and in dry scrub habitats. Invertebrates were not monitored in dry scrub habitats in 2012. Traps were attached around the edges of habitat fragments set at heights between 0.5- 1.2 m. Total captures of Diptera, Arachnidae, Hymenoptera and Hemiptera, as well as other less-frequently encountered taxa (<1%) such as Coleoptera and Lepidoptera recorded in each habitat, providing a cumulative measure of activity-density, were compared between wetland and dry scrub sites. To assess general differences in invertebrate size between habitats, all sampled invertebrates were measured for body length (excluding legs, wings and antennae) and categorised as either small ( $\leq 5$  mm) or large ( $> 5$  mm). This threshold size value is used in other similar studies testing for prey differences for wintering small billed migrant birds for which diet is

primarily comprised of small invertebrate prey (Johnson *et al.* 2005; Jedlicka *et al.* 2006). The difference in distribution of invertebrate size (small and large) was compared between wetland and dry scrub sites. Mean daily temperatures were recorded in each habitat type using temperature loggers (LASCAR EL USB-1).

#### 5.2.4 *Data analysis*

All analysis was undertaken using R version 3.0.3. (R Core Team 2014).

##### 5.2.4.1 *Assessment of Invertebrate Resources: 2012 Wetland habitat analysis*

The invertebrate activity-density across the 2012 study period were analysed with generalized linear mixed-effects models (GLMM; R package “lme4”; Bates *et al.* 2013) using date as a fixed effect and trap location as a random intercept.

##### 5.2.4.2 *Assessment of Invertebrate Resources 2013 and 2014: between-habitat analysis*

Differences in activity-density and the distribution of invertebrate size using the January 2013 and 2014 invertebrate data were analysed using a generalized linear model (GLM) using habitat type (“wetland” or “dry scrub”) and year as factors. Differences in the variances of invertebrate samples between habitat types were tested using an *F*-test.

##### 5.2.4.3 *Assessment of habitat preferences*

We assessed habitat preference among warbler species by modelling probability of occurrence using a binomial GLM with ‘habitat’ as the binary dependent variable (i.e. “dry” or “wet”), and species as an independent variable. Habitat preferences were compared among species using the ‘contrast’ package (Kuhn *et al.* 2013), with positive and negative

parameter values representing closer association with wetlands and dry scrub habitats, respectively.

#### 5.2.4.4 *Body mass, muscle, fat and body size comparisons*

Intra-specific comparisons of body mass and structural body size (wing length) were made for birds occupying both habitats. Body mass and structural body size was not comparable between species because of differences in overall size and shape of species. Comparisons of fat and muscle reserves of birds using both habitat types were made between species as well as within species.

Body mass was compared between habitats for each generalist species (Eurasian reed warbler, subalpine warbler and chiffchaff) using a generalised additive model (GAM) implemented using the “mgcv” package (Wood 2011). Habitat type was modelled as a factor, flattened wing chord, total head length and tarsus length were modelled as linear relationships to control for body size, and time of day was modelled using a cyclic cubic regression spline to allow for the diurnal variation in body mass. We also tested for differences in mass between years, using the same model structure, but with year added as a fixed factor. For birds captured on more than one occasion during the same winter, only the first capture event was included in the analysis, to avoid pseudo-replication. Only six birds were captured in more than one winter, and their recaptures in subsequent years were excluded from the analysis. Residual diagnostic plots from the models were used to verify the assumptions of normality and homogeneity of model residuals, and to test for unduly influential observations (Zuur *et al.* 2010).



Intra-specific differences in the structural body size of individuals between habitat types were compared using a general linear model (GLM), using flattened wing chord as a dependent variable, and habitat type and year as independent effects. An alternative model using the first principal component (PC1) of a principal components analysis (PCA) of the three measures of bird body size (flattened wing chord, tarsus and total head length) as a dependant variable did not improve the fit of the model.

Inter- and intra-specific comparisons of body condition were conducted using muscle and fat scores, since these scores represent an index of energy reserves and allows for direct comparisons of condition between species of different size and morphology (such comparisons using body mass are problematic because of the difficulty in defining lean body mass in live birds). Comparisons between species of fat and muscle reserves are valid because these are size-independent variables (Johnson *et al.* 1985; Brown 1996; Green and May 2001; Bergstrom and Sherry 2008). Since the muscle and fat score methods applied in this study used ordered discrete values (0-3) and (0-8) respectively, a proportional odds regression (a special case of ordinal logistic regression) was used to compare muscle and fat scores between habitats, while controlling statistically for time of day (Lemeshow and Hosmer 2000). Proportional odds regression models were fitted as ordinal regression models, using the “MASS” package (Venebles and Ripley 2002). Before the proportional odds regression was performed, the muscle and fat scores were pooled into one of three levels “0”, “1” and “>1”, so as to distinguish between birds with minimal, low and higher reserves. Pooling together birds with fat score >1 increased the sample size for this category, allowing more powerful contrasts to be made. The ordinal logistic regression analysis generated an odds ratio for each species in a particular habitat. The odds ratio represents the odds of a particular species having a muscle or fat score one unit higher than a reference species, in a particular habitat.

### 5.3 Results

#### 5.3.1 Invertebrate prey resource differences between and within habitats

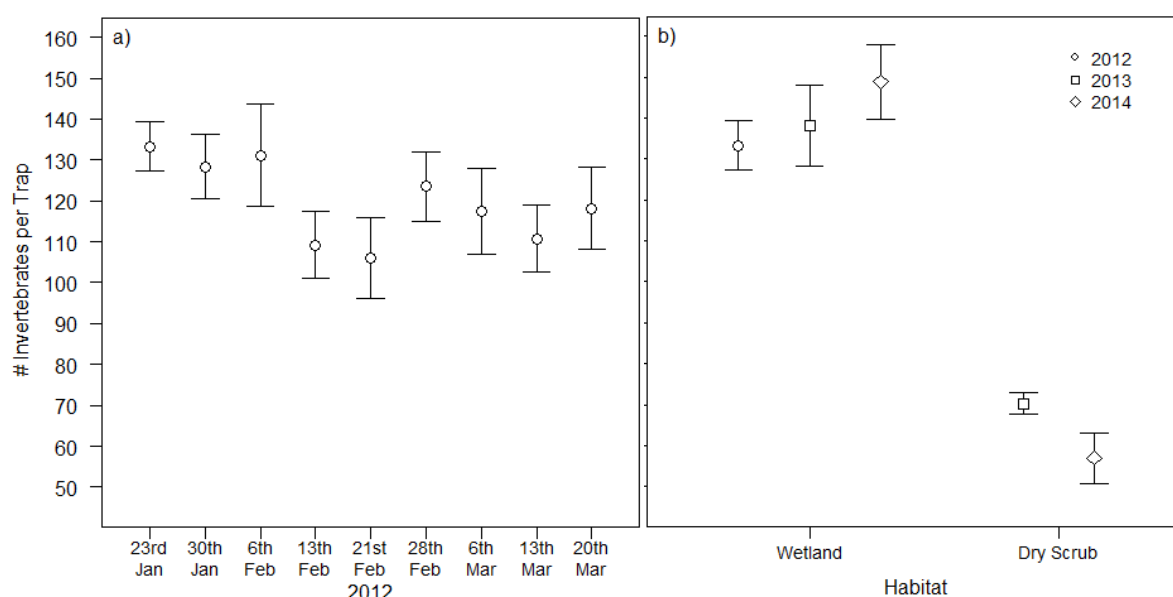
The longer monitoring period in 2012 (three months) revealed a decline of 10.6% in invertebrate abundance over the winter in wetland habitats (GLMM; slope estimate =  $-0.017 \pm 0.002$ ,  $Z = -7.36$ ,  $P < 0.0001$ ; Figure 5.1a). In both 2013 and 2014, wetland and dry scrub habitats supported a similar invertebrate community at the Order level (Table 5.2), but mean abundance of invertebrates per sample in the wetlands ( $135.2 \pm 4.15$ ) was more than double that of the dry scrub habitat ( $57.52 \pm 3.07$ ; GLM:  $F_{141,140} = 182.141$ ,  $P < 0.0001$ ; Figure 5.1b). Variances of invertebrate samples in wetlands were significantly higher than dry scrub in 2013 ( $F_{27,27} = 5.891$ ,  $P < 0.0001$ ) but not in 2014 ( $F_{29,27} = 1.88$ ,  $P = 0.103$ ). There was significant variation in the occurrence of large invertebrates between wetland and dry scrub habitats (GLM;  $F_{1,140} = 37.369$ ,  $P < 0.0001$ ). 2.3% of all trapped invertebrates in wetlands in 2013 and 2014 were large, consisting of Arachnidae, Diptera, Hymenoptera, Lepidoptera and unidentifiable specimens, compared with 1.1% in dry scrub habitats consisting of Arachnidae, Diptera and Hymenoptera (Table 5.2).

**Table 5.2.** Abundances of small and large invertebrates by taxonomic group trapped in wetland and dry scrub sites in PNOD during January 2013 and 2014 combined.

	Wetlands			Dry Scrub		
	Small ( $\leq 5$ mm)	Large ( $> 5$ mm)	<i>n</i>	Small ( $\leq 5$ mm)	Large ( $> 5$ mm)	<i>n</i>
Arachnidae	1	25	26	0	10	10
Diptera	6970	41	7011	2124	20	2144
Hymenoptera	3794	19	3813	496	6	502
Hemiptera	307	0	307	54	0	54
Lepidoptera	0	2	2	0	0	0
Coleoptera	34	0	34	144	0	144
Unknown	431	3	434	367	0	367

Total	11364	263	11627	3185	36	3221
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**Figure 5.1.** Mean numbers of invertebrates per trap ( $\pm$ SE) within a.) Wet habitats between 23 January-19 March 2012 and b.) Wet habitats and dry habitats between 23<sup>rd</sup>-29<sup>th</sup> January 2012, 22<sup>nd</sup> - 30<sup>th</sup> January 2013, and 21<sup>st</sup>-27<sup>th</sup> January 2014



### 5.3.2 Testing for species differences in habitat preferences of warblers

Over the course of the study, 116 Eurasian reed warblers, 89 subalpine warblers and 194 chiffchaffs were caught across wetland and dry scrub habitats (*see Supporting information S5.1*). A total of 151 sedge warblers and 67 African reed warblers were caught in wetlands, and 25 olivaceous warblers were caught in dry scrub habitats. There was no significant variation in habitat preference between generalist species (GLM;  $F_{5, 381} = 0.177$ ,  $P=0.971$ ) with birds caught in the wetlands (in 2013 and 2014) representing 46.4% of all captures of Eurasian reed warblers, 43.3% of chiffchaffs and 17.9% of subalpine warblers.

### 5.3.3 Warbler Body Mass

Time of day was an important determinant of body mass for all species with a significant increase in mass from the early morning to reach a peak in the late afternoon ( $F_{7.874,8.667}=4.872$ ,  $P<0.0001$ ). All else being equal, the estimated mean difference between birds caught at the beginning of the day and those caught in the late afternoon was greatest for Eurasian reed warblers (1.58 g, representing 15.6% of mean winter body mass) and least for chiffchaff (0.49 g, representing 7.0% of mean winter body mass). After controlling statistically for time of day, year and species effects, mass was positively associated with wing length (GAM;  $0.089 \pm 0.009$  g/mm,  $t=10.495$ ,  $P<0.0001$ ), muscle score (GAM;  $0.146 \pm 0.049$  g/integer,  $t=2.971$ ,  $P=0.0031$ ) and fat score (GAM;  $0.355 \pm 0.021$  g/integer,  $t=16.582$ ,  $P<0.0001$ ). The effect of habitat type differed between species (Table 5.3). Eurasian reed warblers and subalpine warblers were significantly heavier in dry scrub than wetlands (by  $0.71$  g (7.0% of mean winter body mass)  $\pm 0.14$  g and  $0.34$  g (4.0% of lean mass)  $\pm 0.15$  g, respectively). Chiffchaffs also weighed more in scrub on average (by  $0.17$  g (2.4% of lean mass)  $\pm 0.11$  g) but the difference was not significant. There was no significant inter-annual variation in body mass for Eurasian reed warbler and subalpine warbler but significant variation between years in chiffchaff with 2014 and 2013 masses significantly greater than 2012 (Table 5.3; Figure 5.2).

**Table 5.3.** Generalised Additive Models of body mass (dependent variable) for each generalist species. Parameter estimates for levels of the factors “Habitat” and “Year”, are relative to the reference levels of “Wetland” and “2012” respectively. Effects shown in bold are significant ( $P < 0.05$ ).

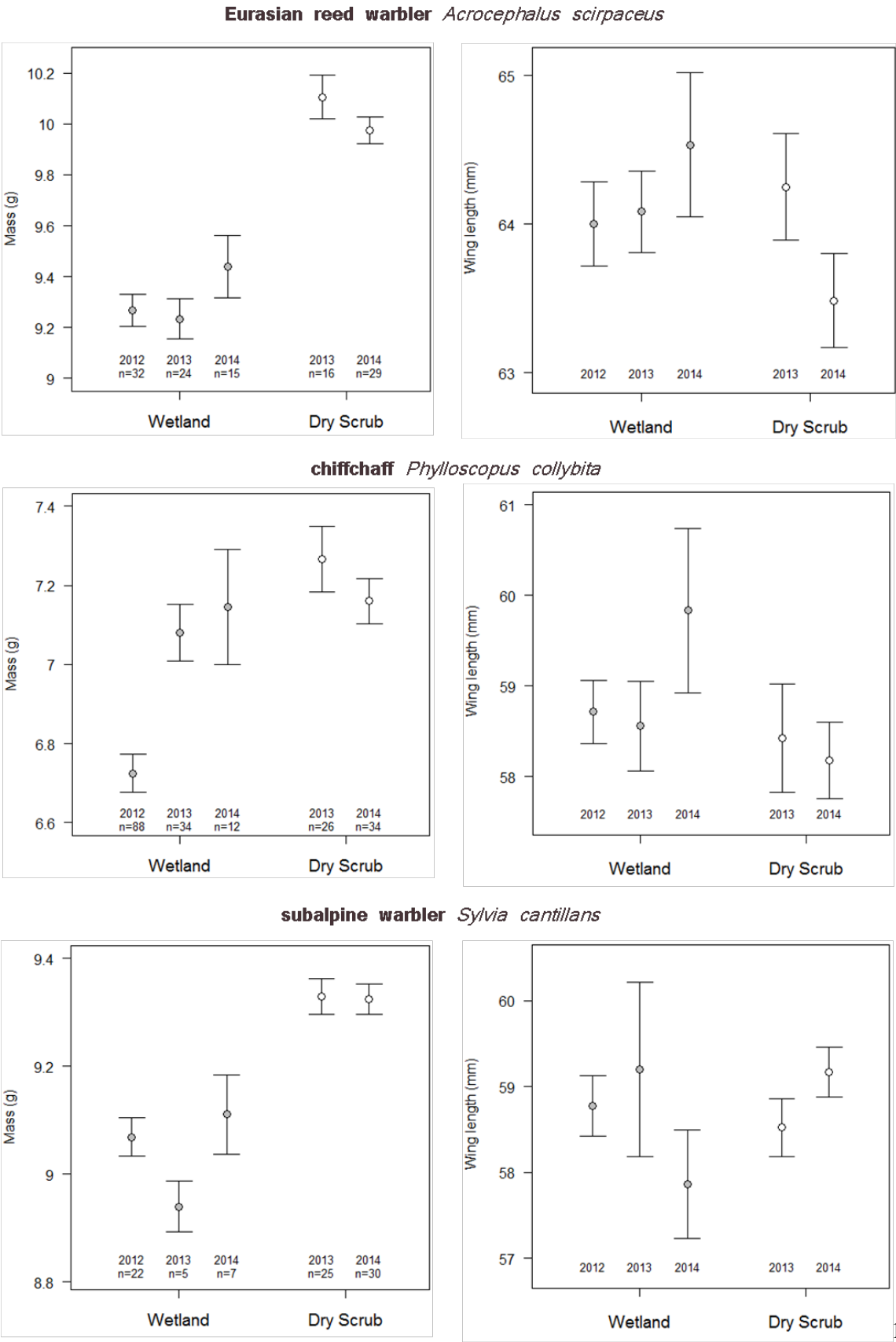
Species	Parameter	Estimate	SE	$z$	$d.f.$	$P$
<i>Eurasian reed warbler</i>	<b>Time(s)</b>	-	-	<b><math>F=4.658</math></b>	<b>3.59, 3.91</b>	<b>0.002</b>
	<b>Habitat Dry</b>	<b>0.708</b>	<b>0.137</b>	<b><math>t=5.157</math></b>		<b>&lt;0.001</b>
	<b>Wing</b>	<b>0.131</b>	<b>0.037</b>	<b><math>t=3.575</math></b>		<b>&lt;0.001</b>
	Total head length	0.131	0.090	$t=1.257$		0.211
	Tarsus	0.132	0.079	$t=1.671$		0.098
	Year 2013	-0.193	0.016	$t=-1.207$		0.230
	Year 2014	-0.106	0.180	$t=-0.591$		0.556
<i>chiffchaff</i>	<b>Time(s)</b>	-	-	<b><math>F=3.665</math></b>	<b>1.85, 2.18</b>	<b>0.024</b>
	Habitat Dry	0.166	0.113	$t=1.470$		0.143
	<b>Wing</b>	<b>0.123</b>	<b>0.016</b>	<b><math>t=7.517</math></b>		<b>&lt;0.001</b>
	Total head length	-0.081	0.065	$t=-1.238$		0.217
	Tarsus	0.090	0.055	$t=1.633$		0.104
	<b>Year 2013</b>	<b>0.471</b>	<b>0.118</b>	<b><math>t=3.995</math></b>		<b>&lt;0.001</b>
	<b>Year 2014</b>	<b>0.387</b>	<b>0.144</b>	<b><math>t=2.684</math></b>		<b>0.008</b>
<i>subalpine warbler</i>	<b>Time(s)</b>	-	-	<b><math>F=4.601</math></b>	<b>1.57, 1.89</b>	<b>0.012</b>
	<b>Habitat Dry</b>	<b>0.346</b>	<b>0.153</b>	<b><math>t=2.258</math></b>		<b>0.027</b>
	Wing	0.028	0.038	$t=0.742$		0.460
	Total head length	-0.004	0.066	$t=-0.055$		0.956
	Tarsus	-0.001	0.089	$t=-0.012$		0.991

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Year 2013	-0.159	0.193	$t=-0.825$	0.412
Year 2014	-0.169	0.186	$t=-0.909$	0.366

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**Figure 5.2.** Body mass ( $\pm$  SE, corrected for structural body size and time of day) and wing length ( $\pm$  SE) of wintering populations of generalist warbler species occupying both wetland and dry scrub habitats.



Controlling statistically for time of day, body size and the extent of fat and muscle, chiffchaff mass was strongly positively associated with the Sahel precipitation index for the preceding wet season (GAM:  $+0.20 \text{ g} \pm 0.04 \text{ g}$ ,  $t=5.764$ ,  $P<0.0001$ ), indicating greater mass following higher rainfall. Of the habitat specialist species, only African reed warbler showed significant variation in mass, exhibiting an increase in mass between 2012 and 2014 (GAM;  $+0.399 \text{ g} \pm 0.177 \text{ g}$ ,  $t= 2.261$ ,  $P= 0.0274$ ; Figure 3).

#### 5.3.4 *Warbler Structural Body Size*

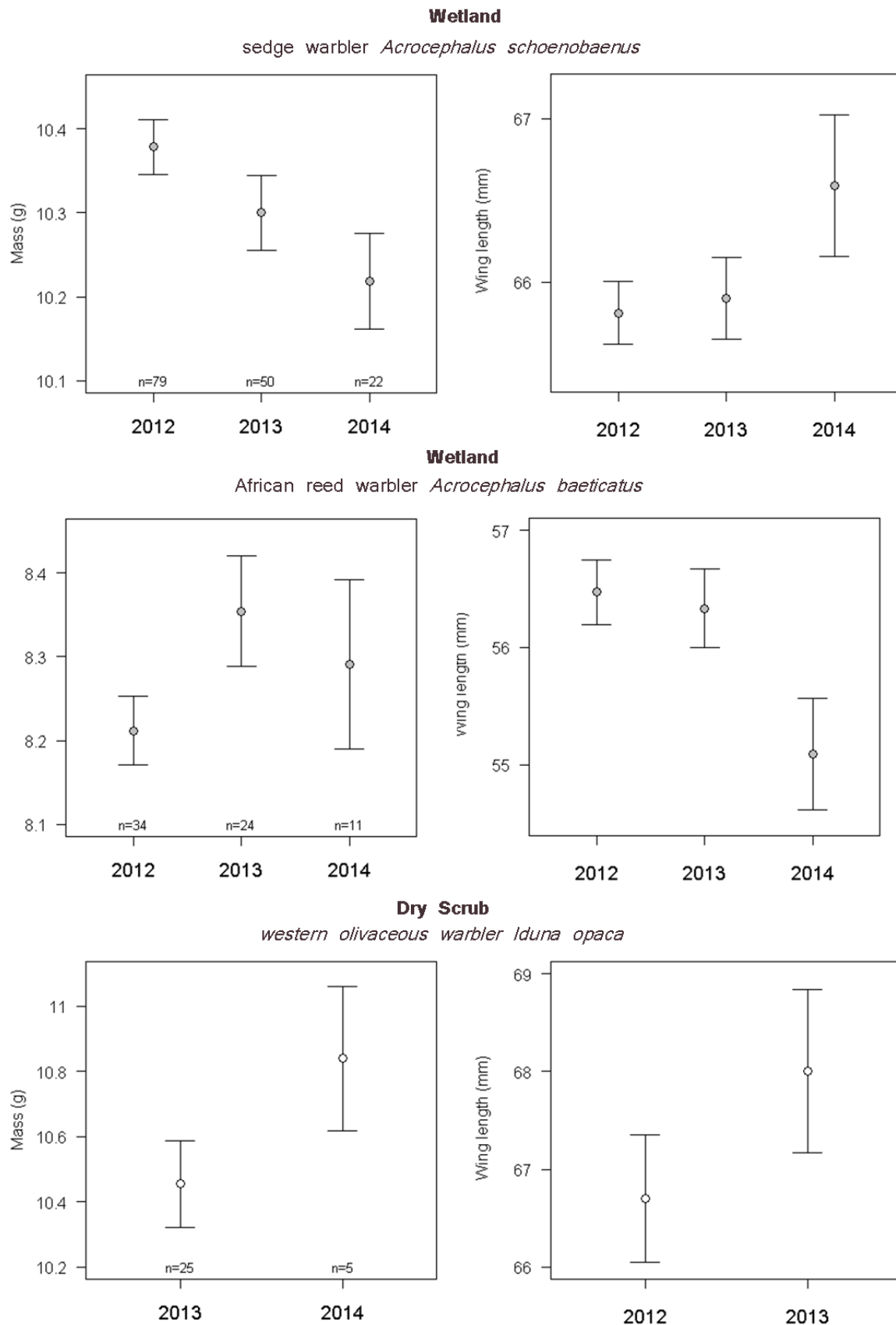
There were no significant differences in structural body size between wetland and dry scrub samples of any of the three generalist species, nor were there any significant differences in size between years (Table 5.4, Figure 5.3). An equivalent model using 2013 and 2014 data only (excluding 2012 on the grounds that there was no habitat contrast available) showed there was no significant year x habitat interaction influencing body size in Eurasian reed warblers ( $t_{83}= -1.683$ ,  $P=0.0963$ ), chiffchaff ( $t_{105}= -1.264$ ,  $P=0.209$ ) or subalpine warbler ( $t_{66}= 1.824$ ,  $P=0.0729$ ), despite some apparent size differences between 2013 and 2014 in Figure 5.2. Of the habitat specialist species, only African reed warbler showed significant differences in the population wing length, with birds in 2014 being  $1.38 \pm 0.561 \text{ mm}$  smaller than birds in 2012 (GLM;  $F_{68,66}= -3.142$ ,  $P= 0.0497$ ; Figure 5.3).



**Table 5.4.** General Linear Model of structural body size (dependant variable) for each generalist species. Parameter estimates for levels of the factors “Habitat” and “Year”, are relative to the reference levels of “Wetland” and “2012” respectively.

<b>Species</b>	<b>Parameter</b>	<b>Estimate</b>	<b>SE</b>	<b><i>t</i></b>	<b><i>df.</i></b>	<b><i>P</i></b>
<i>Eurasian reed warbler</i>	Habitat Dry	-0.451	0.3652	-1.235	112	0.219
	Year 2013	0.330	0.409	0.807		0.421
	Year 2014	0.138	0.445	0.310		0.757
<i>chiffchaff</i>	Habitat Dry	-0.707	0.629	-1.125	190	0.262
	Year 2013	0.091	0.580	0.156		0.876
	Year 2014	0.416	0.725	0.573		0.567
<i>subalpine warbler</i>	Habitat Dry	0.467	0.544	0.859	85	0.393
	Year 2013	-0.529	0.659	-0.802		0.425
	Year 2014	-0.233	0.637	-0.365		0.716

**Figure 5.3.** Body mass ( $\pm$  SE, corrected for structural body size and time of day) and wing length ( $\pm$ SE) of wintering populations of habitat specialist warblers occupying either wetland or dry scrub habitats.



### 5.3.5 *Body reserves*

The proportional odds regression revealed that muscle score was not significantly affected by habitat type ( $t=0.492$ ,  $P=0.6224$ ) or time of day ( $t=1.432$ ,  $P=0.1521$ ). The ordinal logistic regression analysis generates an odds ratio for each species in a particular habitat, which represent the odds of having a muscle score one unit higher than a reference species, in a particular habitat. The only interspecific difference was the wetland specialist species African reed warbler having 1.50 times greater odds ( $P=0.035$ ) of having a muscle score one unit higher than the dry- scrub specialist western olivaceous warbler (Table 5.5). Fat score was significantly affected by habitat type ( $t=-3.944$ ,  $P<0.0001$ ; Table 5.6, Figure 5.4) and time of day ( $t=3.874$ ,  $P=0.0001$ ). The wetland specialist species sedge warbler had 1.26 times greater odds of having a fat score one unit higher relative to the migrant generalist species Eurasian reed warbler occupying the wetland habitat (Table 5.6). Conversely, in the dry habitats, Eurasian reed warbler had 1.70 times greater odds of having a fat score 1 unit higher relative to the dry habitat specialist olivaceous warbler.

**Table 5.5.** Pairwise comparison of proportional odds of species in a particular habitat having a muscle score of 1 unit higher than another species in a particular habitat, or the same species in a different habitat. Displayed odds values relate to species in the vertical column in reference to those in the horizontal row above the matrix. Positive odds values indicate a higher likelihood, and negative odds indicate a lower likelihood. The sign would be reversed to obtain the odds value for the species groups in the horizontal row in reference to those in the vertical column. \*=P<0.05, \*\* = P<0.005, \*\*\*= P<0.0001.

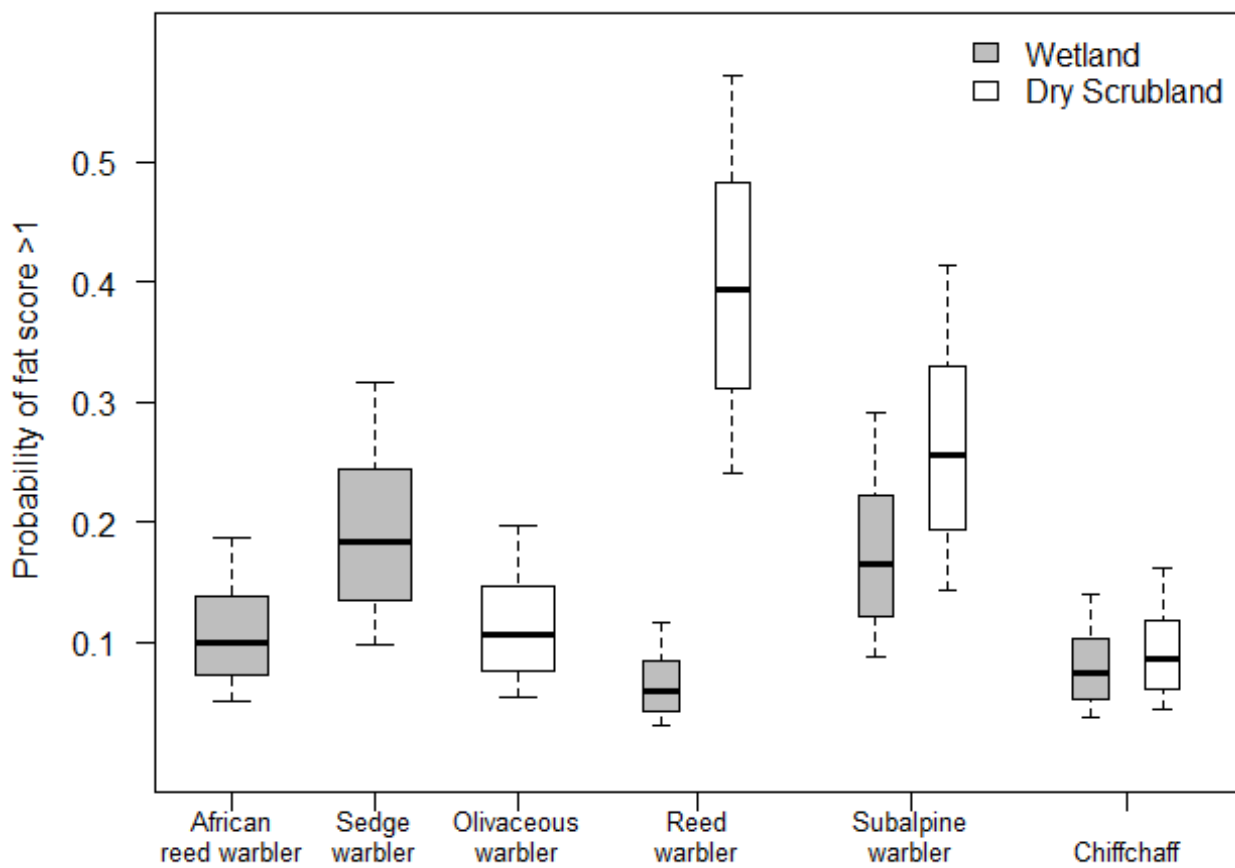
		Wetland Habitat				Dry Scrub Habitat			
		Subalpine Warbler	Chiffchaff	Sedge Warbler	A. Reed Warbler	E. Reed Warbler	Subalpine Warbler	Chiffchaff	Olivaceous Warbler
Wetland Habitat	E. Reed Warbler	-0.82	0.06	-0.88*	-0.74	-0.46	-0.32	0.48	0.29
	Subalpine Warbler		0.88	-0.06	-0.38	0.36	0.49	1.30*	1.12
	Chiffchaff			-0.94**	-1.26	-0.52	-0.39	0.42	0.24
	Sedge Warbler				-0.32	0.42	0.55	1.36**	1.17
	A. Reed Warbler					0.74	0.87	1.68**	1.50*
Dry Scrub Habitat	E. Reed Warbler						0.13	0.94	0.75
	Subalpine Warbler							0.81	0.62
	Chiffchaff								-0.19

The wetland specialist species sedge warbler had 1.26 times greater odds of having a fat score one unit higher relative to the migrant generalist species Eurasian reed warbler occupying the wetland habitat (Table 5.6). Conversely, in the dry habitats, Eurasian reed warbler had 1.70 times greater odds of having a fat score 1 unit higher relative to the dry habitat specialist olivaceous warbler.

**Table 5.6.** Pairwise comparison of proportional odds of species in a particular habitat having a fat score of 1 unit higher than another species in a particular habitat, or the same species in a different habitat. Displayed odds values relate to species in the vertical column in reference to those in the horizontal row above the matrix. Positive odds values indicate a higher likelihood, and negative odds indicate a lower likelihood. The sign would be reversed to obtain the odds value for the species groups in the horizontal row in reference to those in the vertical column. \*=P<0.05, \*\* = P<0.005, \*\*\*= P<0.0001.

		Wetland Habitat				Dry Scrub Habitat			
		Subalpine Warbler	Chiffchaff	Sedge Warbler	A. Reed Warbler	E. Reed Warbler	Subalpine Warbler	Chiffchaff	Olivaceous Warbler
Wetland Habitat	E. Reed Warbler	-1.14*	-0.22	-1.26**	-0.56	-2.32***	-1.68**	-0.39	-0.63
	Subalpine Warbler		0.91	-0.12	0.58	-1.18*	-0.55	0.75	0.51
	Chiffchaff			-1.04**	-0.34	-2.10***	-1.46***	-0.17	-0.40
	Sedge Warbler				0.7	-1.06**	-0.42	0.87*	0.63
	A. Reed Warbler					-1.76***	-1.12*	0.17	-0.07
Dry Scrub Habitat	E. Reed Warbler						0.64	1.93***	1.70*
	Subalpine Warbler							1.29*	1.06
	Chiffchaff								-0.23

**Figure 5.4.** Model predictions for the probability of observing birds in wetlands or dry scrub habitat with a fat score of greater than 1.



## 5.4 Discussion

As expected, wetland habitats supported consistently greater invertebrate resources than dry scrub habitats (Hawke and José 1996; Tschardtke 1999; Bedford and Powell 2005; Schmidt *et al.* 2005). On the basis of food availability, wintering generalist warblers should therefore favour wetlands over the dry scrub habitats. Eurasian reed warblers occupied both habitats and carried substantially larger body reserves in the dry scrub habitat compared to those occupying the wetland habitat, consistent with greater strategic buffering of energy reserves against starvation in the dry scrub habitat where starvation risk is greatest.

Starvation risk is a function of both the overall (mean) level of food availability, and its variance. Reed warblers carried higher body reserves in dry scrub than in wetlands in both years when this comparison was made, including 2013 when variance in prey availability was higher in wetland habitats than dry scrub but the mean abundance remained approximately twice as high in the wetland. This indicates that even the lower end of the range of prey availability in wetlands in 2013 was sufficient to allow birds to maintain low fat reserves without an excessive risk of starvation.

Although muscle was a significant predictor of body mass in this study, the effect-size was low and muscle differed less than fat between habitats. This pattern supports the concept that adaptive changes to mass are likely to involve dynamic fat reserves while loss of functional muscle is more likely to be a consequence of physiological stress (Neto and Gosler 2010). It is also possible that the method of muscle measurement (a three-point scale) provides insufficient resolution to detect a difference between habitats in muscle score. Similarly, the extent to which visible fat scores reflect the relative body-lipid reserves may limit conclusions about adaptive fat deposition (Bergstrom and Sherry 2008). There were no

significant differences in structural body size of reed warblers between habitats or years and, since we were unable consistently to determine the age and sex of the warblers in our study, we were not able to test for intra-specific differences (e.g. age and sex variation) in habitat effects as found in several other studies of migrants in their wintering habitats (Marra and Holberton 1998; Marra 2000; Marra and Holmes 2001; Fernández and Lank 2006). It is thus possible that the distribution of individuals is a result of age or sex-biased habitat segregation, despite the absence of any significant differences in wing length between habitats in our dataset.

These results suggest that mass is regulated strategically among warblers overwintering in the Sahel, rather than being limited directly by food availability. Experimental manipulations of food availability and predictability have shown that birds can strategically increase mass through fat accumulation to buffer against energetic shortfalls (McNamara and Houston 1990; Ekman and Hake 1990; Witter and Cuthill 1993; Witter and Swaddle 1997). A similar effect is evident in the context of migratory fuelling, where larger energetic reserves are accumulated in anticipation of low food availability ahead of large ecological barriers (Jenni-Eiermann *et al.* 2011).

Although higher energy reserves are better for avoiding starvation and for fuelling migration, the extent of muscle and fat accumulation must be balanced against the costs of maintaining higher body mass, such as increased wing-loading costs on flight performance and longer foraging periods, both of which increase susceptibility to predation (Blem 1990). The differences in predator density across wetland and dry scrub habitats in this study are unknown but it is likely that birds inhabiting the dry scrub habitats would have higher



exposure to predators as they must cross open spaces between habitat patches more frequently than in the wetlands. Subalpine warblers and chiffchaffs exhibited similar but less pronounced habitat differences in body reserves than observed in the Eurasian reed warbler (though this habitat difference was non-significant in chiffchaffs). Although subalpine warblers and chiffchaffs were regularly captured in wetlands, it is notable that these captures occurred mainly in the scrub-*Phragmites* interface, rather than in the pure stands of *Phragmites* where Eurasian and African reed warblers and sedge warblers were all regularly captured. This is consistent with the less pronounced habitat difference in body reserves in subalpine warblers and chiffchaffs being due to their more limited exploitation of the invertebrate-rich *Phragmites* stands compared to Eurasian reed warblers and the two wetland-specialist species.

The significantly lower mass for chiffchaffs in 2012 compared with 2013 and 2014 may be due to direct food limitation following the low rainfall (as measured by the Sahel precipitation index) recorded in the preceding wet season, of 2011. This response is contrary to the strategic buffering strategy expected for birds in food-reduced habitats, suggesting direct food limitation in drought conditions. This association with Sahel precipitation index was not observed in the other species in this study, although studies of survival of trans-Saharan migrants indicate that drought can directly limit survival. For example, Sahel rainfall has been found to be significantly associated with survival in the sedge warbler (Peach *et al.* 1991; Foppen *et al.* 1999), reed warbler (Salewski *et al.* 2013), sand martin (Hutto 1980; Szep 1995) and common nightingale *Luscinia megarhynchos* (Boano *et al.* 2004), indicating that drought can impair survival, presumably via the mechanism of food limitation.

We found that habitat specialist species maintained lower energetic reserves than generalist species in their preferred habitats. This was the case for African reed warbler and western olivaceous warbler, but not for sedge warbler. The analysis suggested that sedge warblers were more likely to carry higher fat levels than any other species in the wetland habitat. A possible testable explanation for this is that sedge warblers rely on a narrower range of prey than Eurasian and African reed warblers, with a foraging strategy adapted to exploiting slow moving or sedentary prey (Lima 1986). Although such adaptation is beneficial during seasonal super-abundances of such prey in the pre-migratory grounds (Green and Davies 1972; Bibby and Green 1981; Bayly 2007), it may restrict their wintering habitat to wetlands and limit their foraging time to the cooler parts of the day when active aerial invertebrates are easier to catch. Such limitations may require the accumulation of fat reserves despite the occupation of invertebrate-rich wetland habitat. Another important consideration in the interpretation of these results is that the data were collected during the middle of the dry season, when wetlands have undergone contraction since the time of migrant arrival at the end of the wet season (Janzen 1973; Wolda 1978; Zwarts *et al.* 2009). It is therefore possible that the availability of prey suitable for sedge warblers is particularly low at this time of year. Scarcity of certain prey taxa may explain why sedge warbler populations are particularly vulnerable in the winters following low wet-season rainfall (Peach *et al.* 1991; Foppen 1999). In contrast to sedge warblers, Eurasian reed warblers do not suffer such dramatic population crashes in response to Sahelian drought events (Redfern and Alker 2002; Thaxter *et al.* 2006; Leisler *et al.* 2011). Our results suggest that this may be due to their ability to exploit invertebrate resources in dry habitats in addition to the high quality but intensely competitive and drought-prone wetland habitats.

Although our results suggest an explanation of the presence of different species in a particular habitat or multiple habitats by their ability to exploit resources and survive in these habitats, we are not yet able to explain the process by which community assembly

occurs. It is conceivable that habitat choice may be determined by order of arrival, with earliest arriving migrants (e.g. sedge warblers) occupying the highest quality habitats, while later arriving migrants (e.g. Eurasian reed warbler) must select the secondary habitats. However, this may be unlikely considering the findings of studies of interspecific territorialism and competition for space between reed and sedge warblers on the breeding grounds (Catchpole 1973; Svensson 1978) in which early arriving sedge warblers are often displaced by the later arriving reed warblers.

It is possible that differences in the availability of prey for reed warblers in the dry scrub may not be adequately represented by data collected using yellow sticky traps since this disregards invertebrate prey not attracted to the traps including larvae, spiders and ground dwelling beetles, which may be available at higher densities in dry scrub. This could potentially be overcome through molecular analysis of reed warbler faecal samples which could be compared between habitats, providing the component prey taxa have been identified and included in the reference database. It is also possible that the relative abundances of reed warblers in each habitat may be confounded and biased by the available positions suitable for mist netting. For example, by targeting narrow spaces in wetland habitat, we may be catching higher numbers of reed warblers than we would if we used more open habitat.

In conclusion, the observed patterns of habitat occupation and body condition described in our study are consistent with the hypothesis that when individuals are in food-poor habitats, they utilise strategic buffering to avoid starvation. This mechanism may only be effective above a critical food availability threshold. Below this threshold, bird mass is likely to be directly limited by food availability (Strong and Sherry 2000; Marra 2000; Marra and Holberton 1998). Although there was little evidence for such direct limitation of body

reserves during our study period (other than among chiffchaffs), such patterns of nutritional stress are observed in wintering sand martins *Riparia riparia* (Norman and Peach 2013) and barn swallows *Hirundo rustica* (Van den Brink *et al.* 2000) in the Sahel during drought years and are implicated as a major cause of population-level declines through increased mortality and carry over effects on productivity (Møller 1989; Baillie and Peach 1992; Bryant and Jones 1995). Similarly, impacts of physiological stress have been shown in other contexts, such as in American redstarts *Setophaga ruticilla* (Marra and Holberton 1998; Marra and Holmes 2001) northern waterthrush *Seiurus noveboracensis* (Smith *et al.* 2010) and ovenbirds *S. aurocapillus* (Strong and Sherry 2000; Brown and Sherry 2006) occupying low quality non-breeding habitats in the Neotropics. Such studies suggest that if foraging conditions in the Sahel become worse as a result of climate-driven and anthropogenic habitat degradation, migrant warblers may become increasingly constrained in their ability to use strategic buffering to reduce the threat of starvation and survive the winter.

## Supporting information

### S5.1 Number of birds captured in each habitat in January 2012 (wet only), 2013 and 2014

Species	Year	Wet	Dry	% wet (2013-14)
<i>Eurasian reed warbler</i>	2012	32	-	
	2013	24	16	46.4
	2014	15	29	
<i>common chiffchaff</i>	2012	88	-	
	2013	34	26	43.3
	2014	12	34	
<i>subalpine warbler</i>	2012	22	-	
	2013	5	25	17.9
	2014	7	30	
<i>sedge warbler</i>	2012	79	-	
	2013	50	0	98.6
	2014	22	1	
<i>African reed warbler</i>	2012	34	-	
	2013	24	0	91
	2014	11	3	
<i>western olivaceous warbler</i>	2012	0	-	
	2013	0	20	0
	2014	0	5	0

## **Chapter 6**

**The effects of climate and prey availability on  
survival of Eurasian reed warblers *Acrocephalus  
scirpaceus* breeding in South Wales.**

## Summary

Weather-driven changes to habitat and food availability on the breeding and wintering grounds may affect mortality and survival in local wetland songbird populations. The effects of climate-change may therefore affect patterns of survival and drive changes in population size. In this study, the effects of breeding and wintering ground weather variables on the apparent survival of Eurasian reed warblers *Acrocephalus scirpaceus* are tested using capture-mark-recapture (CMR) models. In addition, the influence of experimental increases in food on survival of adult and juvenile reed warblers was tested using multi-state CMR models. Juvenile survival was positively correlated with mean April temperatures, while adult survival showed an association with the conditions on the wintering grounds rather than those on the breeding grounds. Warmer spring temperatures may enable earlier nesting, increasing survival of broods by avoiding the period of highest predation and enabling longer post-fledging periods prior to autumn migration. Food-supplemented juveniles exhibited marginally higher rates of survival than control juveniles, suggesting nutritional status during dependent stages of life may be a determinant of survival. In adult reed warblers, fed females showed higher survival than control females, while fed males showed lower survival than control males. Adult females may benefit more from increases in food availability in terms of survival. The effects of long term weather variations on survival are measureable, but explain only a small amount of variation in survival, suggesting that reed warblers are very adaptable to environmental change.

## 6.1 Introduction

Weather events can have major direct and immediate influences on the population dynamics of birds, particularly migrants which may be affected by the weather conditions at several locations throughout the year (Møller *et al.* 2008; Salewski *et al.* 2013). Direct effects of weather may include mortality caused by storms or low temperatures (Kennedy 1970; Avery *et al.* 1980; Newton 2007), but indirect impacts such as winter habitat contractions due to drought, or delayed migration may also be important (Peach *et al.* 1991; Brown and Brown 2000; Zwarts *et al.* 2009). By affecting the birds' food availability or habitat quality, weather can influence mortality in a population in any given year (Newton 2007; Moreno and Møller 2011). In the preceding chapters of this thesis, predictions are made about the possible implications of changing conditions on the breeding and wintering grounds, for a long-distance migrant, the Eurasian reed warbler *Acrocephalus scirpaceus* (hereafter 'reed warbler'), based on its responses to changes in food availability and habitat. The associations between prey availability, reproductive success and survival in birds are well-studied and often cited as key mechanisms by which climate may be capable of driving population change (Martin 1987; Hoodless *et al.* 1999; Both and Visser 2005; Pearce-Higgins *et al.* 2010; Studds and Marra 2011; Fokidis *et al.* 2012; Seward *et al.* 2012). Studying the variation in weather is important not least because current predictions of climate change on the breeding grounds in northwest Europe suggest an increase in storm events and droughts which are likely to have consequences for selection in populations (Bumpus 1899; Grant and Grant 2002; Robinson *et al.* 2005). By contrast there are also predictions for warmer conditions earlier in the year (Rasinen *et al.* 2003; Rowell 2005), which in temperate wetland habitats may be associated with increases in food availability earlier in the year (Halupka *et al.* 2008).



Higher rates of adult survival are associated with years of good environmental breeding conditions, possibly due to reduced levels of the physiological stress which has been shown to increase mortality during subsequent migration or over-winter (Alonso-Alvarez *et al.* 2004; Sherry *et al.* 2014). Similarly, higher rates of mortality in breeding adult birds are associated with physiological stress during poor environmental conditions (Martin 1987; Williams 1996). Such effects are also likely to be reflected in offspring survival during these years. There is evidence to suggest that birds fledging earlier in the breeding season have higher survival rates than later fledged birds or those hatched during years of poor environmental conditions (Perrins 1965; Daan *et al.* 1988; Price *et al.* 1988; Møller 1994; Dzus and Clark 1998; Hochachka 1990; Spear and Nur 1994; Verhulst *et al.* 1995). Early fledging may avoid the period of highest nest predation during the middle of the breeding season and give the fledged young a longer period on the breeding grounds, enabling them to gain experience and body reserves before migration (Perrins 1965; Spear and Nur 1994; Dzus and Clark 1998; McKim-Louder *et al.* 2013).

On the West African wintering grounds, temperatures are predicted to increase and precipitation to decrease over the coming decades (Zwarts *et al.* 2009). This is expected to decrease the area and quality of the remaining wetland habitats where many reed warblers overwinter, particularly in association with further anthropogenic habitat-loss (Giorgi and Lionello 2008; Zwarts *et al.* 2009). Such effects have already been linked with major density-dependent mortality in other wetland migrants such as sedge warbler *A. schoenobaenus* (Peach *et al.* 1991; Zwarts *et al.* 2009). The adverse effect of drought in West Africa is thought to be less severe for reed warblers because they can occupy non-wetland habitats (see Chapter 5 *Habitat use and body mass regulation among warblers in the Sahel region during the non-breeding season*); this is supported by several studies across Europe that show no correlation between long-term population trends of reed warbler populations and rainfall in the Sahel (Osterloff and Stolt 1982; Nef *et al.* 1988; Zang and

Heckenroth 2001; Weggler 2005; Zang *et al.* 2005; Reif *et al.* 2006; Thaxter *et al.* 2006). However a recent study by Salewski *et al.* (2013) shows some evidence of an association between reed warbler survival and Sahel rainfall values.

Thus, the predicted long-term changes in environmental conditions may reduce stress-mediated mortality in adults and increase survival in juveniles on the temperate breeding grounds, while selecting for an adaptive response to harsher conditions on the tropical wintering grounds. A less well-understood factor in this prediction is the potential for carry-over effects on survival or fecundity of the conditions experienced in the previous season. For example, good environmental conditions on the wintering grounds may facilitate faster spring migration and earlier arrival on the breeding grounds, presenting the possibility of early nesting and greater opportunity to re-nest (Saino *et al.* 2004; Schaub *et al.* 2011; Harrison *et al.* 2011). Given the potential complexity of these effects, any attempts to anticipate the impacts of climate change on future population dynamics of reed warbler require identification of the weather conditions and phases of the annual cycle for which variation in weather most influences adult survival.

The current study has two main aims. The first is to assess the relative importance of inter-annual variations in weather conditions on both the breeding and wintering grounds to the survival of reed warblers breeding in South Wales. Survival rates were modelled over 34 years using recapture data and related to local spring weather variables (mean April temperature and total rainfall) and the Sahel Precipitation Index (SPI). On the breeding grounds, it is hypothesised that cold and wet conditions are associated with decreased survival in the following year in both adults and juveniles, while warmer and drier conditions are associated with higher rates of survival. Drought conditions on the wintering

grounds (i.e. more negative SPI values) are hypothesised to be associated with lower rates of survival between breeding seasons.

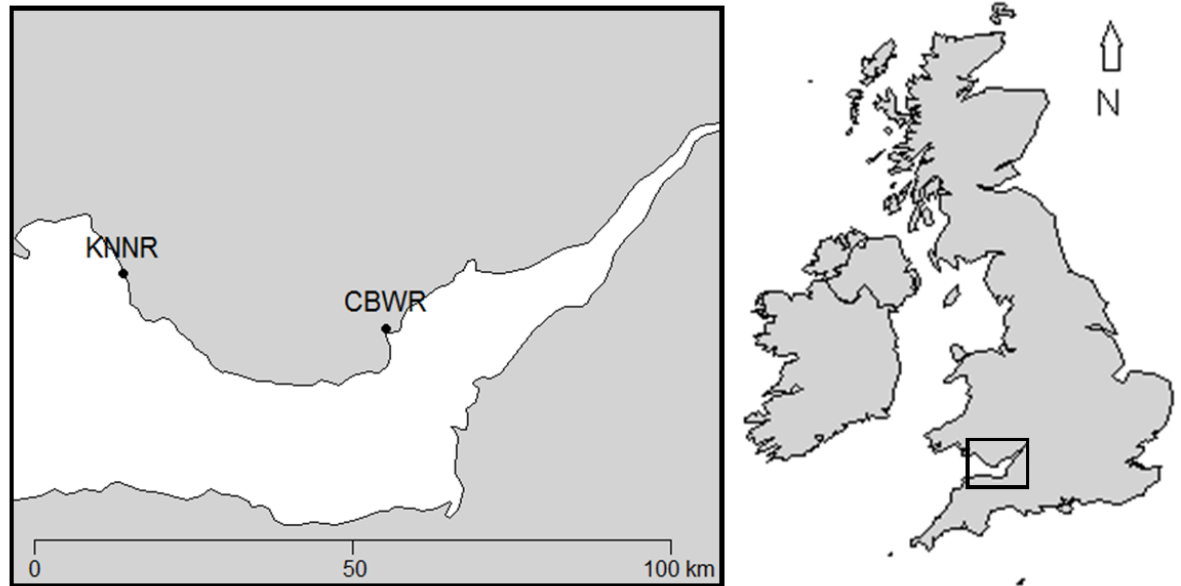
The second aim is to simulate the effect of possible climate-related increases in food availability in the breeding grounds on adult and juvenile survival into the following year. This used a supplementary feeding experiment at a second wetland location that was carried out across two years (2012 and 2013). It is hypothesised that fed treatment adults and juveniles have higher rates of survival than those of control treatment birds. This study, combining long-term observations and short-term experimental manipulations of ecological conditions, provides a strong basis to assess the implications of the impacts of weather variation for future population dynamics in the face of ongoing and predicted future climate change.

## **6.2 Methods**

### *6.2.1 Study sites*

The study site at Kenfig National Nature Reserve (KNNR; 51° 32' 16'' N, 3° 45' 47'' W) is a natural established reed swamp of fringing the shoreline of Kenfig Pool in the county of Bridgend, Wales, UK (Figure 1). Cardiff Bay Wetland Reserve (CBWR; 51° 27' 32'' N, 3° 10' 11'' W) is a wetland site of four hectares consisting of mixed scrub habitat, open pools and large areas of *Phragmites* reedbed in Cardiff Bay, in the city of Cardiff, Wales, UK.

**Figure 6.1.** Wetland study sites in South Wales; Kenfig National Nature Reserve KNNR; Cardiff Bay Wetland Reserve CBWR.



#### 6.2.2 *Kenfig National Nature Reserve KNNR*

Mist-netting of reed warblers took place each year between April and October at KNNR from 1985 to 2013 by members of the Kenfig Ringing Group (including Mr Dave Bull, Professor Peter Morgan, Mr Steve Moon, Mr David Carrington and Mrs Heather Coats). Trapping followed standardised methods as part of the British Trust for Ornithology BTO Constant Effort Sites (CES) scheme (Robinson *et al.* 2007), using six 18m nets in the same locations throughout the study. The newly ringed birds in the final year of the dataset (2013) were excluded from the analysis, as no survival estimate can be calculated for this cohort.

#### 6.2.3 *Cardiff Bay Wetlands Reserve CBWR*

Mist-netting of reed warblers took place each year between April and October at CBWR from 2012 to 2014, following standardised methods as part of the British Trust for Ornithology BTO bird ringing scheme and as part of a supplementary feeding experiment

between 2012 and 2014 (Chapter 5). This experiment involved the experimental increase in prey available to breeding birds and their offspring by providing live and dried mealworms *Tenebrio molitor* larvae (Coleoptera) in 2 litre capacity plastic containers resting on tables at 1.5m height, in two randomly selected areas within CBWR. The feeding stations were supplied with at least 200 mealworms (mean weight  $\pm$  SD of mealworms =  $0.112 \pm 0.026$  g,  $n = 100$ ) and refilled on at least three of every seven days, from early April until the departure on autumn migration of all of the breeding birds and their offspring that were using the feeders (in late August). Over the course of the monitoring, birds were identified to species, sexed and aged following the criteria in Svensson (1992) and Jenni and Winkler (1994) as being in their first year (i.e. captured in their first year of life), or older. During the supplementary feeding experiment, birds were also fitted with a unique combination of colour rings in addition to the BTO registered metal individually numbered ring.

Birds were monitored throughout the breeding cycle using three methods. First, birds attending feeding stations were identified by their colour-ring combination when they landed on perches in front of the containers and recorded with unmanned video cameras (Sony Handycam DCR-SR32, Sony Corporation, <http://sony.co.uk>) in 2012 and 2013, and infrared triggered trail cameras (Bushnell HD, <http://Bushnell.co.uk>) in 2014. Videos were recorded between 06:00 and 18:00 on alternate days throughout the breeding season in 2012 and 2013, and every 24 hours in 2014. The second monitoring method was capturing birds in mist nets as part of regular monitoring. All recaptures were recorded with date of recapture. Thirdly, colour-ringed individuals were identified by observing them in the reedbed via binoculars or taking high resolution digital photographs (e.g. Plate 1). The analysis included all adult and first year reed warblers caught in mist nets over the course of each year as well as ringed nestlings that were later caught in post-juvenile plumage as part of regular monitoring.

**Plate 6.1.** Colour ringed reed warbler identified as R476174 (Left leg (Umber over Orange and Black); right leg (Blue over metal ring); Photo credit: Peter Howlett)



#### 6.2.4 *Environmental variables*

Candidate predictors on the breeding grounds in South Wales included local precipitation (i.e. total rainfall in April, denoted as ‘Rain’) and mean April temperature (derived from daily means; denoted as ‘MAT’) recorded at the Kenfig visitor centre (0.25km from KNNR) and Cardiff Bay Barrage (0.75 km from CBWR). The candidate predictor on the wintering ground was the Sahel Precipitation Index (denoted as ‘SPI’) which represents the difference between observed rainfall in the period June–October for each year and the mean rainfall over the station’s history, across 72 weather stations (Nicholson 1979, 2001, Nicholson and Palao 1993; [http:// jisao.washington.edu/data/sahel/](http://jisao.washington.edu/data/sahel/)).

### 6.2.5 *Survival analysis*

Bird ringing data from KNNR (1985-2013) and CBWR (2012- 2014) were analysed using capture-mark-recapture methods with the program MARK 6.1 (White and Burnham 1999). A series of candidate models were fitted and the relative support for nested models was evaluated using differences in the sample Akaike's Information Criterion (adjusted for small samples;  $\Delta AICc$ ; Burnham and Anderson 2004). Transient structuring was incorporated in all models to account for the effect of transients on resident 'apparent survival' estimates<sup>4</sup>, represented by the notation " $\phi$ " (Cooch and White 2006). 'Transients' are individuals that permanently emigrate after marking and have an apparent survival rate of zero, whereas 'resident' individuals which remain in the study site have the potential to be re-encountered (Peach *et al.* 1990, Peach 1993, Cooch and White 2005).

The analysis started with Cormack–Jolly–Seber (CJS) models to determine whether the data were best described as having a recapture probability " $p$ " (representing the probability that an individual alive in a particular year is detected in that year) as either time-dependent ( $t$ ) or constant ( $.$ ). The models are denoted as ' $\phi(t) p(t)$ ' and ' $\phi(t) p(.)$ ' respectively (Table 6.1; models 1-2). The most parsimonious model, determined by its rank of Akaike's Information Criterion for small sample sizes ( $AICc$ ) and the degree of over-dispersion<sup>5</sup>, was model 2, with a constant recapture probability  $\phi(t)p(.)$ . The second step of the analysis was to test the hypothesis that reed warbler survival  $\phi$  was time-dependent  $\phi(t)$ , constant  $\phi(.)$  or varied with a weather variable ( $\phi SPI$ ,  $\phi MAT$  or  $\phi Rain$ ) in age-structured (models 3-11), juvenile-only

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<sup>4</sup> 'Apparent survival' is used rather than 'survival' as the rates of site fidelity is unmeasured and unknown.

<sup>5</sup> Determined using the median  $\hat{c}$  procedure in MARK using 500 bootstrap simulations (Cooch and White 2011).

(models 12-20) and adult-only (models 21-29) models. In age-structured models, individuals were classified as either adults (in their second year of life or older) or juveniles (bird hatched that year), giving a sample size of 4938 individuals. In juvenile-only models, the data were restricted to birds ringed as juveniles and the first recaptures thereafter, giving a sample size of 3605 individuals. The variable 'sex' was included in adult-only models to test for sex-related effects, giving a sample size of 1575 females and 1599 males. Evidence for trends in survival over time was tested by comparing models in which time was modelled as having general variation or with linear (on a logit scale) relationships. The most parsimonious models (as well as those with  $\Delta AIC_c \leq 2$ , which are considered as having similar support from the data compared to the most parsimonious model ( $\Delta AIC_c = 0$ ) were rerun with the alternative recapture probability ( $p(t)$ ) examined in the first instance to confirm this was the best model. The assumptions<sup>6</sup> underpinning CJS methodology were tested using the computer program RELEASE (available within MARK; White and Burnham 1999) using goodness of fit test diagnostic tools.

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<sup>6</sup> i.e. that birds marked at occasion  $i$  had an equal probability of survival and recapture to occasion  $i + 1$ .



**Table 6.1** *a priori* CMR models tested as part of KNNR 1985-2013 analysis. Basic model notation follows Lebreton *et al.* (1992), with  $\phi$  representing survival, t =full time-dependence, (.)=rate was constant over time, f= feeding group, s= sex,T=linear trend.

Model	Testing	Notation
1	Recapture probability	$\phi(t) p(t)$
2		$\phi(t) p(.)$
3	Age-structured survival	$\phi(.)$
4		$\phi(t)$
5		$\phi T$
6		$\phi SPI$
7		$\phi MAT$
8		$\phi Rain$
9		$\phi SPI/MAT$
10		$\phi Rain/MAT$
11		$\phi SPI/MAT/Rain$
12		$\phi(.)$
13		$\phi(t)$
14		$\phi T$
15	Juvenile survival	$\phi SPI$
16		$\phi MAT$
17		$\phi Rain$
18		$\phi SPI/MAT$
19		$\phi Rain/MAT$
20		$\phi SPI/MAT/Rain$
21	Adult survival	$\phi(.)$
22		$\phi(t)$
23		$\phi(t)s$
24		$\phi T$
25		$\phi SPI$
26		$\phi MAT$
27		$\phi Rain$
28		$\phi SPI/MAT$
29		$\phi Rain/MAT$
30		$\phi SPI/MAT/Rain$

In CBWR, the locations of the experimental feeding territories were different in each year between 2012 and 2014, requiring the use of multi-state models (for recaptures only) rather than standard Cormack-Jolly-Seber (CJS) models to estimate the effect of feeding group (control vs. fed) on apparent survival between 2012 and 2014 (Arnason 1972, 1973, Lebreton 1992, Brownie *et al.* 1993, Schwarz *et al.* 1993, Nichols *et al.* 1994, Nichols and Kendall 1995). The detection parameter “p” represents the probability that an individual alive in a particular feeding treatment group in a particular year is detected in that year. Multistate models also include a transition parameter “phi” representing the probability of switching between the two feeding treatment groups. However, since the probability of being in either feeding treatment group in either year was determined by the position of the feeding stations in this analysis, this parameter “phi”, is constant ‘phi(.)’ and not considered further in this analysis. Global models of juvenile and adult survival were generated allowing  $\phi$  to vary by feeding treatment (f), sex (s)<sup>7</sup> and time (t), which was gradually reduced in complexity in the final constrained model in which  $\phi$  was constant across groups (Table 6.2).

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<sup>7</sup> In adult-only models

**Table 6.2** *a priori* multistate models tested as part of CBWR 2012-2014 analysis. Basic model notation follows Lebreton *et al.* (1992), with  $\phi$  representing survival, (t) =full time-dependence, (.) = rate was constant over time, f = feeding group, s = sex.

Model	Testing	Notation
31	Juvenile survival	$\phi(t)f$
32		$\phi(.)f$
33		$\phi(t)$
34		$\phi(.)$
35	Adult Survival	$\phi(t)s f$
36		$\phi(.)s f$
37		$\phi(t)f$
38		$\phi(.)f$
39		$\phi(t)s$
40		$\phi(.)s$
41		$\phi(t)$
42		$\phi(.)$

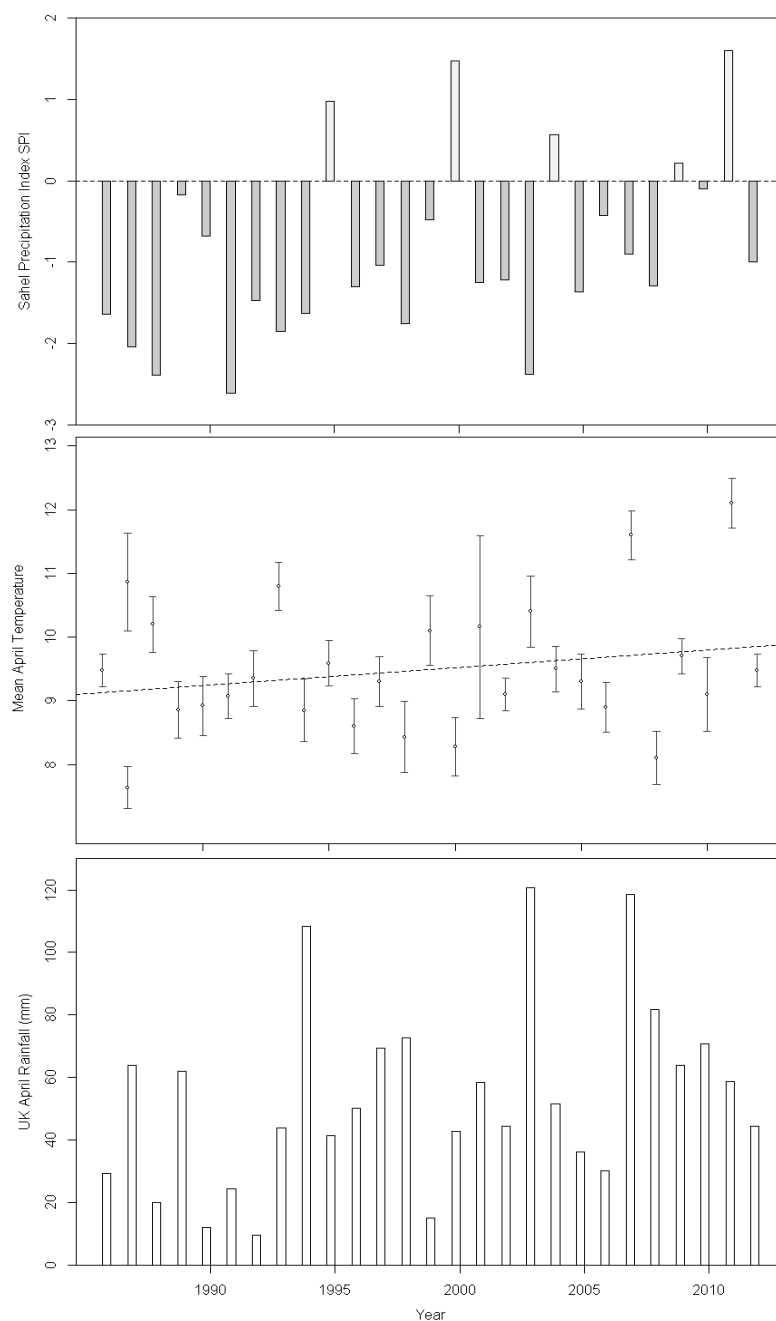
Juvenile-only models included 363 birds ringed as juveniles and the first recapture in the subsequent years. Adult-only models had a sample size of 439 individuals. Parameter estimates and confidence intervals were derived from the models with the lowest AICc weights (Burnham and Anderson 2002; Cooch and White 2005).

## 6.3 Results

### 6.3.1 Climate variables

The majority of the Sahel Precipitation Index (SPI) values for the period 1985- 2013 were negative, indicative of drought conditions, with only five years of positive values (Figure 6.2).

**Figure 6.2.** Weather variables (Sahel Precipitation Index: SPI; UK Mean April Temperature: MAT; and UK April Rainfall: Rain) between 1985 and 2013.



However, there was a significant increase in SPI value over time (linear regression estimate =  $0.061$  units per year  $\pm$  SE =  $0.025$ ,  $F_{1, 25}=5.862$ ,  $P=0.0251$ ). The MAT and Rain values recorded at Kenfig showed no significant trends over time (MAT: linear regression estimate =  $0.028 \pm 0.025$ ,  $F_{1, 25}=1.197$ ;  $P=0.21$ ; Rain: linear regression estimate =  $1.319 \pm 0.700$ ,  $F_{1, 25}=3.551$ ;  $P=0.07$ ).

### 6.3.2 Age-structured models

The best fitting model (with the lowest AICc) was best supported having general temporal variation rather than a linear relationship, indicating no overall trend across the 34 years. There was no clear evidence of a relationship with weather (Table 6.3). As expected, the best model identified a lower survival estimate for first year birds ( $0.20 \pm 0.115$ ) compared with adults ( $0.34 \pm 0.115$ ).

**Table 6.3.** Comparison of the top-ranking *a priori* CMR models of age-structured reed warbler survival  $\phi$  at KNNR, ranked according to their AICc values, with  $\phi$  representing survival, (t) = full time-dependence, (.) = rate was constant over time, SPI = Sahel precipitation index, MAT = Mean April temperature, Rain = rain.

Model	no. parameters	$\Delta$ AICc	Deviance
$\phi(t)$	101	0.0000	681.5020
$\phi$ SPI	57	14.6871	704.1026
$\phi$ Rain/MAT	62	23.1219	714.5164
$\phi$ MAT	57	23.9237	740.4044
$\phi(.)$	6	131.7774	1007.1030

### 6.3.3 Juvenile survival

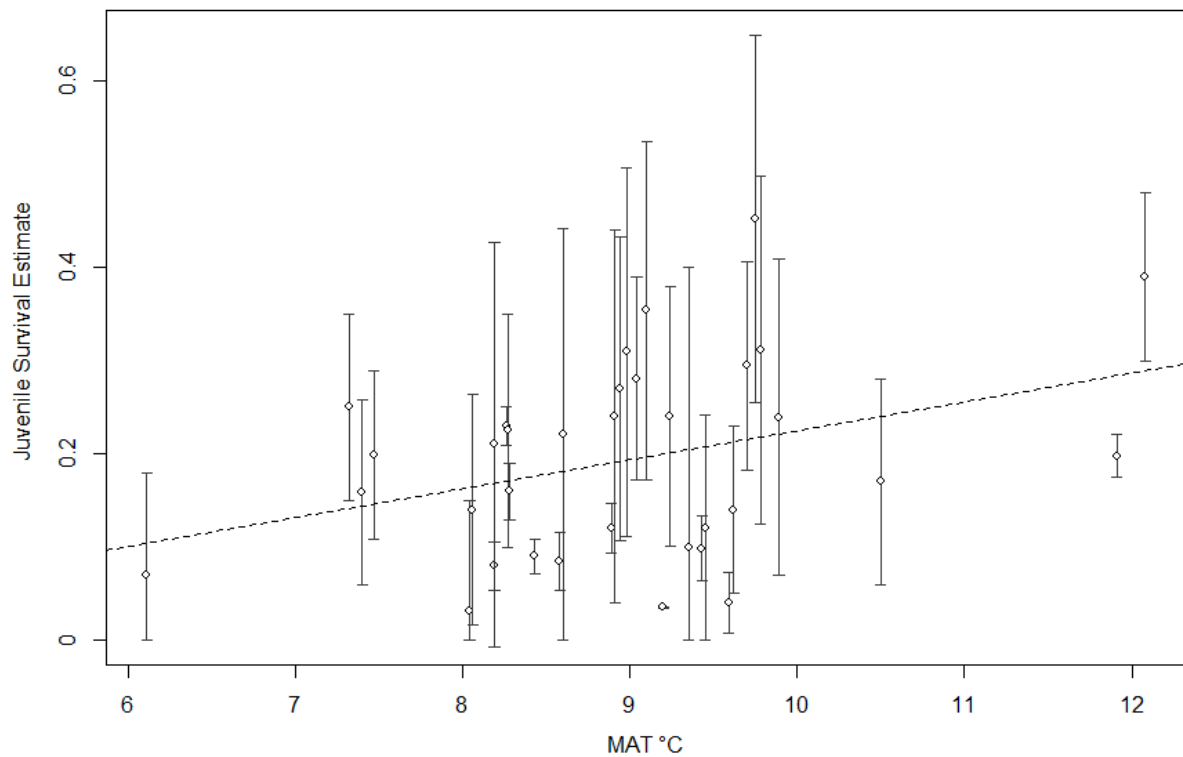
In juvenile-only models there was strong support for weather affecting survival rates. The inclusion of time with an interaction with April temperature had the lowest AICc (Table 6.4; Figure 6.3) followed by the interaction of time with both April temperature and rain. The inclusion of rain only (Figure 6.4), SPI (Figure 6.5) and time (Figure 6.6) reduced the  $\Delta\text{AICc}$  by 3.9-12.129.

**Table 6.4.** Comparison of the top-ranking a priori CMR models of juvenile reed warbler survival  $\phi$  at KNNR, ranked according to their AICc values, with  $\phi$  representing survival, (t) = full time-dependence, (.) = rate was constant over time, SPI = Sahel precipitation index, MAT = Mean April temperature, Rain = rain.

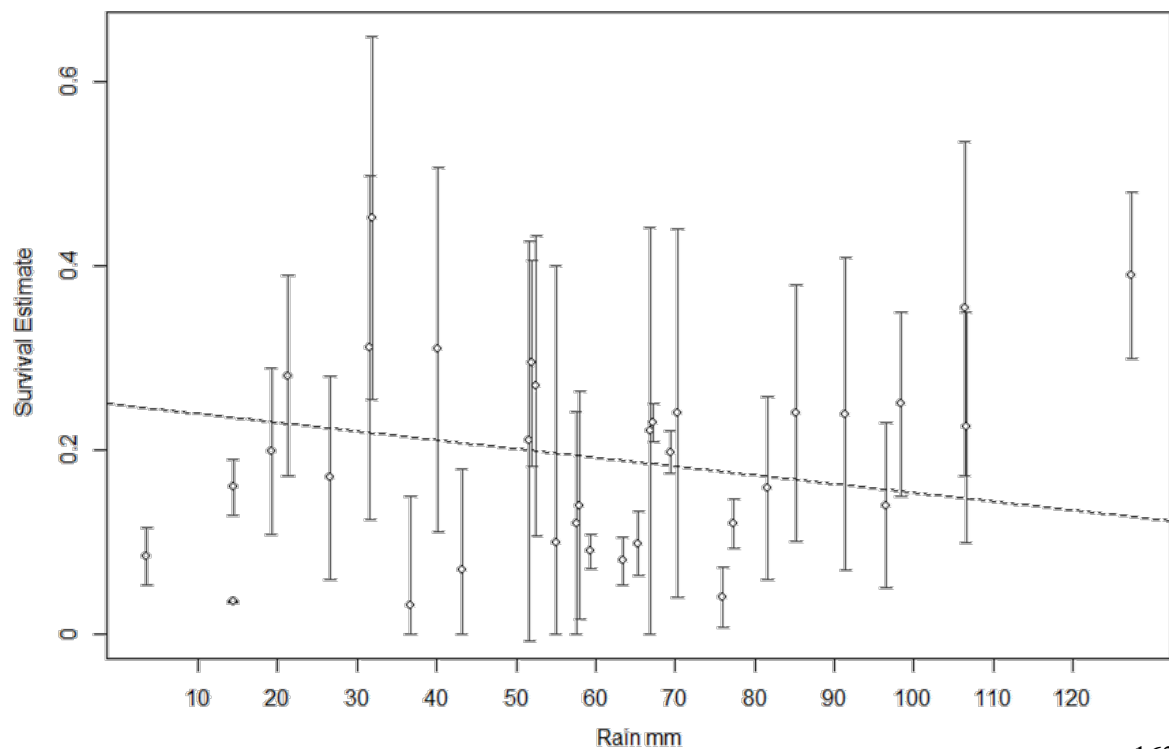
Model	no. parameters	$\Delta\text{AICc}$	Deviance
$\phi\text{MAT}$	37	0.0000	296.1421
$\phi\text{Rain/MAT}$	39	2.0440	299.3241
$\phi\text{Rain}$	37	3.9128	304.2214
$\phi\text{SPI}$	37	8.1312	309.2419
$\phi(t)$	68	12.1290	312.9105
$\phi(.)$	2	21.2735	387.9403

The direction of the effects of weather variable effects were as hypothesised, with higher survival rates associated with high MAT values and lower survival associated with higher Rain values and more negative SPI values. The survival estimates only showed a significant correlation with MAT values (Linear regression estimate 0.031 ( $\pm 0.015$ )  $F_{1,32}=4.431$ ,  $P=0.0432$ ), while the other variables were non-significant.

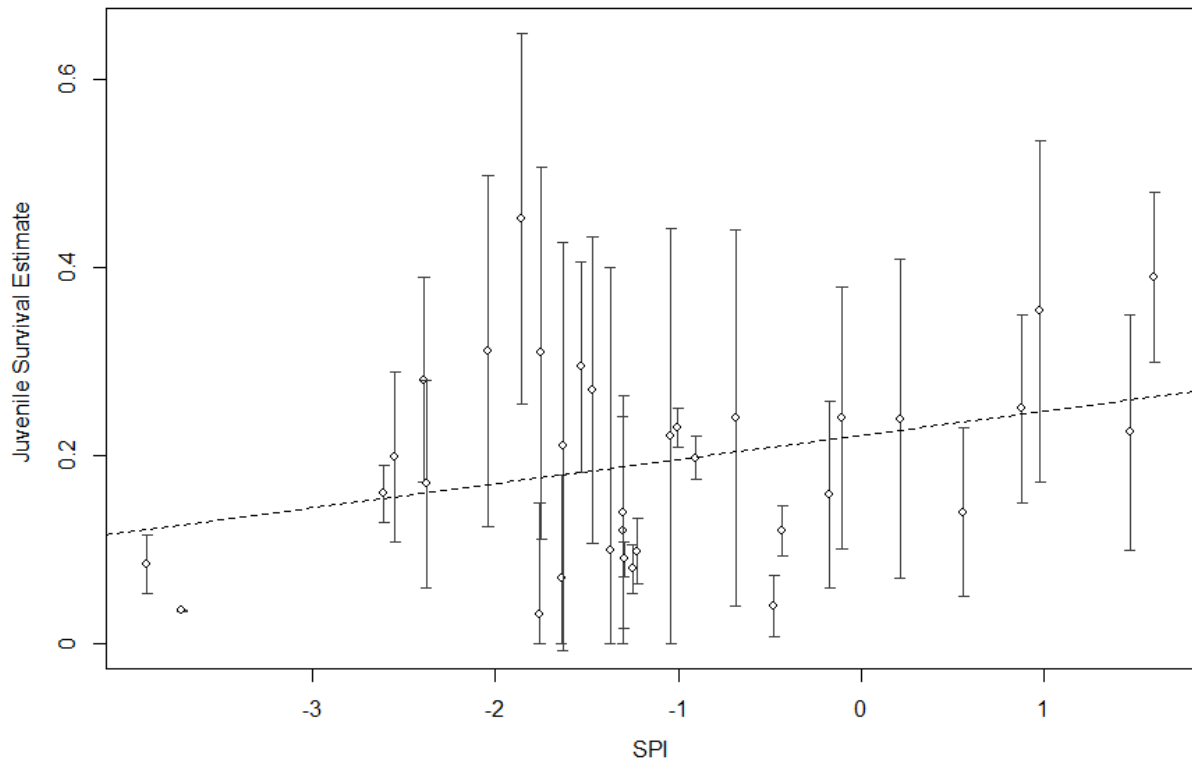
**Figure 6.3.** Survival estimates ( $\pm$  SE) of juvenile reed warblers at Kenfig National Nature Reserve 1980-2013 plotted against mean April temperature (MAT). Linear regression line represents parameter estimate of  $+0.031 (\pm 0.015)$   $F_{1,32}=4.431$ ,  $P=0.0432$ .



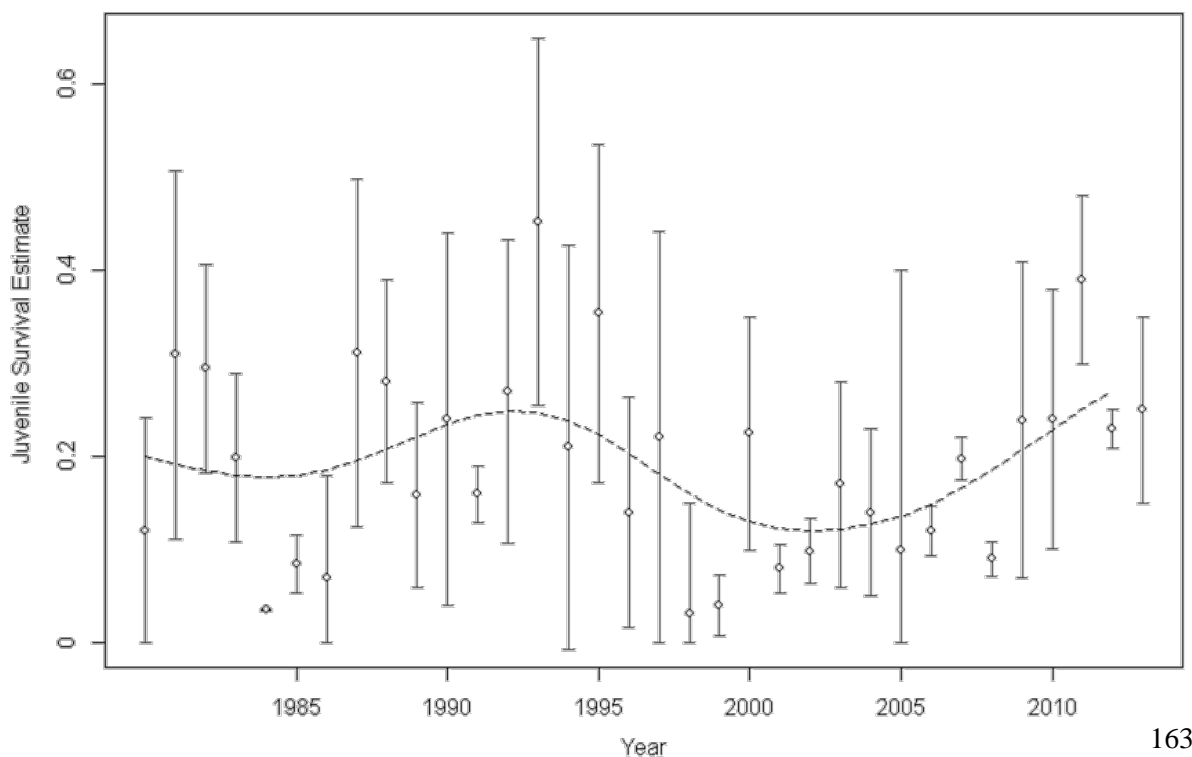
**Figure 6.4.** Survival estimates ( $\pm$  SE) of juvenile reed warblers at Kenfig National Nature Reserve 1980-2013 plotted against total rain. The fitted linear regression line represents parameter estimate of  $-0.001 (\pm 0.001)$   $F_{1,32}=2.975$ ,  $P=0.0942$ .



**Figure 6.5.** Survival estimates ( $\pm$  SE) of juvenile reed warblers at Kenfig National Nature Reserve 1980-2013 plotted against Sahel Precipitation Index (SPI). The fitted linear regression line represents parameter estimate of 0.025 ( $\pm 0.013$ )  $F_{1,32}=3.591$ ,  $P=0.0672$ .



**Figure 6.6.** Survival estimates ( $\pm$  SE) of juvenile reed warblers at Kenfig National Nature Reserve 1980-2013 with the dashed line representing the non-linear survival trend ( $F_{5,654,32}=6.121$ ,  $P=0.0477$ ).





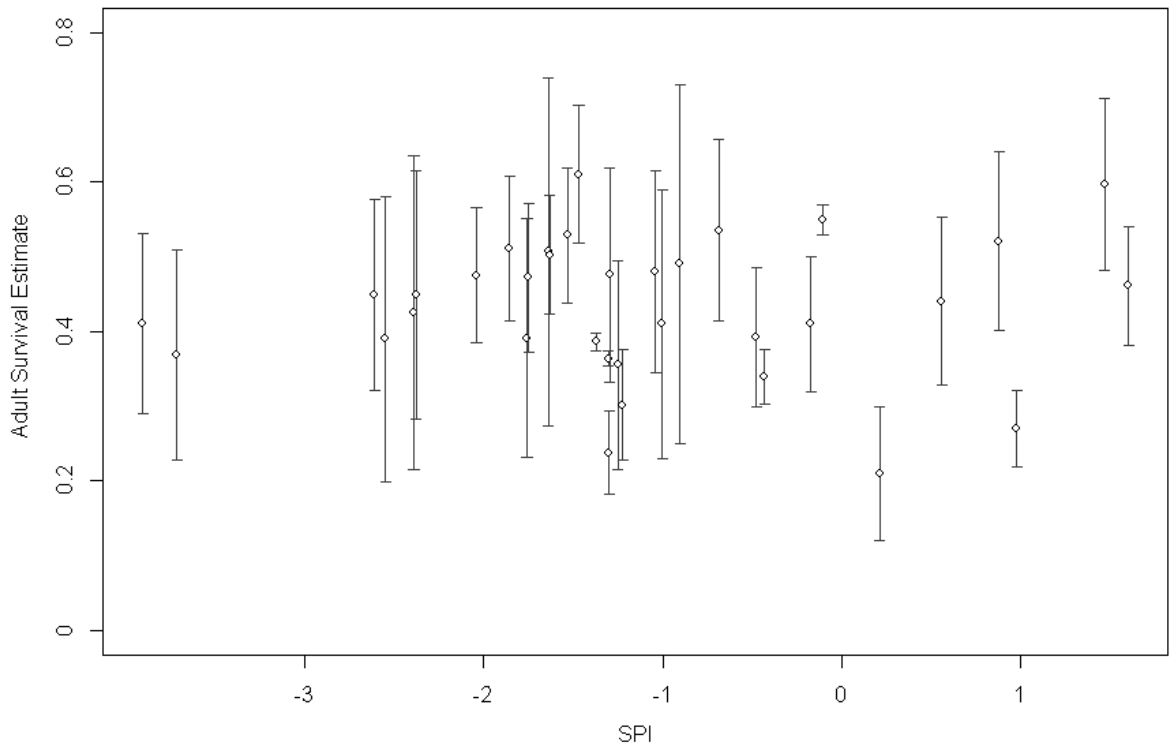
#### 6.3.4 Adult survival

The best supported model using the adult-only data included SPI (Table 6.5, Figure 6.7). The next best supported model included Rain ( $\Delta\text{AICc} = 1.009$ ; Figure 6.8), MAT ( $\Delta\text{AICc} = 1.197$ ; Figure 6.9) and time only (with general temporal variation  $\Delta\text{AICc} = 6.147$ ; Figure 6.10). There was little support for the inclusion of sex in the models ( $\Delta\text{AICc} = 18.18$ ). The survival estimates were weakly correlated with each of the three weather variables with no significant trends identified (Figure 6.7-6.9).

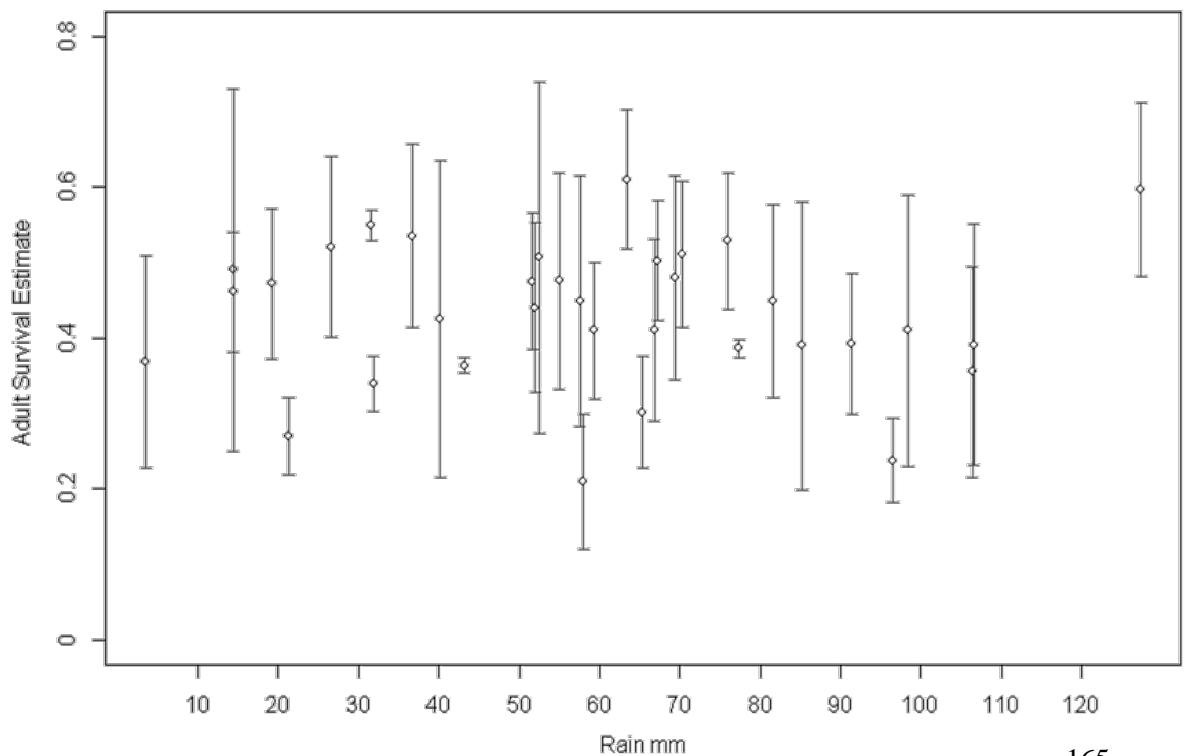
**Table 6.5.** Comparison of the top-ranking a priori CMR models of adult reed warbler survival  $\phi$  at KNNR, ranked according to their AICc values, with  $\phi$  representing survival, (t) = full time-dependence, (.) = rate was constant over time, S = sex, SPI = Sahel precipitation index, MAT = Mean April temperature, Rain = rain.

Model	no. parameters	$\Delta\text{AICc}$	Deviance
$\phi\text{SPI}$	37	0.0000	585.1624
$\phi\text{Rain}$	37	1.0091	585.1768
$\phi\text{MAT}$	37	1.1972	585.3240
$\phi(t)$	68	6.1472	589.3940
$\phi(t)\text{S}$	133	18.1807	591.5611
$\phi(.)$	2	28.5411	632.1167

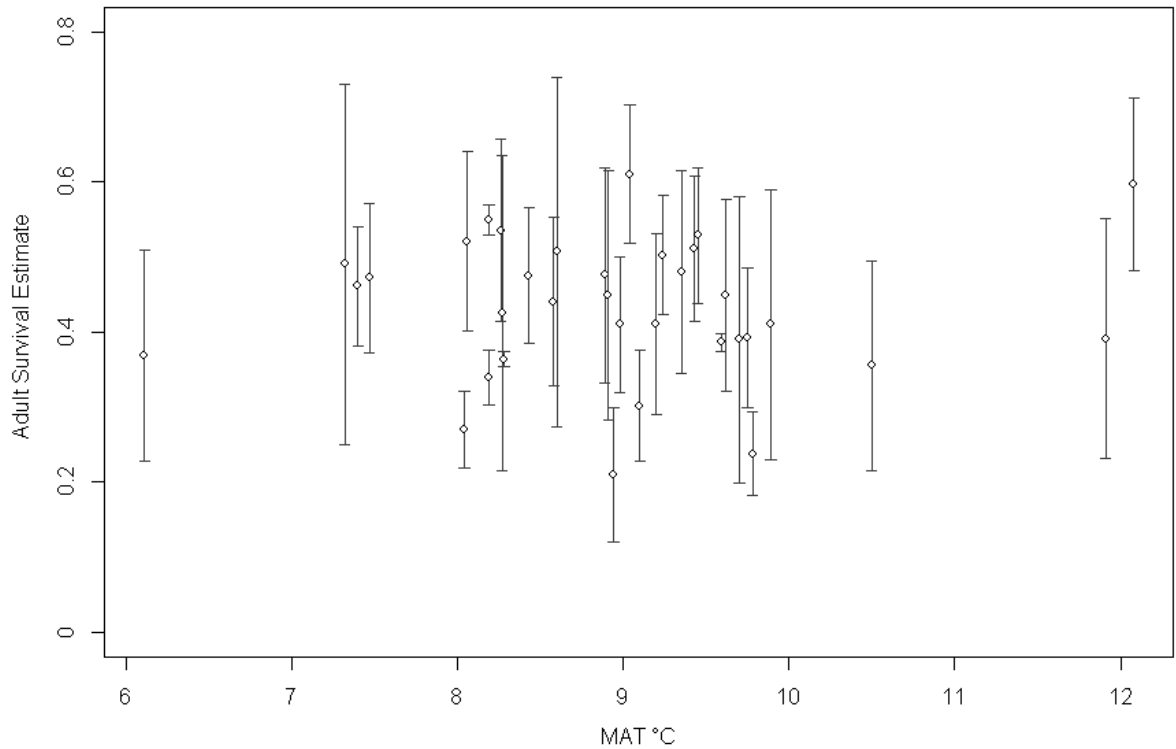
**Figure 6.7.** Survival estimates ( $\pm$  SE) of adult reed warblers at Kenfig National Nature Reserve 1980-2013 plotted against Sahel Precipitation Index (SPI). There was no significant linear trend ( $0.003 \pm 0.013$ ,  $F_{1,32}=0.061$ ,  $P=0.8070$ ).



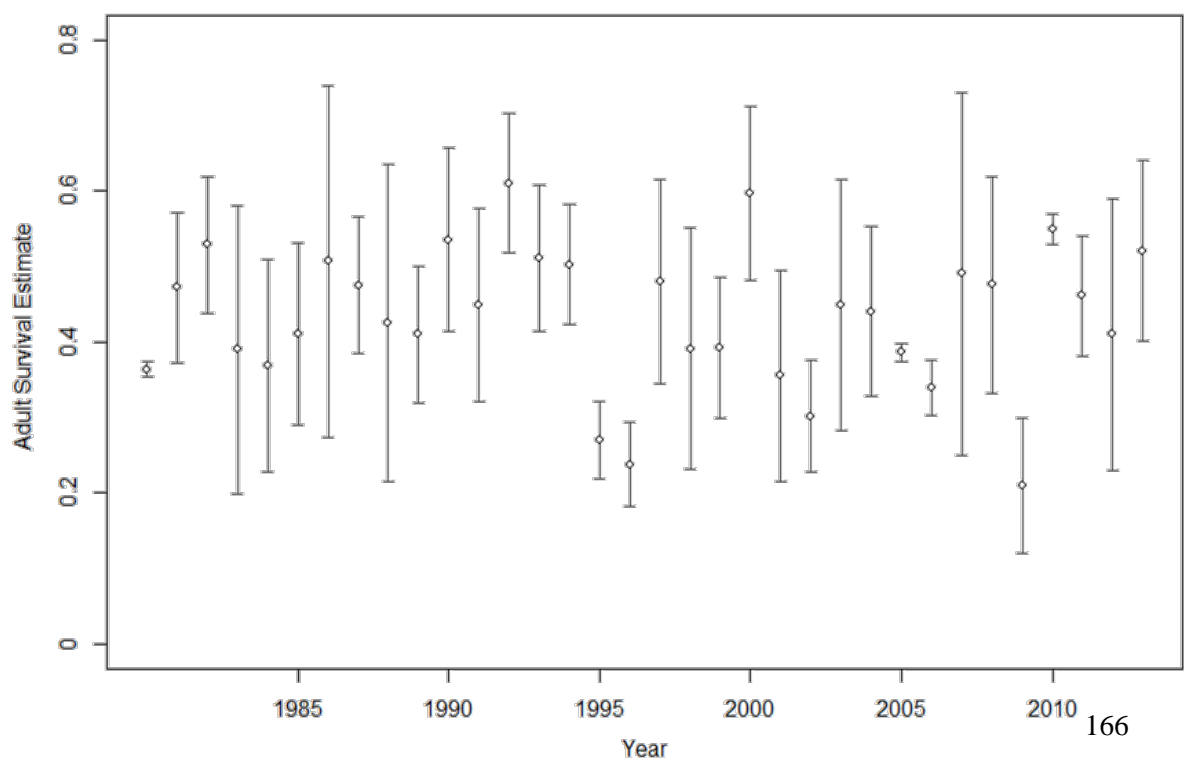
**Figure 6.8.** Survival estimates ( $\pm$  SE) of adult reed warblers at Kenfig National Nature Reserve 1980-2013 plotted against total rain. There was no significant linear trend ( $-0.000 \pm 0.000$ ,  $F_{1,32}=0.061$ ,  $P=0.8060$ ).



**Figure 6.9.** Survival estimates ( $\pm$  SE) of adult reed warblers at Kenfig National Nature Reserve 1980-2013 plotted against mean April temperature (MAT). There was no significant linear trend  $-(0.001 \pm 0.014, F_{1,32}=0.0127, P=0.9108)$ .



**Figure 6.10.** Survival estimates ( $\pm$  SE) of adult reed warblers at Kenfig National Nature Reserve 1980-2013



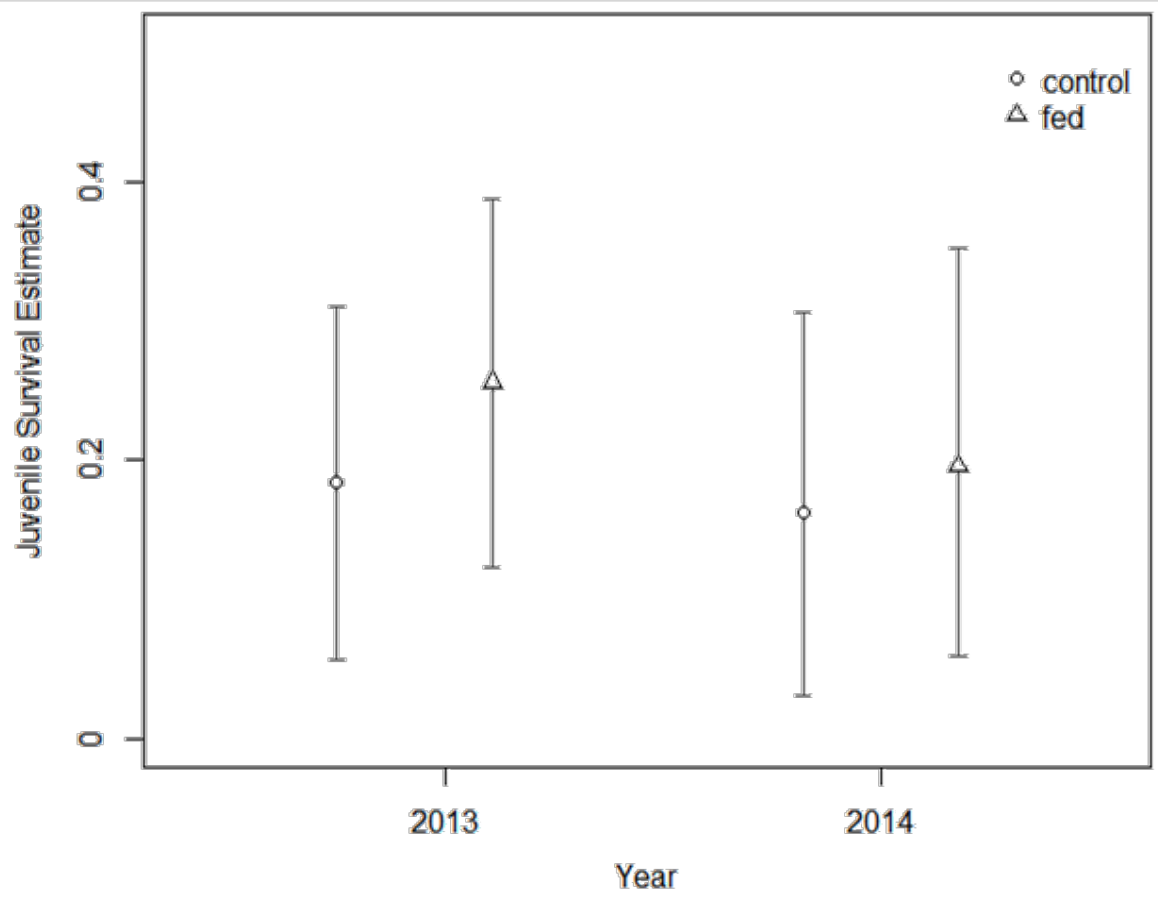
### 6.3.5 *The effects of supplementary feeding on juvenile survival in CBWR*

The best-supported model for survival estimates included separate time-variable survival parameters ( $\phi$ ) for control and fed treatment birds followed by a time-dependent only model which provided similar support (Table 6.6). The low  $\Delta\text{AICc}$  of the time-dependent model indicates that the support for a treatment effect on juvenile survival is weak and the effect size is small (95% CI Limits = 0.033-0.072).

**Table 6.6.** Comparison of the top-ranking a priori multistate models of juvenile reed warbler survival  $\phi$  at CBWR, ranked according to their AICc values, with  $\phi$  representing survival, (t) =full time-dependence, (.) =rate was constant over time, f= feeding group.

Model	no. parameters	$\Delta\text{AICc}$	Deviance
$\phi(t)f$	6	0.0000	7.3618
$\phi(t)$	4	0.0718	5.3916
$\phi(.)$	2	3.4276	4.6314

**Figure 6.11.** Survival estimates ( $\pm$  SE) for juvenile reed warblers in control and fed treatments in Cardiff Bay Wetland Reserve 2013- 2014.



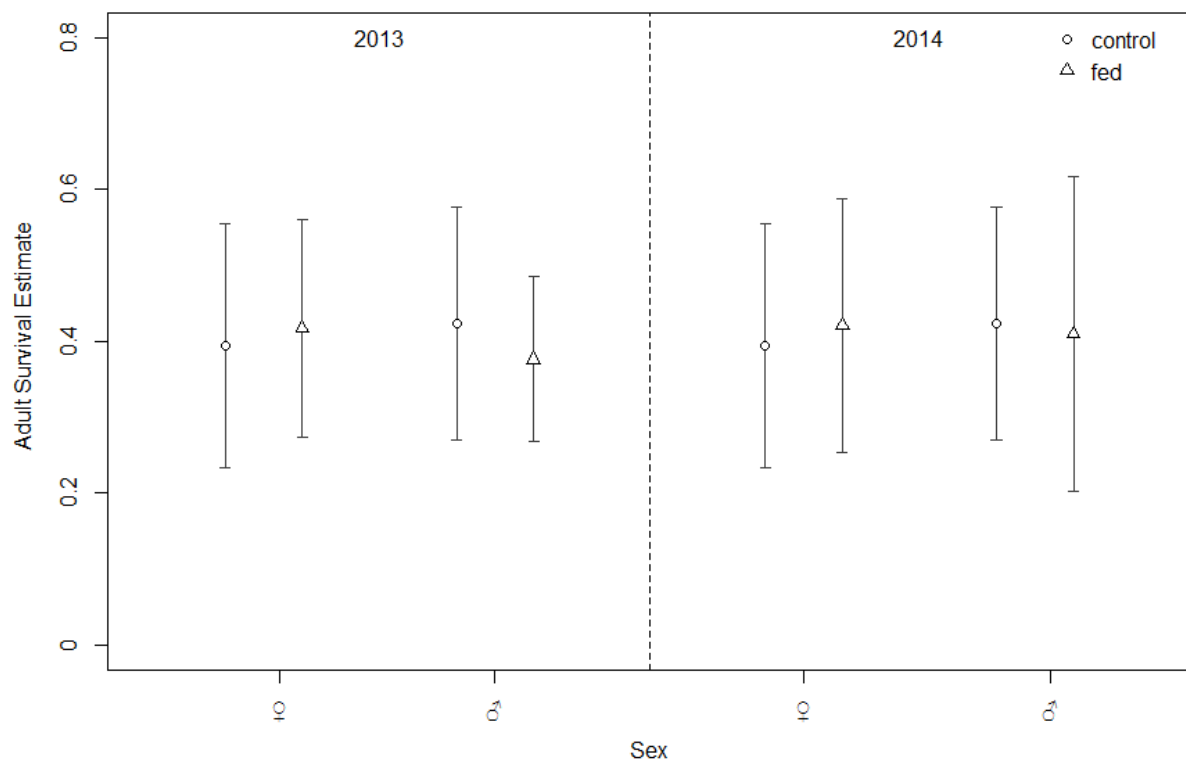
#### 6.3.6 *The effects of supplementary feeding on adult survival in CBWR*

The best-supported model for survival estimates included treatment and sex, followed by a sex model which provided similar support (Table 6.7). The survival estimates showed no significant variation between treatment or sexes although fed females had a higher mean survival than control females ( $0.417 \pm 0.143$  (fed 2013) and  $0.420 \pm 0.167$  (fed 2014) compared with  $0.395 \pm 0.161$  (control 2013) and  $0.395 \pm 0.161$  (control 2014); Figure 6.12). In contrast, fed males showed a decreased survival compared with control males ( $0.376 \pm 0.109$  (fed 2013) and  $0.410 \pm 0.207$  (fed 2014) compared with  $0.423 \pm 0.153$  (control 2013) and  $0.423 \pm 0.153$  (control 2014)).

**Table 6.7.** Comparison of the top-ranking a priori multistate models of adult reed warbler survival  $\phi$  at CBWR, ranked according to their AICc values, with  $\phi$  representing survival, (t) =full time-dependence, (.) =rate was constant over time, f= feeding group, s = sex group.

Model	no. parameters	$\Delta\text{AICc}$	Deviance
$\phi(t)f\ s$	7	0.0000	9.6807
$\phi(t)s$	6	1.8873	12.5874
$\phi(t)f$	6	3.1762	14.6617
$\phi t$	4	4.2661	14.9817
$\phi(.)$	2	5.6771	16.3812

**Figure 6.12.** Survival estimates ( $\pm$  SE) for adult reed warblers in control and fed treatments in Cardiff Bay Wetland Reserve 2013- 2014.



## 6.4 Discussion

The predicted effects of climate-change across the migratory range of Eurasian reed warblers are substantial and include rising mean spring temperatures on the breeding grounds and more frequent low rates of precipitation on the wintering grounds (Zwarts *et al.* 2009). Despite these predictions, the historical data between 1980 and 2013 show that SPI values have become increasingly positive (i.e. the Sahel has become wetter) while the increases in mean spring temperature and spring rainfall are minor and not statistically significant. Perhaps in light of this, this study reveals relative stability in the survival of a South Wales breeding population with little influence of the tested weather variables on survival.

Reed warblers, as long-distance migrants that exploit the conditions in different biomes carry a high cost of migration as is the case for other long-distance migrants. Indeed, the survival estimates obtained from both KNNR and CBWR models (ranging between 0.30 and 0.59), are comparable to other similar studies (Bibby 1971 (0.44-0.64); Green 1975; 1976; Redfern 1978 (0.43-0.57); Thaxter *et al.* 2006 (0.41-0.68)). Reed warbler age was identified as an important factor in survival models, with juveniles estimated to have a lower rate of survival than adults by a mean of 0.24. It is well-established that juveniles have a lower apparent survival rate than adults on the basis of age-related differences in mortality and lower rates of natal site philopatry (Greenwood and Harvey 1982; Thaxter *et al.* 2006; Fulton 2010). By separating juveniles from adults, the analysis revealed a positive relationship between survival and mean April temperature. The mechanisms behind this relationship may be that warmer spring temperatures are associated with earlier nesting, a factor that is often correlated with higher rates of offspring survival (e.g. great tit *Parus major*: Perrins 1965; pied flycatcher *Ficedula hypoleuca*: von Haartmann 1967; house martin; Bryant 1975; European blackbird *Turdus merula*: Snow 1955). Aside from the potential survival benefits of hatching at a period of greater food availability, earlier nesting

allows nestlings to avoid the period of greatest predation that typically occurs during the peak of the breeding period and facilitates a longer period on the natal grounds prior to autumn migration (Perrins 1965; Daan *et al.* 1988; Price *et al.* 1988; Møller 1994; Spear and Nur 1994; Dzus and Clark 1998; McKim-Louder *et al.* 2013). Juvenile survival was related to April rainfall and the Sahel precipitation index on the basis of the AIC model comparisons, but the correlations were weak. The significant non-linear temporal trend in juvenile survival suggests there is a temporal pattern relating to juvenile survival, although the cause has not yet been identified. One avenue of enquiry is the influence of weather conditions later in the breeding season on the survival of recently fledged birds. For example, this period has been implicated as of importance for the survival of juvenile spotted flycatchers *Muscicapa striata* (Freeman and Crick 2003).

The adult-only models showed weak correlations with all weather variables although the model including the Sahel precipitation index was best supported. Wetland habitats in the Senegal Delta and Inner Niger Delta are vulnerable to the effects of prolonged droughts as well as the habitat losses from agriculture and hydrological intervention (Zwarts *et al.* 2009). However, wintering reed warblers are less constrained to wetlands than other wetland-breeding migrants such as sedge warblers, and are found occupying the surrounding dry scrub habitats as well as the moist savannahs and tidal mangroves further south. Therefore, climate-driven loss of wetland habitat may not represent such an important influence of overwinter survival as is the case for sedge warblers (Peach *et al.* 1991; Leisler and Schulze-Hagan 2011; Zwartz *et al.* 2009). These findings, of minimal influence of weather conditions on survival, are mirrored by similar studies of reed warbler population trends in the UK (Thaxter *et al.* 2006), Sweden (Osterlof and Stolt 1982), Belgium (Nef *et al.* 1988), Germany (Zang *et al.* 2005; Berthold and Fiedler 2005), Switzerland (Wiggler 2005) and the Czech Republic Reif *et al.* 2006). A lack of strong correlation of survival with conditions on the wintering grounds has been shown in other studies of small migrant birds (Stokke *et al.*



2005, Robinson et al. 2008; Schaub et al. 2005; Jarvinen 1987; Foppen et al. 1999; Salewski et al. 2013) and may indicate that breeding success and productivity may be better predictors of population dynamics rather than survival (Zwarts *et al.* 2009). Improving conditions on the breeding grounds may not improve the actual survival of birds as such, but may ensure a better rate of retention of breeding birds at the breeding site because of higher philopatry, which may translate into a higher rate of apparent survival (Schultze-hagen 1993).

The effect of the supplementary-feeding treatment in the CBWR study on juvenile and adult survival was equivocal on the basis that models excluding the feeding treatment were as well supported as models including it. Juvenile survival estimates were marginally higher in the fed treatment than control, which suggests that either the nutritional status of birds during the dependant stage or the timing of hatching in this treatment may have some importance as a determinant of survival. In adult-only analysis, the model including sex and feeding treatment was best supported, suggesting important sex-related variation in the effect of the feeding treatment. As discussed in Chapter 4, food supplementation in our study may have compensated for periods of low natural food availability, thereby reducing nutritional stress, reducing the workload of feeding dependent offspring, and of fuelling for migration. All of these benefits would be expected to increase survival of adults due to lower reproductive costs and improved body condition at the onset of migration. However, only females showed increases in survival as a result of fed treatments, while fed males showed lower survival. Since females showed a stronger response to the fed treatment compared to males (e.g. by increasing mass to a greater extent; see Chapter 4) in combination with higher rates of inactivity on the nest, females may gain greater survival. By contrast, by responding at all to greater food availability (e.g. by increasing mass), male reed warblers may reduce their physiological stress during the breeding season but may increase their risk of predation since males, unlike females, must maintain and patrol their breeding territories throughout the breeding season.

Although the measures of environmental conditions on the breeding and wintering grounds used in this study show evidence of a weak effect on survival, this does not preclude the possibility that conditions experienced at these places or on migration will account for a significant proportion of the variation in apparent survival. Equally, identifying and quantifying variables that indicate important carry-over effects is a major challenge in this work. For example, the beneficial effects on survival of improved conditions on the breeding grounds may be offset by the deterioration of habitats on the wintering grounds, and vice versa. The inconclusive results could be due to the use of too-general weather variables in the separate models, each of which explain only small proportion of variation in apparent survival, or not including the conditions of the more critical periods (e.g. post fledging). The remaining variation could be due to factors unrelated to weather such as variation in habitat quality, competition, and disease or predation pressure. Alternatively, the effects may be diluted through the population, which may consist of individuals with differing migration routes and wintering areas (Prochazka et al. 2009; Zwartz et al. 2009; Leisler et al. 2011). In addition, the power to detect changes in survival may have been limited by the relatively low detection probabilities compared with some other long-distance migrants (Seward et al. 2012; Salewski et al. 2013), high rates of dispersal or a large proportion of transient individuals. Reed warbler populations are notoriously difficult to sample comprehensively as they are a skulking species that inhabit dense stands of tall and often dense vegetation, sometimes in deep water that cannot be accessed or practically monitored using mist nets (Leisler et al. 2011; Møller et al. 2009).

Finally, the present study and analysis assumes, perhaps simplistically, that birds are passive and respond in binary outcomes to changes in basic climatic measures, ignoring the capacity to respond using phenotypic plasticity or evolution. Birds are well-studied and their behaviour, distribution, breeding output and migration have been monitored intensively over the course of the greatest change in climate history in the last 200 years. In this time birds

have responded to climate change by shifting their distribution, the timing of laying, and migratory behaviour (Thomas and Lennon 1999; Dunn and Winkler 2010; Fiedler 2003). It is therefore possible that, particularly in adaptable species like reed warbler, birds can adjust to their changing environment sufficiently for population size to remain largely stable over several decades.

## **Chapter 7**

### **General Discussion**

## **7.1 The effects of climate-driven changes in food availability and habitat quality on migratory birds**

There is growing evidence that migratory birds are affected by climate change directly through the effects of weather, as well as via indirect effects of climate-driven changes to habitat quality and food availability (Crick 2004; Pearce-Higgins *et al.* 2010; Pearce-Higgins *et al.* 2011; Seward *et al.* 2013). Both short and long-term changes to the abundance and distribution of prey may have a variety of implications for the different stages of the annual cycle for migrant birds. In this study, I have assessed the mechanisms and impacts of climate-driven changes on the breeding and wintering ecology of a long-distance migrant bird, the Eurasian reed warbler, using a combination of observational and experimental approaches with the aim of addressing ‘gaps in knowledge’ identified in Chapter 1, to provide a holistic understanding of how the study system may be influenced by climate. Eurasian reed warblers are particularly well suited for this study because their biology and ecology are well understood. Despite this knowledge, and the recent attention on climate change in the last 30 years, little is known about the mechanisms by which climate affects reed warblers. The general aims of this thesis were to review and test the effects of climate change on reed warbler biology, as a case study of the mechanisms by which climate may affect migratory songbirds in general. The specific aims were to determine:

1. The importance of local and larger-scale weather conditions in determining the availability of invertebrate prey resources (Chapter 2).
2. How associations of invertebrate prey availability with short-term weather variation can reveal long-term trends that may have occurred in relation to climate change (Chapter 2).

3. How experimental manipulations of temperature can explain differences in shoot emergence timing and growth rate of *Phragmites*, and the emergence and availability of invertebrate prey for reed warblers (Chapter 3).
4. How weather conditions and food availability affect body condition and breeding performance of adult reedbed warblers (Chapter 4).
5. How differences in food resources among habitats in the tropical non-breeding grounds affect body condition (Chapter 5).
6. The importance of inter-annual variations in weather conditions on the European breeding and African wintering grounds to the survival of reed warblers (Chapter 6).
7. The influence of food availability on reed warbler survival (Chapter 6).

In Chapter 2, the monitoring study confirms the prolonged period of mid-summer invertebrate prey availability in temperate wetlands and reveals the effects of mean air temperature, the cumulative effect of temperature (i.e. “growing degree day”), and short-term influences of wind and rain on invertebrate availability. The strong correlation of invertebrate availability with cumulative temperature provides support for an effect of rising temperatures on invertebrate abundance, while the short term influences of temperature, rain and wind account for differences in activity. This indicates that climate-driven increases in temperatures will increase invertebrate activity-density earlier in the year by affecting development and emergence phenology of invertebrates as well as their current activity levels. The extrapolations of these patterns using historical weather datasets showed a relatively small advance of ~4.8 days across 34 years in the timing of a hypothetical threshold minimum invertebrate availability value. The results provide conceptual and

empirical support for the influence of rising temperatures on the timing of invertebrate availability and indicate that climate-driven increases in temperature earlier in the spring are likely to result in correspondingly earlier increases in invertebrate abundance which may extend over a longer period. This work builds upon similar studies monitoring the effect of weather variables on Arctic invertebrates as a food resource for breeding shorebirds (Høye and Forschhammer 2008; Tulp and Schekkerman 2008) and those using chironomids as proxies for environmental change (Larocque and Hall 2002; Woodward and Shulmeister 2006; DeChaine and Martin 2006). Although there are many experimental studies of invertebrate responses to temperature manipulations (Taylor 1963; MacLean and Pitelka 1971; Briers *et al.* 2003; Goulson *et al.* 2005; Høye and Forschhammer 2008), there is limited literature available for the influences of weather variables on natural abundances of wetland invertebrates in the context of invertebrate prey for migratory warblers.

In Chapter 3, temperature manipulation experiments revealed faster *Phragmites* growth in the elevated temperature treatments and earlier, larger peaks in invertebrate emergence. This provides experimental evidence that climate change is likely to cause earlier availability of suitable nesting vegetation and sufficient prey levels for breeding reed warblers. These experimental temperature manipulations build on the work of Taylor (1963); Haslam (1974); Zemlin *et al.* (2000); Bale *et al.* (2002); Briers *et al.* (2003); Goulson *et al.* (2005); Eggermont and Heiri (2012) by providing a focussed perspective on the effects of rising temperature treatments on the resources required by a particular consumer species, the reed warbler.

In Chapter 4, I used experimental food supplementations to test for evidence that food abundance limits key aspects of reed warbler breeding biology, in order to understand the mechanisms by which climate driven changes in food supply may affect the demography of

the species. Breeding reed warblers in the food supplemented group significantly advanced their laying date, reduced their laying interval and incubation period, and increased nestling growth rates. This provides evidence for food limitation on these aspects of breeding biology, and such limitation appears to be particularly strong early in the breeding season. This study builds on the observational work on breeding phenology in reed warblers and their congeners undertaken by Crick and Sparks (1999); Schaefer *et al.* (2006); Halupka *et al.* (2008); Dyrce and Halupka (2008) and the supplementation studies on other bird taxa in habitats such as woodland, where the peak in food availability is much shorter than in reedbeds (Kallander 1974; Rodenhouse and Holmes 1992; Desrochers 1992; Svensson and Nilsson 1995; Kallander and Karlsson 2013). This study also revealed patterns of adult mass change in control (non-supplemented) birds that are consistent with the energetic stress hypothesis, as found in other species during the breeding season (Johnston 1993), particularly those studied at natural breeding densities (Cucco and Malacarne 1997; Nagy *et al.* 2007; Neto and Gosler 2010). Food supplementation led to large increases in body mass during the prelaying stage, providing further support for food limitation (under current climatic and foraging conditions). Food-supplemented reed warblers maintained high mass throughout the breeding period which may indicate preparation for a second breeding attempt. Together, the results from Chapters 2-4 suggest that warmer spring temperatures will increase the availability of food for breeding reed warblers which may increase breeding productivity by enabling earlier fledging (which is associated with higher rates of survival and subsequent recruitment of chicks (Perrins 1965; Price *et al.* 1988; Daan *et al.* 1989; Spear and Nur 1994; Mckim-Louder *et al.* 2013) and enabling earlier initiation of a second breeding attempt (which is associated with a higher total annual breeding productivity (Halupka *et al.* 2008).

Chapter 5 focused on the role of food availability on the non-breeding grounds in West Africa. Reed warblers occupying wetland habitats maintained lower body reserves in this



food-rich habitat than conspecifics occupying relatively food-poor dry-scrub habitats. This is consistent with strategic buffering of reserves against starvation in food-poor habitat, indicating that birds occupying prey-rich habitats can reduce body reserves while those occupying prey-poor habitats generally carry an increased level of body reserves as a strategic buffer against starvation. The ability to occupy poor quality habitats (at the cost of carrying higher reserves) may release reed warblers from a strict dependence on wetland habitats during periods of greatest food limitation and competition. Models of climate change are inconclusive regarding the direction of changes in future Sahel rainfall (Hulme *et al.* 2001; Zwarts *et al.* 2009; Atkinson *et al.* 2014), but if wetlands can be maintained or increased in the Sahelian wintering grounds due to higher rainfall, this may facilitate higher survival of migratory birds including reed warblers. Conversely, decreasing rainfall in the region is likely to increase the pressure on wetlands causing continuing declines in wetland-specialist migrants (e.g. sedge warblers) while reed warblers may be able to avoid such strong declines through the use of dry scrub. The study helps to fill the current gaps in understanding about the distribution, habitat use and foraging ecology of reed warblers two habitat types in Africa, since no other study has looked at these issues in the Sahel region, other than body mass regulation during migratory fuelling (Jenni-Eiermann *et al.* 2011) and correlations of annual survival with environmental conditions in Africa (Hutto 1980; Peach *et al.* 1991; Szep 1995; Foppen *et al.* 1999; Boano *et al.* 2004; Thaxter 2006; Salewski *et al.* 2013). The study also builds on the wintering mass regulation studies undertaken in temperate zones (McNamara and Houston 1990; Ekman and Hake 1990; Witter and Cuthill 1993; Witter and Swaddle 1997) and the extensive habitat quality gradient work undertaken in the Neotropics (Marra and Holberton 1998; Marra 2000; Strong and Sherry 2000; Marra and Holmes 2001; Fernández and Lank 2006; Brown and Sherry 2006; Smith *et al.* 2010).

In Chapter 6, the variation in adult survival was best described by conditions on the wintering grounds while first year survival was best described by conditions on the breeding

grounds. This provides support for a strong effect of warmer springs on juvenile reed warbler survival. Provision of supplementary food during the breeding season showed a minor increase in juvenile annual survival but did not affect annual survival of adults, suggesting that the nutritional status of birds during the dependant stage or the timing of hatching in this treatment may have some minor importance as a determinant of survival. This builds on the work of other survival studies on reed warblers particularly Bibby (1971); Green (1975; 1976); Redfern (1978); Berthold and Fiedler (2005); Thaxter (2006); Salewski *et al.* (2013), and extends these studies by using an experimental manipulation to test the importance of food availability on the breeding grounds.

## **7.2 Considerations**

Although this study presents robust findings based on original research, as with most scientific work, there are several shortfalls and weaknesses that need to be addressed and justified.

### **7.2.1 *Population-level effects***

The responses of reed warblers to changes in their environments were reported in terms of the population (e.g. the means and standard errors) and were, depending on the study, split by year, experimental treatment group, sex and age. While the study revealed important and significant population-level effects, the heterogeneity in response due to individual differences are overlooked. The importance of this individual variability and the heritability of traits are discussed below and will be investigated in detail in further work investigating the role of phenotypic plasticity and the heritability of traits.

### 7.2.2 *Shortfalls of first brood-only results*

The data collected as part of the breeding season study included only first brood data. One of the core findings of this chapter is that Eurasian reed warblers advance the start of their breeding season in response to spring temperatures and food availability. The assumed benefits of this response are considered to be i) lower clutch/nestling predation, ii) higher juvenile survival and iii) earlier nest completion leading to higher chances of successful second broods. While the first two benefits are testable by comparing early and late nestlings, the third benefit cannot be confirmed in this study as second broods were not recorded. This omission represents a major weakness in the ability of the study to confirm this benefit, which may represent the mechanism by which reed warbler populations are increasing and expanding their distribution. The collection of such data was due to practical considerations in the first year and attempted in the second and third year but with insufficient data. The difficulty in locating second nests lies in the low percentage of birds participating (estimates for European populations are 0-30%; Halupka *et al.* 2008) as well as the difficulty in finding them in full growth, often partly-collapsed reed swamp. This is a difficulty experienced by other researchers studying this species (Pers comm. David Leach). Future work will assign more effort and man power to fulfilling this important aim.

### 7.2.3 *Molecular Analysis*

The thesis initially included a study of warbler diet using molecular identification of the components of diet, using warbler faecal samples. This study would test for potential dietary partitioning of resources between species breeding in wetland habitats e.g. difference between reed warblers and sedge warblers and track changes in diet composition across seasons and years, as well as testing the efficacy of sticky traps in representing the range of taxa included on the *Acrocephalus* menu. Although the study was designed, faecal samples

were collected, DNA extracted and sequencing carried out using tested methodologies by experienced and trained personnel, many of the samples failed due to insufficient genetic material in the DNA extractions for the fusion primers to act on. The viable data come from pooled samples representing species diets over short timeframes (within one to two weeks) and reveal important prey species but is insufficient to support the intended studies. The value of this preliminary work is that it provides an initial assessment of reed warbler diet at our study sites, and informs the refinement of this procedure for further work in this rapidly evolving field.

## **7.2 Are reed warblers typical migratory songbirds?**

Reed warblers are unusual among long-distance migratory songbirds, in that their European breeding populations have increased over recent decades, whereas populations of many other such species have decreased (Burfield *et al.* 2004; Bulmer *et al.* 2013). There is evidence that the climate in the UK has increased by 1°C in the last 30 years (Watts *et al.* 2014). The detailed studies described in this thesis suggest that by having an adaptable foraging strategy, occupying prey-rich breeding habitats and prey-poor wintering habitats, reed warbler populations may be profiting from the benefits of climate change while avoiding the detriments. The propensity to exploit spatially and temporally varying prey resources may enhance an individual's survival when resources are limited or when occupying unknown and unpredictable habitats (e.g. during migration stopovers; Morse 1971; Overington *et al.* 2011). In addition, the ability to maximise nestling development by provisioning at a high rate (and reducing the period of nestling vulnerability) will be strongly favoured by selection in wetlands, where there are high rates of nest predation (Ricklefs 1969; Duckworth 1992; Kleindorfer *et al.* 1997). Adaptable foraging strategies are also reported in chiffchaff *Phylloscopus collybita*, whitethroat *Sylvia communis* and subalpine warbler *S. cantillans* which have stable European populations at the decade-scale,

with declines in individual years associated with factors (e.g. loss of wintering habitat) unrelated to diet specialisation (Wilson and Cresswell 2006; Stevens *et al.* 2010 Baillie *et al.* 2013). The occupation of *Phragmites*-dominated habitats during the breeding season is a trait shared by great reed warblers *A. arundinaceus*. The effect of warming spring temperatures on the development of *Phragmites* and the earlier availability of invertebrates will represent benefit for these species but the mechanisms may differ. Great reed warblers show population increases in response to warmer conditions by increasing clutch size and nesting success but show less pronounced phenological advances than reed warblers in response to warmer springs (Schaefer *et al.* 2006; Dyrce and Halupka 2008). This may be related to a lower requirement for avoiding periods of higher competition and predation, which represent more important selective pressures in reed warblers (Schaefer *et al.* 2006; Dyrce and Halupka 2008). By contrast other similar *Acrocephalus* species, e.g. aquatic warbler *A. paludicola* and marsh warbler *A. palustris*, occupy non-*Phragmites* breeding habitats that are threatened by degradation through agricultural drainage (Leisler *et al.* 2011), and so have different pressures.

Reed warblers are able to inhabit alternative habitats on their wintering grounds and thus appear to avoid the high rates of density-dependent mortality associated with drought conditions as found with sedge warbler and great reed warbler (Altenburg and van Spanje 1989; Zwarts *et al.* 2009). This is also true for other species with flexible habitat selection strategy including subalpine warbler and chiffchaff, which have stable populations. It is likely that the combination of these traits has enabled reed warblers to maintain their population size and even to expand into north-western Europe where the breeding conditions are improving.

## 7.4 Further work

In order to achieve the modest aims of this thesis, a wide range of potentially important aspects of wetland, plant, invertebrate and bird ecology are largely ignored. For example, in terms of bird ecology alone, the effect of climate change on the interspecific interactions between species (e.g. cuckoos *Cuculus canorus* and great reed warblers), migratory flight range and departure fuel loads, as well as the wider threats from habitat loss, land management and invasive species are briefly mentioned but not considered in detail. By dispensing with these issues, the true future for these birds cannot be reflected with confidence. However such an approach enables a clearer focus on a set of key questions and a means to establish an understanding of these issues to serve as a starting point for future research.

### 7.4.1 *Determining the phenotypic plasticity or adaptive evolution of heritable traits.*

This study has revealed that individuals showing plasticity in response to environmental variation have the potential to gain fitness benefits. The behavioural traits that determine these responses, with their potential gains to fitness, include clutch initiation date, propensity to exploit temporally and spatially abundant food supplies, chick provisioning rate and ability to occupy alternative wintering habitats. Evidence from a range of bird species suggests that phenotypic plasticity (rather than evolutionary change) is the primary mechanism underlying observed changes to laying date in response to recent variation in environmental conditions (Przybylo *et al.* 2000; Both and Visser 2001; Schiegg *et al.* 2002; Sergio 2003; Sheldon *et al.* 2003), whereas changes in morphology and the timing, direction and fuelling aspects of migratory behaviour are associated with genetic adaptation within populations (Dhondt 1983; Berthold *et al.* 1992; Bearhop *et al.* 2005; Knudson *et al.* 2011; Gienapp *et al.* 2007). High levels of phenotypic plasticity for particular traits such as the

propensity to exploit temporally and spatially variable food resources can be beneficial for species living in unpredictable environments, allowing them to track current conditions within the “normal” range of variability (Pulido and Berthold 2004). However, if phenotypic plasticity alleviates selection pressure on populations, this may impede long-term adaptation for changed conditions, beyond the range of current conditions to which phenotypes have the capacity to respond (Pulido and Berthold 2004). The considerable genetic variation within and among bird populations (Pulido and Berthold 2004) and the occurrence of heterogeneous dispersal of birds with divergent life histories (e.g. those breeding or wintering in different areas; Møller and Hobson 2004; Coltman 2005), suggest there is potential for adaptive evolutionary change. In reed warblers, populations are likely to support high levels of gene flow and divergence following the species’ rapid westerly range expansion across Europe over the last half century (Prochazka *et al.* 2011). In order to better determine which traits limit or promote the adaptability of populations to current and future environmental change, it is important to understand the relative extent that responses are due to either plasticity or differential selection.

Further work to determine the extent of phenotypic plasticity in these traits would continue monitoring individual responses in the study population in response to natural and experimentally simulated variation in food availability over several seasons and generations, to quantify the overall level of phenotypic variation in the population, the level of individual phenotypic variation, the heritability of each trait and the impacts of variation in each trait on survival and/or fecundity. Integral projection modelling (IPM; Coulson 2012; Smallgange and Coulson 2013) can be used to assess the degree to which either plasticity or adaptive evolution in these traits (or both) could be responsible for changes in response to environmental conditions, and ultimately what might happen in response to a range of predicted selection gradients.

## 7.5 Does it matter? The consequences of the research for the discipline.

By combining the study of climate effects on *Phragmites* habitat, invertebrate prey populations and the responses of birds to such changes, this thesis presents an integrated line of enquiry providing evidence for plausible mechanisms for the effects of climate change on reed warbler populations. This builds on the vast body of research undertaken by countless researchers over at least six decades. Specifically, this study:

- 1) Provides strong support for a climate-driven advance in *Phragmites* growth and invertebrate availability for reed warblers breeding in South Wales;
- 2) Confirms the breeding parameters most affected by increases in food availability;
- 3) Provides evidence of the mechanism by which reed warblers are able to avoid high vulnerability to poor wintering conditions in the Sahel;
- 4) Provides support for higher rates of survival in first-year birds with warmer springs on the breeding grounds.

These findings represent an important step towards understanding the mechanisms which may underlie current levels of population growth in what might be one of the few long-distance migratory European songbird populations currently benefiting from climate change.



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**Appendix I**    **Published Article:** Habitat Use and Body Mass Regulation among Warblers in the Sahel Region during the Non-Breeding Season. **Plos One 2014.**