Impacts of Climate Change on Woodland Birds; From Individual Behaviour to Population Change

Thesis submitted in part fulfilment of PhD

Jeremy Alexander Smith

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Abstract

Long-term demographic studies are vital for understanding trends in population size, such as the rapid decline of many bird species. Studies of trophic cascades provide a mechanistic understanding of how populations respond to climate change. The mis-match between timing of food availability and food requirements of nestlings is implicated in the rapid declines of woodland-breeding bird populations. I report the decline of the Pied Flycatcher, *Ficedula hypoleuca*, and investigate and model its demographic changes.

I used a long-term citizen-science dataset of Pied Flycatcher population characteristics (collected 1990-2016 in south Wales), and conducted studies linking weather conditions, invertebrate availability and breeding biology (2016-2018). I used these data to investigate the consequences of laying date on adult annual survival and recruitment, and examined the consequences of changes in the timing of breeding in consecutive years and generations.

The study population has declined by 66%. Temperature and rainfall had interacting and non-linear impacts on the breeding cycle. Fledging success was a significant predictor of the next year's population size. Warmer and more variable conditions were associated with earlier invertebrate phenology and variation in availability, with a phenological mis-match between peak chick food demand and caterpillar availability. Most Pied Flycatcher nesting attempts were timed to allow for successful fledging, but later nests tended to be less successful. Early-laying birds a had higher fledging success and a higher probability of surviving.

A stochastic Integral Projection Model predicts that the ongoing decline in the population will continue, leading to extinction within the next 5-15 years. A greater consistency in laying dates of early laying individuals leads to higher annual adult survival. Between-year consistency in laying date had the greatest impact on population growth, and appears to be the strongest mechanism by which this population could avoid extinction.

1 General Introduction

1.1 Multi-trophic phenological matching

Phenological matching, the synchronising of one organisms life events to those at other trophic levels, in order to maximise survival and reproductive success, is a key process in community ecology (Stenseth and Mysterud 2002; Cole and Sheldon 2017). Breeding success in many taxa is dependent on synchronising breeding with the timing of abundant food resources. Breeding productivity of insectivorous songbirds, for example, is strongly constrained by the availability of insects and other invertebrates in spring and early summer, when the parent birds feed their nestlings, and when newly fledged chicks must learn to forage independently of their parents (e.g. Seward *et al.* 2014; Vafidis *et al.* 2016). Parent birds therefore attempt to time their breeding such that the nestling and fledging periods coincide with abundant food resources (Stenseth and Mysterud 2002). Synchrony is frequently beneficial for one species (e.g. a predator) to the detriment of another (e.g. a prey species), the result of which can be the prey attempting to adjust their timing so that they are asynchronous with the predator. These concepts allow us to understand the mechanisms by which species interact and to predict how a species or group of species might change if the ecosystem is perturbed.

Weather variation is a common cause of ecosystem disturbance. As environmental conditions do not remain constant, individuals must be behaviourally flexible to respond to changes in their environment. The ability to respond to a change in local conditions such that the trait expressed (e.g. date of bud burst, egg hatching or bird laying date) is altered, is known as phenotypic plasticity (Hollander and Bourdeau 2016). Examples of phenotypic plasticity can be found in a wide variety of organisms (Parmesan 2006), including trees (MacKenzie *et al.* 2018), invertebrates (Durant *et al.* 2007) and birds (Burgess *et al.* 2018), with many of these interannual adaptations arising through direct effects of weather (e.g. temperature and rainfall) or indirect effects of weather on food availability. The phenology of life cycles in many organisms is driven by environmental cues (e.g. changes in, or thresholds of, temperature and rainfall). A variety of specific cues may be involved, as different species use different cues to determine life cycle phenology e.g. winter temperature and minimum spring temperature for bud burst in trees (Cole and Sheldon 2017), or minimum temperature for caterpillars, and photoperiod for birds (Gwinner 1996). The interconnection of organisms within and between ecosystems means that it is not just individual species that are affected by changes in weather but also interspecific relationships (Walther 2010).

1.2 Climate change effects on phenology

While the concept of global climate change is not new (Fourier 1827), the intensity with which its biological impacts have been studied has accelerated markedly over the past four decades, leading to an increased awareness of the nature and extent of its impacts, including its effects on ecosystems, species and individual organisms (Parmesan 2006). The Intergovernmental Panel on Climate Change (IPCC) report in 2018 stated that global surface (air/water) temperatures had increased by approximately 0.5 - 1°C during the 20th Century (IPCC 2018). While this provides an estimate of mean global temperature increase, the degree of temperature change varies spatially and temporally, such that different localities and ecosystems are affected by climate change to differing extents, in different ways and over different timescales (Wiens 1989). In temperate zones, for example, temperature is predicted to increase by 1 - 2°C between 1990 and 2050 (Tyrrell 2019), and the rate of increase is accelerating, as Europe has experienced an increase of 0.2°C per decade during the previous 25 years (Jenkins *et al.* 2008). In addition to the increases in mean conditions, there are predicted to be increases in seasonal variability in temperature and particularly precipitation (Kahl *et al.* 2019). For example, increased rainfall in winter, and decreased rainfall in summer, result in a more varied annual rainfall but a relatively stable annual mean precipitation (Jenkins *et al.* 2008).

Whilst many studies have focussed on the biological impacts of mean temperature and rainfall changes, extreme events can have important impacts upon ecosystems (European Environment Agency 2015). For example, heavy rainfall events during summer result in leaf-dwelling invertebrates being washed from leaves leading to a subsequent reduction in food availability for predators (Whitehouse *et al.* 2013). The frequency of such extreme events has increased and is projected to increase more rapidly in the future, the result of which will be larger impacts on ecosystems (IPCC 2018). These impacts will disproportionately affect ecosystems at higher altitudes and latitudes, which are already under greater pressure from climate change (European Environment Agency 2015). The impacts of increased and more variable temperatures, and variability in precipitation, cascade across trophic levels; as one species responds so another must also respond. For example, increased winter warming and precipitation advance the onset of flowering in temperate ecosystems, leading to a mis-match between trophic levels as herbivores are less able to adjust (Arfin Khan *et al.* 2018). The increases in populations of resident and short distance migrant birds, but decreases in populations of long-distance migrants (Pearce-Higgins *et al.* 2015) has generally been associated with a temperature increases in central England by 0.45°C in the past 25 years (Jenkins *et al.* 2008). Increased Winter temperatures increase the survival of resident species, but increased spring temperatures can result in mis-match of predator-prey phenology (Visser *et al.* 2004).

1.3 Spatial and temporal adaptations to climate change

The rapid changes in climate are leading to breakdowns in phenological matching between trophic levels, as species respond to climate changes at different rates (Thackeray *et al.* 2010). An ecosystem-level, or even global-level, understanding of the biological effects of climate is therefore vital to understand how species succeed or fail in responding to the changing conditions (either through phenotypic plasticity or through evolutionary adaptation), as well as in understanding what novel ecological and evolutionary pressures they may face. These mis-matches can occur across time and space, resulting in species altering the timing of certain life history traits, or moving location to coincide with the responses at trophic levels. Specifically, responses to warmer Spring temperatures can include (i) advancing Spring phenology, (ii) moving to higher latitudes, (iii) moving to higher altitudes, or (iv) some combination of each of these responses (European Environment Agency 2015).

Up to 6,300 species at risk of extinction after the disappearance of their associated species have been reported (Koh *et al.* 2004). Those species which are not at the extremes of their range will have to either undergo non-plastic adaptations such as range shifts (Pateman and Hodgson 2015) or respond in some way to the new conditions, either through evolutionary adaptation or phenotypic plasticity. It is now considered that phenotypically-plastic responses are more common than evolutionary responses (at least over decade-scale timescales), with many of the apparent evolutionary responses previously described being more recently reclassified as examples of phenotypic plasticity (Gienapp *et al.* 2008). As one species responds to the new conditions, so each of the species with which it interacts will also need to respond. In this way, the response of each species to environmental change will have cascading impacts throughout the ecosystem (Post *et al.* 1999).

Understanding the cascading impacts of climate change across trophic levels requires insight into the responses of individuals to climatic variables, as well as the impacts of these responses on demographic traits (e.g. bud burst, laying date, egg hatching) and, ultimately, on changes in population size at each trophic level (Bellard *et al.* 2012). In part, this requires an appreciation of the timing of biological events and the consequences of appropriate or inappropriate timing on individuals and populations.

A measure of spring phenology recorded historically throughout the UK has been the date of bud burst in oak (*Quercus* spp.) leaves (Parmesan 2006). Bud burst initiation occurs in winter when trees experience frost, with the subsequent temperature increase in spring resulting in the bud formation and opening. Bud burst has been shown to influence the timing of caterpillar hatching; this is believed to have evolved to maximise the fitness of caterpillars (Feeny 1970; Coyle *et al.* 2010). Early emerging caterpillars feed on fresh leaves that are low in tannin levels and grow rapidly, obtaining higher body mass and better survival (Tikkanen and Julkunen-Tiitto 2003). As individual oak trees are highly synchronised between years (early trees are always early), caterpillars must match their hatching to the phenology of that particular tree (Tikkanen *et al.* 2000). Mis-match can happen when moths or butterflies from two different trees, with different phonologies, mate and produce offspring. These caterpillars are likely to exhibit an intermediate hatching date and, as a result, be mis-matched with the host tree (Tikkanen and Julkunen-Tiitto 2003).

Woodland insectivorous passerines need to match the timing of their egg laying to result in peak chick demand (8-10 days post hatching) coinciding with peak availability of caterpillar prey (Visser *et al.* 2006). Chicks of parents which achieve this matching experience higher post fledging survival and recruitment into the breeding population (Visser *et al.* 2006). The ability of a breeding bird to time the initiation of its egg-laying to match the phenology of their prey, depends upon their migratory strategy. Resident birds are able to use cues from the local environment to decide when to lay (Durant *et al.* 2007) but migrants are constrained in their timing of departure from the wintering grounds (Knudsen *et al.* 2011). As a result, the degree of mis-match between migrants and food resources is greater than between residents and food, particularly in years where spring temperatures increase earlier in the year.

1.4 Differing bird migration strategies and their sensitivities to climate

The phenological matching of breeding with abundant trophic resources may be disrupted if organisms at different trophic levels are differentially affected by climate change (Walther 2010). In the case of many long-distance migratory birds, warming spring temperatures have led to substantially earlier growth of vegetation on the breeding grounds, and an earlier spring emergence of invertebrates, which the birds use to provision their chicks (Visser and Both 2005). Unfortunately, for many migrants, the timing of their arrival to the breeding grounds, and the onset of breeding, is constrained by the timing of departure from their wintering grounds, which, in turn, is primarily determined by day-length cues rather than climate (Pulido 2007). As a result, as spring temperatures have increased over recent decades, many long-distance migrants now arrive in their breeding habitat too late to exploit the much earlier invertebrate availability for provisioning their chicks – leading to a trophic mis-match. This has been implicated in the declines of many long-distance migrant species' populations (Wright *et al.* 2004). The pattern of these declines has not been the same for all such songbird species (Marchant 1992; Morrison *et al.* 2013), because of their differing behaviours, ecologies and demographic processes including differing wintering areas and propensity to double brood. To understand the roles of these factors, we need to model the demographic processes by which climate variations lead to population change.

Long distance migratory birds cannot always adapt to conditions during specific periods of their life cycle (e.g. breeding) if it reduces their fitness at another part of the life cycle (Visser *et al.* 2003). Migrants also cannot advance their arrival / breeding dates if the conditions during migration are unsuitable (i.e. there is a temporal mis-match between conditions on stop-over sites and those on breeding grounds). Arriving early relative to the onset of spring in any given year could result in a paucity of available prey for the parents after a long and potentially swift migration; this would be likely to result in a lower body condition prior to breeding.

Of the 18,043 bird species globally (Barrowclough *et al.* 2016), approximately one in five are migratory (Birdlife International 2019). Of these, approximately 50 species migrate from northern Europe to sub-Saharan Africa to spend the Palearctic winter (Moreau 1972; Berthold *et al.* 1992), many of which have suffered population declines in the past three decades (Jones *et al.* 1996). As 32% of European species are threatened, near threatened, declining or depleted on a Europe wide scale (European Commission 2015), their continued survival and abundance is an important conservation issue. The general decline in Northern hemisphere long distance migrant birds compared to short distance and resident birds is well documented (Morrison *et al.* 2013). For example, the longest-running systematic study of migrant birds in the world (Heligoland, Germany), running from 1909 to the present, has shown population declines in many long distance migrant bird species (Hüppop and Hüppop 2011). Such declines are not necessarily uniform; for some such species showing overall declines there have been shorter-term population increases during this time-frame (Marchant 1992). This is important as it means that we cannot just calculate a linear rate of decline for a species and extrapolate indefinitely into the future. Instead, more detailed investigations of the underlying causes are needed to understand the drivers, predict future trends and develop conservation interventions

1.5 Tri-trophic woodland ecosystem (Oaks, Caterpillars and Pied Flycatchers)

The majority of temperate ecosystems, but not all (see Vafidis *et al.* 2016), are strongly seasonal (Both and Visser 2001). One particularly well studied example of phenological matching in a strongly seasonal ecosystem is the “tri-trophic” (3-trophic levels) system of Oak trees, Lepidopteran caterpillars, and woodland birds (Burgess *et al.* 2018). Acidic, free-draining soils in south-west England, northern England and throughout Wales support upland Oak woodlands. In these habitats, Sessile Oak (*Quercus petraea*) dominates, although there are sporadic occurrences of Pedunculate Oaks (*Quercus robur*) and hybrids of the two species (Rackham 2012). The post-glacial landscape of what is now Wales was primarily an Oak-dominated mix of broadleaved tree species, but by 2010, only 13% of Wales was covered in broadleaf and coniferous woodland. Furthermore, much of this woodland cover is now greatly fragmented; approximately 70 % of upland woods are less than 10 ha in area (Mitchell and Kirby 1990). The decline in land-cover of Oak woodlands is expected to continue, and increase in their ecological impact, as other pressures, such as warmer springs and increased variability in precipitation, are exerted on species populations (Northrup *et al.* 2019).

1.6 The Pied Flycatcher as a model study species

One long-distance Oak woodland-breeding migratory songbird of current conservation concern is the Pied Flycatcher (*Ficedula hypoleuca*). The species and its ecosystem provide a classic model for examining cascading impacts of global climate change across trophic levels (Both and Visser 2001; Lundberg and Alatalo 2010; Samplonius *et al.* 2018). The Pied Flycatcher is a small trans-Saharan migratory passerine bird which breeds in many forested areas of the Palaearctic region, and migrates to over-winter in tropical West Africa between the Sahara Desert and the Gulf of Guinea (Cramp and Perrins 1993; Lundberg and Alatalo 2010). Europe contains 75 % of the world’s population of Pied Flycatchers, which is estimated at between 33 and 52 million (BirdLife International 2018). This suggests an European population estimate of between 25 and 38.8 million mature individuals (Birdlife International 2015).

Much research has been carried out on Pied Flycatchers over recent decades, particularly so in the context of climate change and European populations (Both and Visser 2001; Both *et al.* 2006). The propensity for this species to breed in nest boxes in Western Europe has made it a very popular “model” species for breeding studies (Lundberg and Alatalo 2010). These latter studies have examined the associations between climate variables and Pied Flycatcher population size, timing of arrival at the breeding grounds, phenology of egg-laying, clutch size, chick growth and annual survival of adults and fledglings from one breeding season to the next (Both and Visser 2001; Both *et al.* 2006; Samplonius *et al.* 2018). The preference of Pied Flycatchers for occupying artificial nest boxes in preference to natural tree cavities (Eeva and Lehikoinen 1996; Lundberg and Alatalo 2010) means that it is possible to capture the birds whilst in the nest box (adults as well as chicks) marking them individually with metal leg-rings, enabling subsequent individual identification (Lundberg and Alatalo 2010). The result of such studies is that over two million Pied Flycatcher nestlings have been ringed in Europe during the last four decades (Both 2010). As a result, the breeding biology of the species is understood in great detail. To date, however, relatively little is known about Pied Flycatcher wintering ecology (but see (Ouwehand and Both 2017).

1.7 Population abundance and declines in Pied Flycatchers

In the UK the British Trust for Ornithology coordinates the annual Breeding Bird Survey (BBS). This allows population trends to be assessed using standardised and comparable methodology. The results of this survey show that Pied Flycatchers have declined more than 60 % in the 20 years between 1994 and 2014 with a recent increase (Figure 1.1) (Woodward *et al.* 2018).

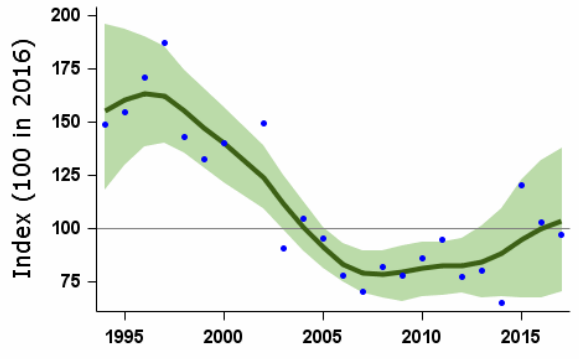

Figure 1.1 Historic trend of Pied Flycatcher abundance in the UK using data from the Breeding Bird Survey from 1994 – 2017 (reproduced from Woodward et al. 2018)

The spatial distribution of Pied Flycatchers is not uniform across the UK, with a skew towards Wales and the south of Scotland, in association with the distribution of woodlands dominated by Oak (*Quercus* spp.). The Welsh population is estimated at 7800 - 9800 breeding pairs (Harris 2019 *in litt.*), with spatial variation between Welsh breeding sites in the local population trajectories (Smith *et al. unpubl.* – see Chapter 5).

In the Pied Flycatcher's preferred breeding habitat – Oak woodlands – the spring peak of invertebrate availability is relatively brief (typically peaking across 1-2 weeks). This makes long-distance migrants, whose ability to advance their egg laying is constrained by the timing of migration, vulnerable to trophic mis-matches. In contrast, resident bird species (e.g. titmice *Parus* spp.) do not have such constraints on the timing of egg laying, and so have been better able to track the rapidly advancing invertebrate phenology (Both and Visser 2001).

Although the concept of trophic mis-match is well established in the field of climate change biology, the nature of the links between phenology (e.g. laying date of migrant songbirds), and the demographic and population-level consequences of trophic mis-matches, has yet to be examined in detail. Many previous studies have identified links between climate variables and the timing of arrival of migratory birds back to the temperate breeding grounds (Jonzén *et al.* 2007). They have also identified responses of various breeding parameters (e.g. nest productivity) to changes in a multitude of environmental factors such as food availability and local weather conditions (Siikamäki 1995). There remains a need, however, to understand how and why trophic mis-matches may drive demographic changes and population declines, and (ii) to assess the role of trophic mis-matches in driving population change, in the context of the whole of the annual cycle.

1.8 Modelling of patterns and mechanisms of population change

Patterns in weather variables and population trends have been well-described and correlated (Pearce-Higgins *et al.* 2015) but the underlying processes linking weather and populations remain poorly understood. Knudsen (2011) highlighted that there was a greater body of evidence of patterns (observations of what has changed) rather than mechanisms (how and why these changes have occurred) and consequences for individuals, populations and species interactions. Subsequently, a major aim of this thesis is to develop a mechanistic understanding of the processes underlying such patterns, and to model the consequences of these mechanisms at the level of population size and the interactions between trophic levels. This addresses the question of how individual-level demographic responses lead to changes in population size and the evolution of demographic traits. Previous studies have rarely integrated these individual patterns and processes in an over-arching conceptual framework, to understand and predict how the impacts of climate on individual aspects of the annual cycle together act to create demographic and population changes. This research need was highlighted by Vickery *et al.* (2014) who suggested that one of four of the main foci of research on declining migrant birds should be to use the abundance of data from the European breeding-grounds to identify spatial and temporal patterns in demographic parameters.

Classical modelling frameworks in systems ecology evolved from looking at linear relationships between single or multiple variables (typically using General Linear Models), to identify associations (e.g. between temperature and breeding productivity), or differences between groups (e.g. differences in clutch size between first-year and more experienced females). These approaches identified patterns (associations and differences) in demographic variables, but not the causal mechanisms underlying population change. More recent approaches have looked at the individual to try to theorise as to the processes. These Individual-Based Models (IBMs) predict how individuals would have to behave (e.g. with regards to exploration/dispersal and territoriality) in order to match the observed population changes (Green Woodhoopoe - *Phoeniculus purpureus*, du Plessis 1992). These individual-based models are primarily used to identify hypotheses that could then be tested using real world data. They tend to be so specific as to lose generality to other situations and are therefore not widely applicable (Grimm and Railsback 2005).

Other research has taken a population-level approach, by using Matrix Population Models (MPMs) to determine population level dynamics. Here, researchers group populations by categories (e.g. age class) and using empirical data provide estimates of demographic parameters (e.g. survival and reproduction). For many study systems, this has proven effective as estimated population growth rates have been shown to be relatively accurate (Jones 2019). MPMs use categorical variables (e.g. reproductive state) to create predictions for life history traits as organisms transfer from one category to another e.g. from juvenile to adult. A major disadvantage of MPMs is that there is no scope for modelling differences between individuals within groups. For example, all individuals of age class “adult” are assumed to have the same reproductive output and survival probabilities. In practice, individuals within categories may exhibit substantial variability in key traits that are intrinsically linked to demographic parameters, and hence to population growth rates.

IBMs are excellent at creating scenarios with which processes can be hypothesised but where no empirical data are used to formulate these and population level parameters are not the focus. MPMs, in contrast, provide good estimates of population level parameters but ignore individual-level variation. This can, to an extent, be mitigated by increasing the number of classes and decreasing the difference between classes i.e. instead of having “adult” and “juvenile” age classes have “year 1”, “year 2”, “year 3”, etc. This allows for a greater resolution between groups and a more representative population model. Categorical variables which are divided into infinite numbers of classes can be considered to be continuous.

Easterling (2000) advanced the method of MPMs by changing the input variable from categorical to continuous, creating an Integral Projection Model (IPM). These models, initially applied to an endangered plant (Northern monkshood, *Aconitum noveboracense*), used differences in a growth variable to separate individuals. No longer were the individuals separated by age category, but by a continuous explanatory (independent) variable (e.g. stem diameter), which could change between individuals within the same year, and within individuals between years. The result is an IPM which is informed by four sub-models (describing Survival, Growth, Fecundity and Inheritance) using the continuous trait as the explanatory variable. Populations of mammals, birds and amphibians have subsequently been modelled using multiple continuous independent variables (e.g. body mass, laying date and parasite load (Ozgul *et al.* 2010; Childs *et al.* 2016; Metcalf *et al.* 2016) to explain trends in survival, recruitment, *etc*. The effects of these independent variables on demographic parameters are then integrated by the IPM to project population growth rates.

In this thesis, an IPM will be used to model the demographic and population-level consequences of phenological matching / mis-matching between breeding birds and their invertebrate food supplies. The IPM framework conceptualised by Easterling (2000) brings the benefits of IBM and MPM concepts together under a unifying framework. IPMs use the individual nature of the IBM and the population level outputs of the MPM by using a continuous, rather than categorical, trait - specific to each individual - to identify how the population changes under different conditions.

Despite the wealth of data available there are currently very few IPMs conducted on birds. The three published examples to date identify genetic differences in a resident population of Great Tits (Childs *et al.* 2016), the effects of habitat management on migratory Black-tailed Godwits (Kentie *et al.* 2018) and how body size and condition alter reproductive success in the Eurasian Hoopoe (*Upupa epops*) (Plard *et al.* 2018). To date, there are no published IPMs on migratory passerines. This is a clear research need, given the benefits of the IPM approach and the rapid population crashes currently being observed among long-distance trans-equatorial migrants.

1.9 Predicting population trajectories of a migratory passerine using an Integral Projection Model

In this study, populations of Pied Flycatchers breeding in Wales are used to test a series of interlinking hypotheses addressing the ecological and behavioural mechanisms underlying historic, current and future changes in demography and population size. This study is, therefore, the first to analyse demographic mechanisms in a declining migratory passerine using an IPM. I use laying date as a continuous trait variable, to explain adult survival, fecundity and recruitment in the Pied Flycatcher. Once an IPM has been built, *in silico* experimentation in the form of sensitivity analysis allows us to understand the effects of hypothetical changes in individual demographic parameters on population trajectories. This experimental manipulation approach is often impossible to implement in the field, but is readily implemented within an IPM, and so adds to our understanding of the mechanisms driving population declines. It also allows us to understand how particular conservation strategies might affect population trajectories.

1.10 Thesis structure and hypotheses

The thesis comprises of three data chapters, starting with a long-term study of demography and the effect of weather, moving to understanding how food supply is affected by weather and its effect on flycatcher demography, building to specifying an IPM studying the impacts of laying date changes on population trajectories.

Utilising 25-year datasets on Pied Flycatcher breeding phenology, productivity and local weather, I aim to test the hypothesis that inter and intra-annual variation in weather variables (e.g. temperature and rainfall) resulted in long term population declines, by means of changes in demographic variables (e.g. clutch size and fledging success) (Chapter 2).

By monitoring seasonal variation in invertebrate abundance in broad-leafed woodlands, I test the hypothesis that peak invertebrate abundance occurred earlier in years with elevated spring temperature (potentially leading to a greater trophic mis-match and a subsequent reduction in Pied Flycatcher breeding success (Chapter 3).

Using an Integral Projection Model framework, I will test whether birds which laid early in a given year, relative to the population mean laying date, had a greater reproductive fitness than later-laying individuals, and examine how perturbations to demographic parameters (e.g. laying date) change future population viability (Chapter 4).

My aims are (i) to aid in understanding of the role of climate-driven trophic mis-matches in influencing songbird population trajectories, (ii) to investigate the impacts of perturbations of demographic parameters of population growth rates, and (iii) to create a model general enough to predict the effects of variation in laying date on breeding productivity and population change, in other songbird populations.

2 Population Decline and Demographic Changes in a Breeding Population of Pied Flycatchers in South Wales over 26 years

2.1 Abstract

Long-term demographic studies are vital for understanding trends in population size; for example, the on-going and rapid decline of many bird species across Europe. This chapter reports the population change of one such species, the Pied Flycatcher, *Ficedula hypoleuca*, from a population in south Wales, UK, over 26 years, and investigates the demographic changes accompanying its population change. The study was carried out at Cwm Clydach; a low altitude oak woodland, where laying date, clutch size, brood size and number of fledglings have been recorded annually between 1990 and 2016, allowing a detailed study of changes in breeding biology. Population size and demographic parameters were examined across a 26-year study period to i) describe temporal changes in demographic parameters, ii) assess the extent to which variation in those parameters could be accounted for by weather, and iii) assess whether breeding-related demographic changes explain the observed population changes. The results of these analyses show that i) the Cwm Clydach Pied Flycatcher population has declined faster than the UK average, with the number of breeding pairs falling by approximately 66 % and nest box occupancy falling by approximately 77 % between 1990 and 2015. After an initial increase (1990-1997), the number of breeding pairs declined from a maximum of 111 in 1997 to 15 pairs in 2015, and occupancy declined from 50 % to 10 % of nest boxes. Ii) Temperature and rainfall had impacts on different stages of the breeding cycle. Clutch initiation was earlier when April temperatures were higher, and fledging success was correlated with rainfall in April, but the strength and direction of this effect depended primarily on rainfall during May. Fledging success was a significant predictor of the next year's population size, indicating a measurable effect of breeding productivity on population change. The population in Cwm Clydach is at risk of extirpation if the current rate of decline continues.

2.2 Introduction

There are contrasting population trends within temperate woodland bird species, depending predominantly on their migratory strategies (Amar *et al.* 2006). The populations of many resident temperate woodland bird species (e.g. Blue Tit, *Cyanistes caeruleus* and Great Tit*,* *Parus major*) are stable or increasing, whereas populations of long-distance migrants (e.g. Pied Flycatcher, *Ficedula hypoleuca* and Common Redstart, *Phoenicurus phoenicurus*) are generally declining (Morrison *et al.* 2016). In addition, there is spatial heterogeneity between population trends at a continental scale. For example, migratory species in North-Western Europe are declining less rapidly than those in Southern Europe (PECBMS 2015). In the UK, approximately half of woodland-breeding bird species are red or amber-listed in the latest assessment of *Birds of Conservation Concern* (Eaton *et al.* 2015), due to their breeding population having declined by more than 50 % (red-listed), or by 25 - 50 % (amber-listed) over the past 25 years. Eaton and colleagues (2015) specifically highlighted concerns about the declines in woodland-breeding and long-distance migratory species, such as the Pied Flycatcher.

As a long-distance migratory woodland bird breeding in the UK, which preferentially chooses artificial nest boxes over natural nest sites (Huhta *et al.* 1998), the Pied Flycatcher is a valuable model species for understanding the links between environmental, demographic and population changes (Lundberg and Alatalo 2010). In terms of diet, migration and breeding biology, Pied Flycatchers are broadly representative of many insectivorous long-distance migrants which breed in North-Western Europe and winter in sub-Saharan Africa (Zwarts *et al.* 2010).

With resident woodland-breeding species generally becoming more widespread and abundant, and woodland-breeding migrant species declining in abundance and geographical range, there is a need to understand the mechanisms driving their contrasting population trends (Amar *et al.* 2006). Stressors faced by migratory species are spatially heterogeneous, with many stressors occurring in the wintering grounds, including habitat loss and shifts in vegetation phenology - leading to a reduction in the availability of food prior to departure from the wintering grounds (Saino *et al.* 2017; Awa *et al.* 2018). Major reviews of population changes among woodland birds in the UK identified conditions on the sub-Saharan wintering grounds were a major cause of population decline among trans-Saharan migratory species (Fuller *et al.* 2005). Overwinter conditions may affect overwinter survival and have carry-over effects on fecundity in the subsequent breeding season. Ockenden *et al.* (2013) found that climate change on the breeding grounds explains more variation in fecundity than carry-over effects from wintering grounds. Further detailed research on understanding the impacts of changes in individual-level demographic variables on population change is, however, required in order to understand the demographic mechanisms underlying population changes.

Although migrant and resident bird species within a woodland breed in the same location, their behavioural responses to the environment may be different. For example, resident Blue Tits adapt their reproductive phenology to that of the Lepidopteran caterpillar larvae found in Oak (*Quercus* spp.) woodlands, resulting in the peak in food demand of Blue Tit chicks closely matching the peak in the availability of caterpillars (Visser *et al.* 2004). This phenological match results in continued high breeding success despite these climate-driven ecological changes. Increased over-winter survival rates of resident birds, due to milder winters, have also contributed to increased population sizes of resident species (Askeyev and Askeyev 2002). In contrast, long-distance migrant species are less adaptable to phenological changes on the breeding grounds than resident birds (Bartosova *et al.* 2014). A trans-Saharan migrant's arrival date is constrained by its departure date from the wintering grounds, which is primarily driven by photoperiod rather than climate variables (Gwinner 1996). The inability of long-distance migrants to adapt fully to the changing phenology of their invertebrate prey under climate change, has, in years with an early spring, resulted in a phenological mis-match between the nutritional demands of the nestlings and the availability of their invertebrate food supply. For example, the peak availability of caterpillars in broadleaved woodlands now occurs too early to coincide with the peak food demand for nestling Pied Flycatchers (Both and Visser 2001).

Demographic changes associated with climatic variables, such as temperature and rainfall, result in variation in breeding productivity. The behavioural response of migrants to the inverse relationship between arrival date and monthly temperature has been to advance their arrival dates by 1.6 days per decade (Croxton *et al.* 2006). This advance in arrival date has been achieved primarily by accelerated migration following departure from Africa (Both 2010). Nevertheless, the advance in arrival time on the breeding grounds has been insufficient to keep pace with the advance in peak caterpillar abundance. Suboptimal timing of arrival (late arrival) results in late laying and reduced breeding productivity (Thomas *et al.* 2001), with impacts on population size. For example, breeding productivity has been shown to be the most important driver of population change in Willow Warblers, *Philloscopus trochilus;* population size increased in years when annual survival and breeding productivity were both high (Morrison *et al.* 2016).

Ambient temperature and rainfall affect the breeding productivity of songbirds, both directly (e.g. by increasing thermal costs of endothermy and incubation), and indirectly (e.g. by reducing the availability / activity density of invertebrate prey) (Seward *et al.* 2014; Vafidis *et al.* 2016). A meta-analysis of 283 studies showed that low temperatures result in smaller clutches and smaller eggs, which have a lower probability of hatching and the resultant chicks have a lower probability of fledging (Krist 2011). Shifts in temperature therefore influence breeding success (Golawski 2008). Clutch size has been shown to vary in some species, based upon parental food availability during the pre-laying period (Hall *et al.* 2018), and clutch size declines across the breeding season (Czeszczewik 2004). The proportion of eggs which hatch depends, initially, on the number of eggs fertilised and then, on investment in incubation by the female parent (only the female parent incubates in the Pied Flycatcher), as embryo development ceases below an internal egg temperature of 26 °C (Conway and Martin 2000).

Invertebrate abundance in oak woodlands is affected by weather variables. Temperature increases in Spring trigger the emergence of terrestrial invertebrates from their eggs or from dormancy, coinciding with leaf growth of food plant species (Bauer *et al.* 2010). Lower Spring temperatures result in delayed leaf growth and subsequent delays in caterpillar emergence. Low temperatures, particularly frost, after oak leaf burst can result in the death of leaves (pers. obs.) making them unpalatable to caterpillars. Reductions in invertebrate availability can result from caterpillars being washed off leaves due to heavy rainfall in May (Thom 1986). As many woodland birds, including Pied Flycatchers, glean caterpillars from leaves (Stowe 1987), heavy rain events and low temperatures can both reduce and delay the availability of food for the parent birds to collect and provide to their chicks (Leech and Crick 2007).

Chick survival and growth are indirectly affected by food availability, and directly by climatic effects of temperature and rainfall (Oeberg *et al.* 2015). Rainfall which can wet the plumage of parent birds may lead to reduced or less efficient incubation of eggs and brooding of chicks. This indirect effect of rainfall, and the direct effect of particularly low temperatures on nest temperatures, can cause chilling of eggs and hypothermia in chicks resulting in mortality (Leech and Crick 2007). Likewise, high temperatures can cause chicks to overheat, as they are not able to thermo-regulate fully until eight days after hatching (Sturkie 1976). Once hatched, the proportion of chicks that successfully reach fledging depends upon both their ability to maintain an appropriate body temperature and a high enough food intake, to facilitate growth of feathers and to gain enough mass to leave the nest in good condition. It is predominately the combined and cumulative effect of diet and weather that determines whether chicks survive to fledging or not (Siikamäki 1995). The increase in UK Spring temperatures over the last three decades (Hart *et al.* 2010) has occurred simultaneously with a decline of more than 60 %, in the number of breeding Pied Flycatchers in the UK (Woodward *et al.* 2018).

Within the UK, the core range of Pied Flycatchers is Wales, SW England and SW Scotland; areas that contain broad-leafed woodlands, dominated by Sessile Oak, *Quercus petrea,* and are characterised by steep-sided upland woodlands. Some of these sites have long-term (25+ years) data time-series which have been systematically collected. The design and consistency of these studies enables both the identification of trends over long periods of time, as well as determining the environmental variables acting upon the populations (Hart *et al.* 2010; Burgess 2014).

In this chapter, the changes in abiotic parameters, and how they affect Pied Flycatcher demographics in a woodland in South Wales over a 25-year period, are explored. Long-term declines in the Pied Flycatcher breeding population have been observed in Cwm Clydach (H. Coats, *pers. comm.*). The nature and rate of population change in this woodland is described to determine and understand its drivers. If breeding productivity in one year has a significant effect on population size of Pied Flycatchers in the subsequent year, then it should be possible to show that variables which affect breeding productivity also affect the population size.

The overall hypothesis to be tested is that Pied Flycatcher population change is driven by changes in weather that, in turn, affect breeding productivity. The rate of decline in the breeding population at Cwm Clydach study site will firstly be quantified and compared with simultaneous national (UK) population change. Next, the associations will be examined between year to year variations in different weather variables (temperature, rainfall) and breeding parameters (laying date, clutch size, hatching success, brood size and fledging success). These data will be used to i) test the hypothesis that weather explains annual variation in breeding productivity, and ii) investigate which demographic parameters are most sensitive to changes in weather. Finally, iii) associations between breeding parameters and subsequent changes in population size will be used to identify whether breeding productivity is the primary proximate driver of population change.

2.3 Methods

2.3.1 Study Site

Cwm Clydach is a nature reserve of approximately 50 hectares (centred on 51°42’ 25 N, 3°54’ 18” W) in the administrative area of Neath - Port Talbot, South Wales (Figure 2.1). The site comprises steep-sided sessile oak woodlands on either side of the Clydach River, with elevations ranging between 40 and 110 m a.s.l. Much of the woodland is owned and managed by the Royal Society for the Protection of Birds (RSPB), with all nest box recording conducted by the Gower Ornithological Society (GOS).

Figure 2.1 Cwm Clydach study site, South Wales. Images obtained from Google Earth (left) and modified from OS maps (right)

2.3.2 Data Collection

The dataset comprises Pied Flycatcher breeding data from Cwm Clydach across 30 years (1986-2015, excluding 2001 when a Foot and Mouth disease outbreak prevented access to the study site). Wooden nest boxes (275 mm x 145 mm x 19 mm, with 32 mm front facing hole) have been fixed to trees at approximately 1.5 m above ground level. Nest box availability varied between years, increasing from 13 boxes in 1986 to a maximum of 302 in 1998. Availability of boxes remained above 250 from 1996 onwards. Due to limited sample size (fewer than 150 boxes) (Figure 2.3), population abundance data from 1986 to 1989 has been excluded from the main analysis.

Nest box occupancy and breeding data were collected by volunteers according to the protocols used in the Nest Record Scheme (NRS), co-ordinated by the British Trust for Ornithology (BTO) (Crick *et al.* 2003). Nest boxes were checked weekly, with clutch size, brood size and chick mortality recorded for each box, along with first-egg laying date, individual ring number of parents and nestlings, hatching success (proportion of eggs that hatched), fledging success (proportion of chicks that fledged) and fledging date, recorded wherever possible. If laying date was not recorded directly, then it was estimated based on an assumption of one egg laid per day, and incubation starting from the day of completion of the clutch (Both *et al.* 2005). If a female was found to be brooding young and the laying date was unknown, then the calculation was based on an assumption of one egg per day plus 14 days for incubation, plus the apparent age of the chicks (Laaksonen *et al.* 2006). Young were ringed at 7-10 days old. Nest boxes were emptied and cleaned between seasons.

In 2003 and 2004, the frequency of visits by volunteers and their timing prohibited brood size from being recorded. Also, in 1992, 1996, 1997, and 1999-2006, laying dates were not recorded, meaning that data for laying date was available for 18 years. Although there are gaps in the resulting dataset, the long-term nature of the study allows for long-term relationships between demography and weather to be examined.

2.3.3 Weather data

Monthly rainfall and temperature data, 1990 – 2015, were downloaded from the Meteorological Office website (Met Office *et al.* 2017), and data extracted for the 5 km^2 cell containing the Cwm Clydach study site from the national spatially-smoothed weather dataset (UKCP09 gridded observation datasets). Four variables were used to quantify weather during the breeding season, calculated separately for each month April – June inclusive (i.e. 12 variables in total): 1. number of heavy rain days (> 10 mm rain falling in a day), 2. mean rainfall (mm), 3. number of nights on which ground frost occurred, and 4. mean temperature (℃). These specific temperature and rainfall variables were chosen as they had previously been found to be useful predictors of bird breeding biology, with specific anticipated effects on the woodland ecosystem (Bagchi *et al.* 2012): 1. Heavy rainfall washes caterpillars off oak leaves reducing the foraging efficiency of insectivorous birds and chilling adults and chicks (Burgess 2014), 2. Mean rainfall influences the rate of advancement of the growing season (Amar *et al.* 2006), 3. Frost causes damage to newly opened oak leaves affecting the abundance of food available for caterpillars which in turn affects flycatcher foraging success (Moreno *et al.* 2015), and 4. Mean daily temperature influences when the oak leaves will start budding and the caterpillars will emerge from their eggs (Visser *et al.* 1998).

2.3.4 Statistical Analysis

All analyses were conducted using R v3.5.1 (R Core Team 2018) with additional packages lme4 (Bates *et al.* 2015) and mgcv (Wood 2011) used for linear and non-linear modelling, respectively. Statistical methods followed Thomas *et al*. (2017).

2.3.5 Principal Component Analysis

Tests for multi-collinearity between weather variables were conducted and, on finding that multiple variables were substantially correlated with each other, a Principal Component Analysis (PCA) was conducted to summarise the main axes of variation in weather following methods in Shariati-Najafabadi *et al.* (2016). The first five principal components (PCs) were retained, as they exceeded the eigenvalue retention threshold of 1 (following Thomas *et al.* 2017). These five PCs accounted for 87 % of the variation within the weather variables. Using PCs from a PCA, the impacts of inter-related weather variables could be identified together rather than assessing impacts of each variable independently. The combining of variables is biologically relevant as temperature and rainfall co-vary in nature and the effect on the ecosystem is in response to both variables. Using PCA both variables can be investigated whilst reducing redundancy.

Table 2.1 Eigenvectors for each of the input weather variables of a Principal Components Analysis at Cwm Clydach (1990 and 2015). Each new principal component was described by using the corresponding emboldened numbers identifying the original weather variables that were most strongly correlated with each Principal Component.

	PC1	PC2	PC3	PC4	PC5	Total
Variance explained (%)	**32.0**	**18.6**	**15.7**	**12.0**	**9.2**	87.5
Apr Rain > 10 mm	0.246	-0.039	**0.599**	-0.004	0.148	
May rain > 10 mm	**-0.344**	-0.036	**0.378**	0.215	0.110	
Jun rain > 10 mm	**0.408**	-0.098	0.050	0.100	**0.428**	
Apr temperature	**-0.305**	-0.262	-0.248	-0.188	**0.493**	
May temperature	0.223	**-0.491**	-0.192	-0.164	-0.242	
Jun temperature	-0.274	**-0.393**	0.125	0.166	-0.174	
Apr rain 1 mm	0.299	-0.175	**0.501**	-0.073	-0.183	
May rain 1 mm	**-0.371**	-0.257	0.142	0.162	0.223	
Jun rain 1 mm	**0.390**	-0.039	-0.168	0.102	**0.505**	
Apr frost	0.166	0.202	-0.238	**0.607**	-0.255	
May frost	-0.168	**0.507**	0.153	0.182	0.213	
Jun frost	-0.048	**0.358**	0.055	**-0.641**	-0.049	

PC1 summarised the timing of spring warming and rainfall, with high PC1 values representing colder than average conditions in April, drier conditions in May but more than average rain in June. PC2 summarised the strength of a breeding season cold snap with high PC2 values representing frost and low temperatures in May and June. PC3 summarised the amount of April rainfall with high PC3 values representing higher than average heavy rainfall in April and May, and a cold May. PC4 summarised the temperature in April with high PC4 values representing higher than average April temperature. PC5 summarised the probability of a dry cold June with high PC5 values representing a higher than average chance of a dry frost in June. All five Principal Components were used as candidate independent variables in the statistical models described below, as indices of weather conditions during the Pied Flycatcher breeding season at Cwm Clydach.

2.3.6 Temporal trends

Trends in population size, nest box occupancy and nest productivity variables were analysed using Poisson, quasibinomial and binomial error terms and square root, log and logit link functions respectively. Non-linear temporal trends were modelled using Generalised Additive Models (GAMs) with the degree of non-linearity (fitted using thin-plate splines) selected by using generalised cross validation (Wood 2006). Long-term linear trends, in these previously described dependent variables, were modelled separately using Generalised Linear Models (GLMs) All of these GAM and GLMs contained only “year” as the independent variable therefore no model refinement was required. Link function selection was conducted by using Akaike Information Criterion (AIC) values. Models with the lowest absolute AIC values were selected as the most parsimonious following Thomas *et al.* (2017).

2.3.7 Weather impacts on demography

Relationships between variations in nest productivity (dependent variable) in relation to the five identified principal components of weather (fixed independent effects) were examined using a Generalised Additive Mixed Model (GAMM), with a binomial error family and complementary log-log link function. Random independent effects of year and location (woodland subsection) were included to control statistically for inter-annual variation and spatial pseudo-replication respectively. Prior to refinement all five weather PCs from the PCA were initially included in the full model along with all 2-way interactions. Subsequent model refinement, using the AIC, resulted in PC1, PC2 and PC3 being retained in the most parsimonious model with an interaction between PC1 and PC3.

The relationship between the current year’s population size (dependent variable), the previous year’s population size and previous year’s breeding productivity (independent variables) were modelled in a GLM with a Poisson error family and log link transformation.

2.4 Results

2.4.1 Population size and nest box occupancy

The number of nesting attempts by Pied Flycatchers at Cwm Clydach increased from 80 in 1990 to a maximum of 108 in 1997, after which there was a steep decline in the number of breeding attempts, with only 27 nests recorded in 2015 (Figure 2.2). The overall decline in the number of nesting attempts between 1990 and 2015 was 66 %, although the decline was not linear during this period (Figure 2.2: GAM; χ^2 = 470.6, edf = 7.799, p <0.001, deviance explained 95.6 %).

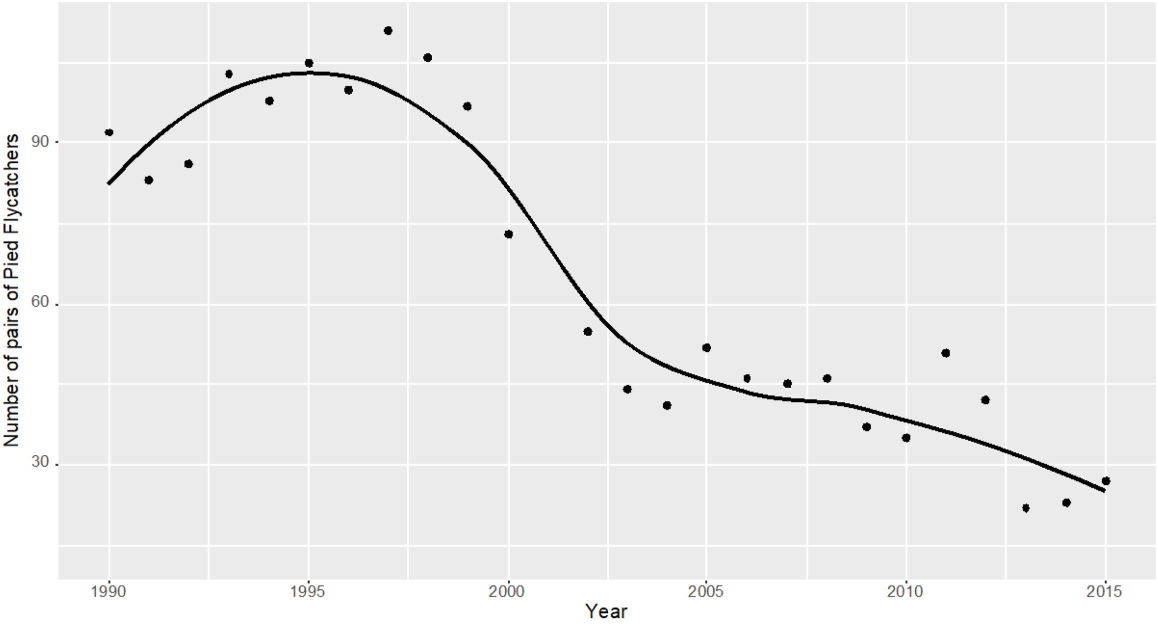

Figure 2.2 Historic trend in the numbers of Pied Flycatchers breeding in nest boxes at Cwm Clydach, from 1990 – 2015, with fitted modelled line (solid) and 95 % CI (dashed).

Nest box occupancy, adjusting for the varying number of nest boxes available through time, showed a similar decline to the number of nests (comparing Figure 2.3 with Figure 2.2). The frequency at which Pied Flycatchers occupied nest boxes remained relatively stable at 40-50 % between 1990 and 1996, but then the occupancy declined by 50 %, falling from an occupancy of 40 % to 20 % between 1996 and 2003. By 2015, nest box occupancy had fallen to nearly 10 % (Figure 2.3). This decline in percentage of nest boxes occupied was significantly non-linear (Gamma GAM; edf = 5.82, ref.df = 6.95, F = 42.7, p< 0.001, deviance explained = 94.2 %).

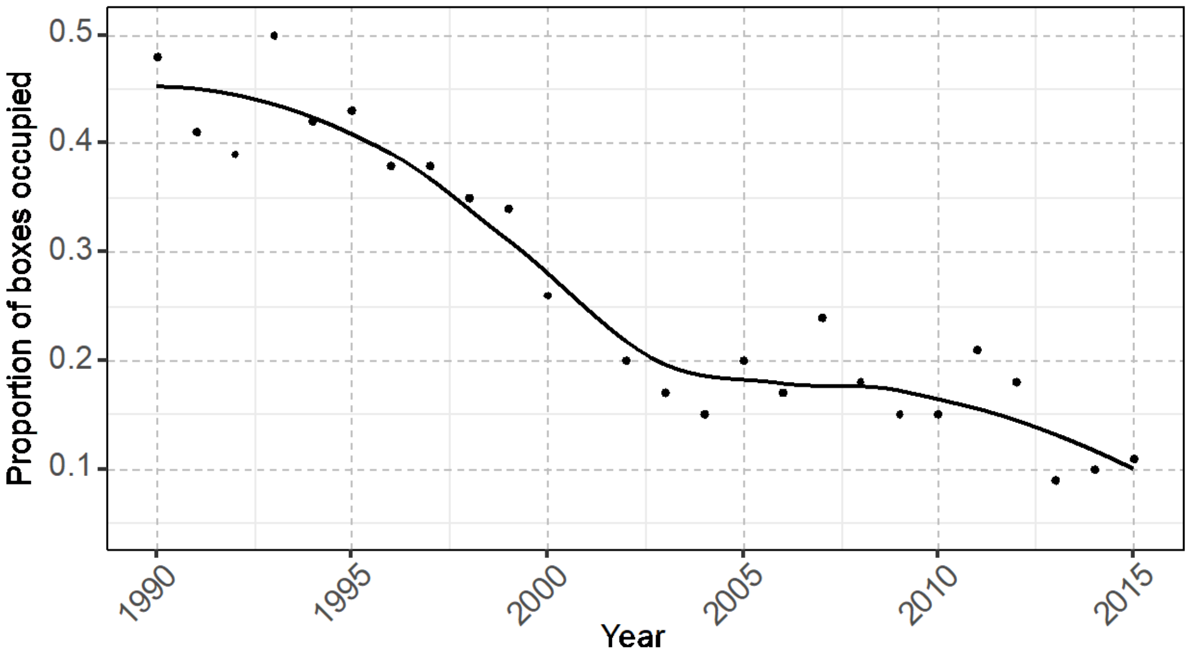

Figure 2.3 Trend in proportional nest box occupancy (1990 – 2015) with fitted modelled line (solid) and 95% CI (dashed).

Table 2.2 Annual number of boxes checked in Cwm Clydach between 1986 - 2015

Year	No. boxes checked	Year	No. boxes checked	Year	No. boxes checked
1986	13	**1996**	266	**2007**	187
1987	65	**1997**	292	**2008**	252
1988	87	**1998**	302	**2009**	240
1989	144	**1999**	285	**2010**	241
1990	193	**2000**	276	**2011**	240
1991	202	**2002**	280	**2012**	240
1992	218	**2003**	262	**2013**	240
1993	208	**2004**	272	**2014**	240
1994	235	**2005**	265	**2015**	240
1995	242	**2006**	267		

2.4.2 Inter-annual variation in April weather and laying date

Over the period of decline in the Pied Flycatcher populations, mean April temperatures increased by 1.5 °C (GLM; mean increase ± SE = 0.059 ± 0.003 °C per year, $F_{1,1576} = 306.5$, $p < 0.0001$, $R^2 = 0.16$), The was also a long-term advancement of laying date of 1-2 days across the study period (Figure 2.4), this estimate was robust to removal of outliers where individuals laid after day 55 (where clutches might be replacements). There was no difference in the slope when all dates were included (slope = -0.074) or when the replacement clutches had been removed (slope = -0.071). Intra-annual variability in laying date was much greater than inter-annual variation. Laying date was negatively (mean ± S.E. = -0.03 ± 0.001, $p < 0.0001$) and significantly associated with mean April temperatures (Figure 2.5) whilst there was no association with rainfall in April ($p = 0.211$) (GLMM: $Chi_{1,765} = 12.9$, $R^2 = 0.09$). Annual mean laying date was approximately seven days earlier in the warmest versus coldest observed April conditions across the study period Figure 2.5).

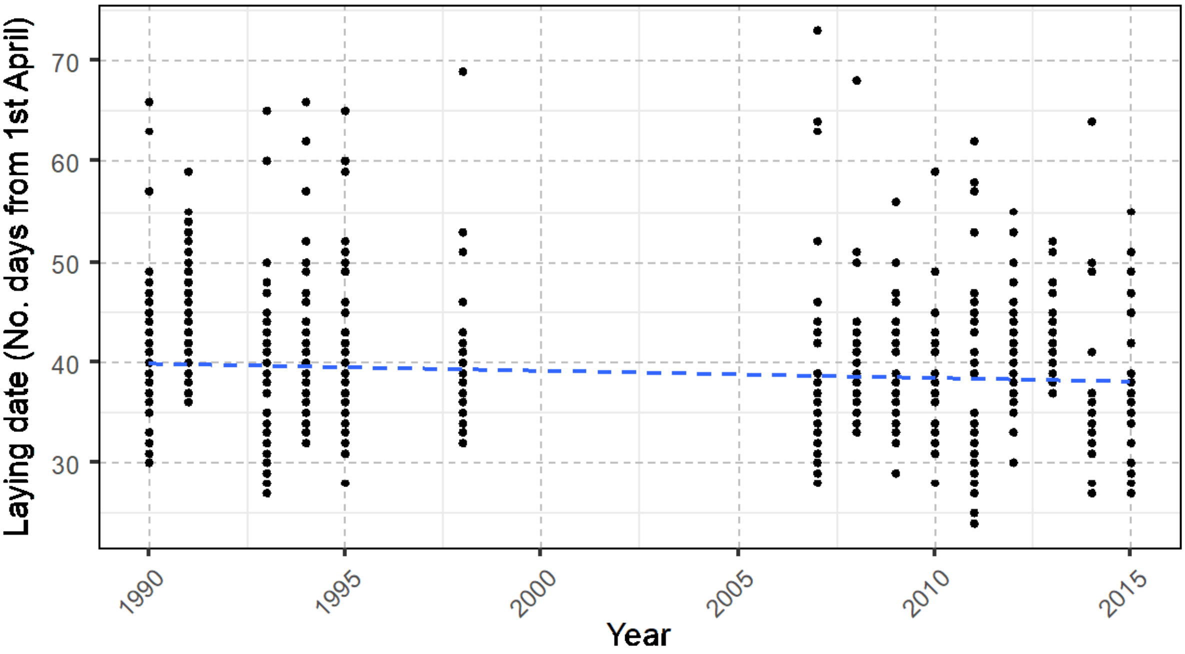

Figure 2.4 Pied Flycatcher first-egg laying date (no. of days from 1st April) 1990-2015.

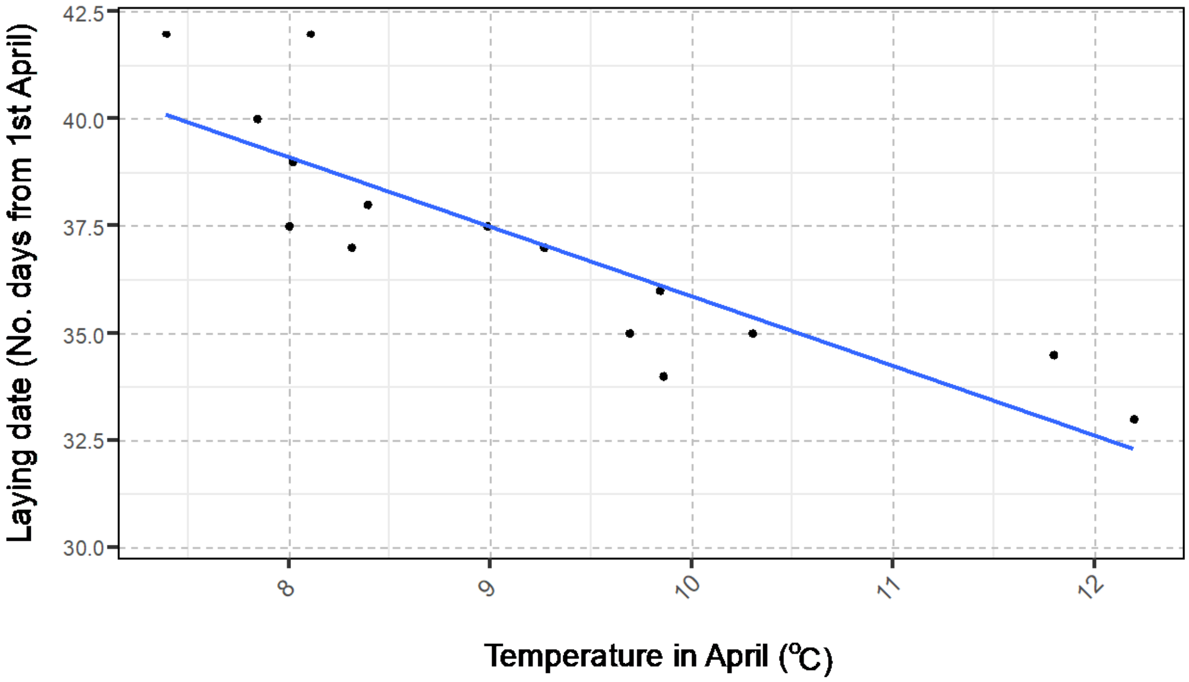

Figure 2.5 Shifts in laying date in relation to temperature at Cwm Clydach between 1990 and 2015

There was a strong correlation between laying date and clutch size (GLMM; slope ± SE = -0.01 ± 0.002 eggs per day, $p < 0.0001$) with larger clutches, mean of 7.7 eggs, laid at the beginning of the season (30 April) compared with a mean of 4.7 eggs at the end of the season (12 June).

There was significant inter-annual variation in all of the demographic parameters recorded (clutch size, brood size, number of chicks fledged) (Figure 2.6) (Table 2.3). There was also significant inter-annual variation in the calculated metric of hatching success (GLM: LRT = 524.54, df = 22, p< 0.0001) with an annual mean hatching success range of 50 – 87%.

The analysis identified long-term negative trends in the number of chicks which fledged (GLM; mean ± SE = -0.006 ± 0.001, $F_{1, 1501} = 273.6$, $p < 0.0001$, $R^2 = 0.1536$) and the proportional of chicks which fledged of 2 % per year (GLM; mean ± SE = -0.02 ± 0.006 decrease per year, t = -3.54, pseudo $R^2 = 0.007$). The other demographic parameters showed no significant long-term trends (p = 0.143, 0.330 and 0.751 for clutch size, hatching success and brood size, respectively).

The modal clutch size across the whole study period was seven eggs (mean = 6.8 eggs, range = 4 - 9 eggs), and the modal brood size was seven chicks (mean = 6.01, range = 0 - 9 chicks), yet there was substantial and significant inter-annual variation in both clutch (range of annual mean values 5.7 - 7.3 eggs per clutch) (Figure 2.6a), and brood (range of annual mean values 3.5 - 6.1 chicks per brood) (Figure 2.6b) size.

Of the 1,540 nests recorded during the study, 215 contained eggs but did not result in any fledglings (14%) but from nests which fledged chicks, the modal number of fledglings was six, giving a modal fledging success of 85 %. Predation of the nests by mammals (primarily Grey Squirrel, *Sciurus carolinensis*, Common Weasel, *Mustela nivalis* and Wood Mouse, *Apodemus sylvaticus* and birds (primarily Great Spotted Woodpecker, *Dendrocopos major*) at the study site was minimal, with desertion of the clutch or starvation of the brood being the primary cause of nest failure (H. Coats pers. comm.).

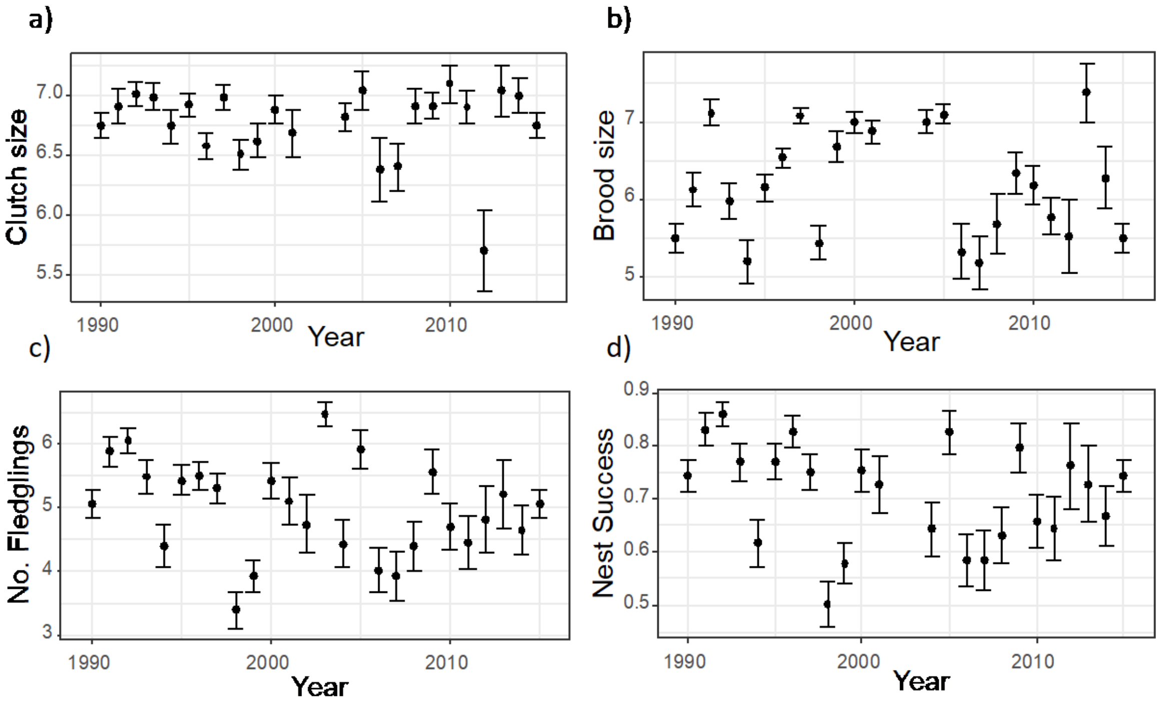

Figure 2.6 Variation in a) clutch size, b) brood size, c) number of fledglings produced per nest, d) nest productivity (proportion of eggs which resulted in fledged chicks) at Cwm Clydach 1990 – 2015. Annual means ± standard error are given.

Table 2.3 Inter-annual variation in demographic parameters (Clutch size, Brood size and number of chicks which fledged)

Variable	Chi statistic	Degrees of freedom	p-value	Pseudo-R^2
Clutch size	124.5	22, 1441	<0.0001	0.65
Brood size	175.5	22, 1012	<0.0001	0.79
No. fledged	142	24, 1478	<0.0001	0.69

There were no significant linear increases or decreases in any of the weather patterns described by PCs 1-5 during the course of the study (p = 0.053, 0.081, 0.813, 0.065 and 0.833, respectively) (Figure 2.7).

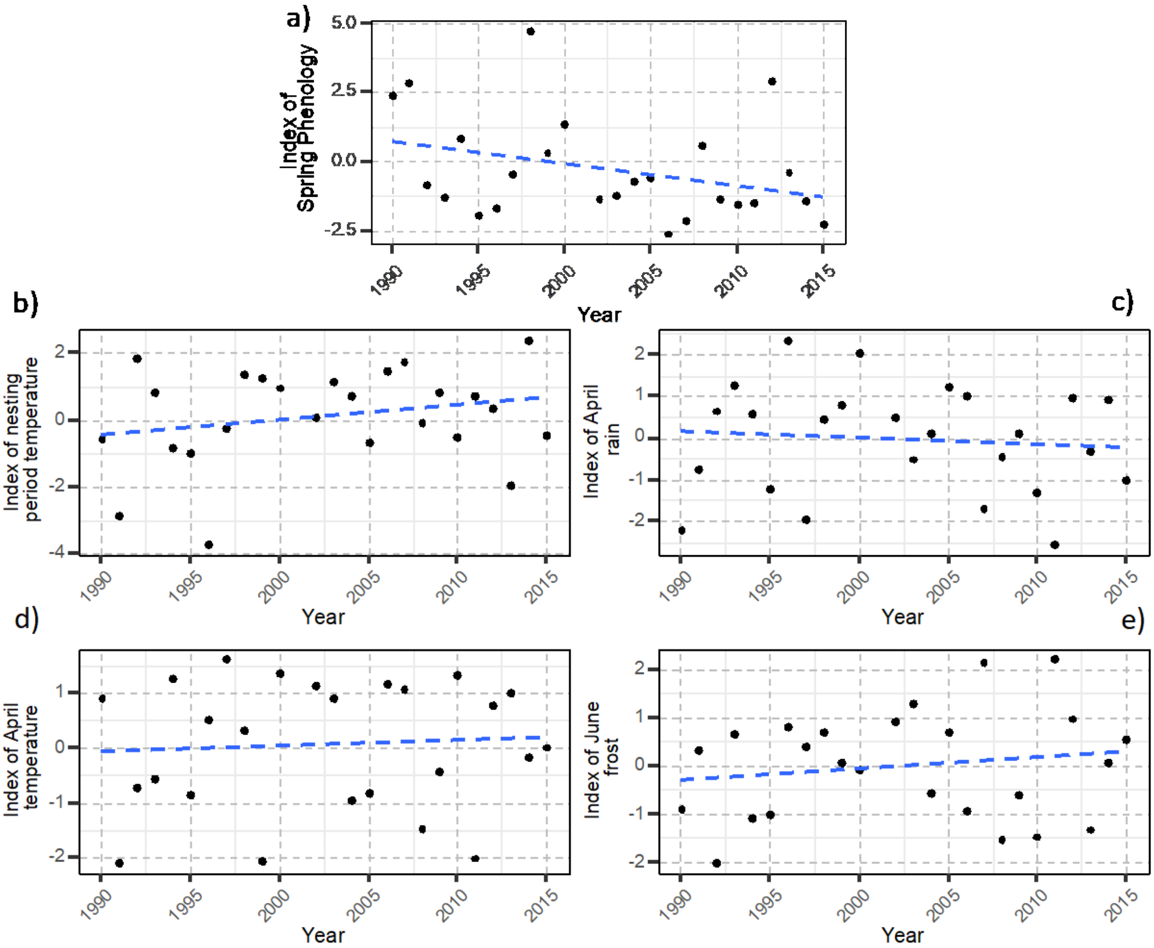

Figure 2.7a-e. Weather variation between 1990 and 2015 at Cwm Clydach, all dependent variables are scaled by long-term mean. a) Inter-annual variation in Spring phenology (summarised by PC1). High values of the spring phenology index represent warm April temperatures, dry May and wet June. b) Index of temperature during the nesting period (May and June). High values represent warmer conditions. c) Index of rainfall in April. Larger positive values represent higher frequency of heavy rainfall events and a greater quantity of rain. d) Index of temperature in April. Larger values indicate a warmer temperature. e) Index of frost in June. Higher positive numbers represent an increase in the number of days with frost. Dashed line represents the non-significant trend.

2.4.3 Effects of weather on fledging success

The three PCs which explained the most variation in weather (PCs 1 - 3) were retained in the GAMM explaining fledging success after AIC-based model selection. These were indices of spring timing, April rainfall and the degree of frost in May. The effect of April rainfall on fledging success was impacted significantly by how early spring started in a given year ($F_{2,2}$ = 4.77, p = 0.009) and varied non-linearly in its effect across the range of rainfall index values. In years which had a drier April/May (low PC3 values; Figure 2.8, left hand end of red line), fledging success was very high (80-100 %). It was also high when a wet

April was followed by a wet May and then a dry June (Figure 2.8). When rainfall conditions differed in April and May, nesting success was low, more so in years when April was very wet (high PC3 values) and cold (low PC1 values), followed by a very dry May (high PC1 values). In years when the conditions were poor, the fledging success of a brood was as low as 40 %.

The probability of fledging was higher at times of no frost in May, compared to heavy or frequent frost (high PC2 values) (Figure 2.9). It was also higher in years when April had a lower than average temperature and a drier than average May (high PC1 values).

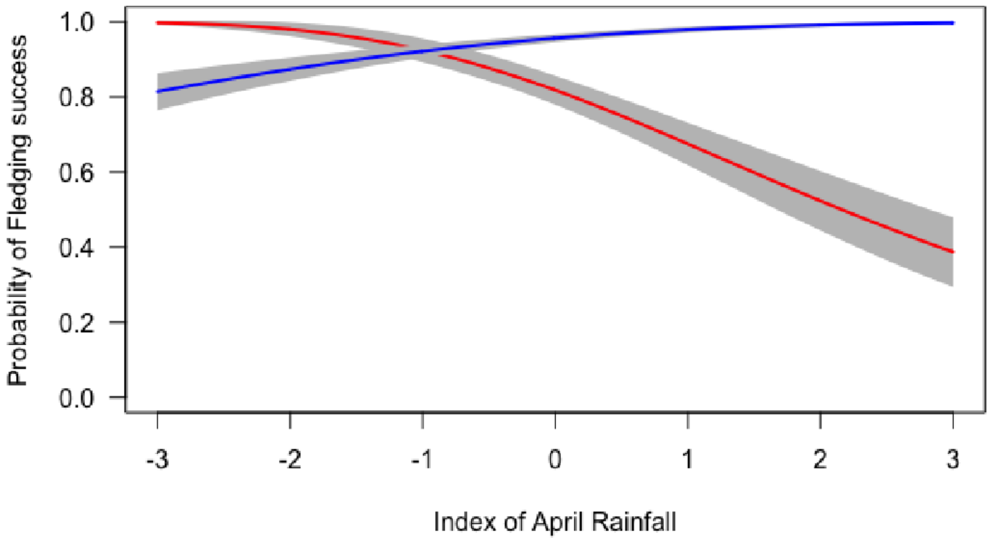

Figure 2.8. Probability of fledging success per nest in different rain conditions in April (PC3), mediated by rain in May and June (PC1). Blue: High May-June rainfall index. Red: Low May-June rainfall index.

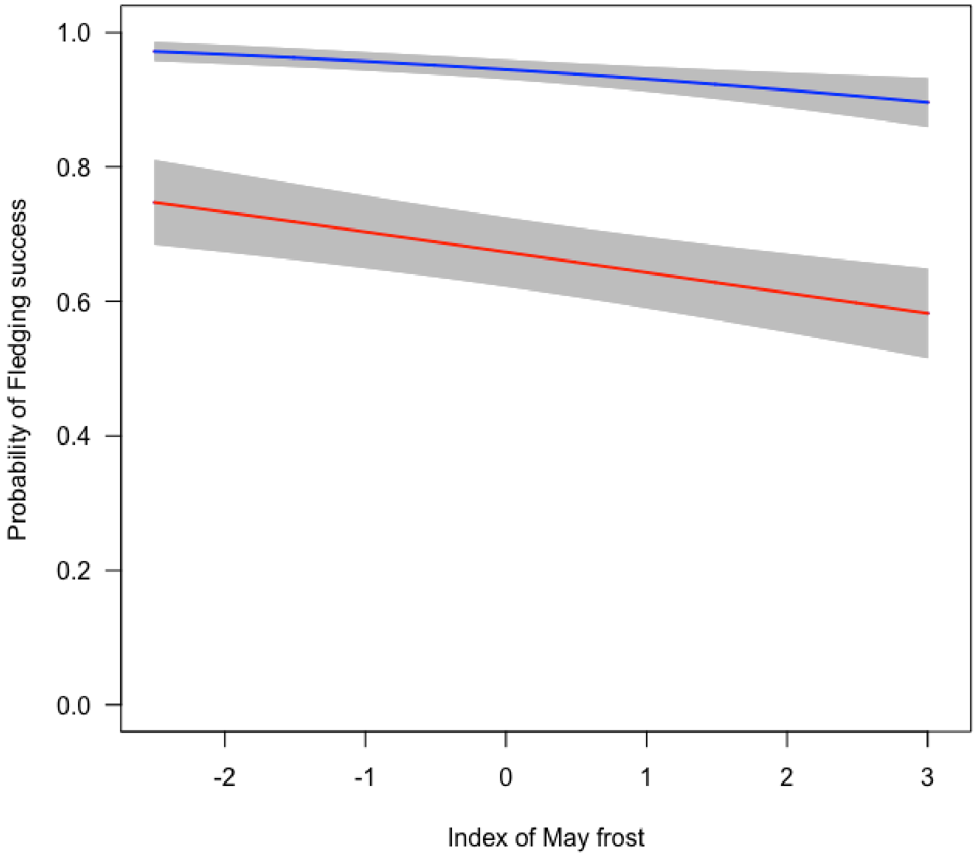

Figure 2.9 Probability of nest fledging success under varying temperatures and rainfall conditions. Wet May followed by dry June (blue), dry May followed by wet June (red).

Mean annual fledging success was a significant predictor of the subsequent population size (GLM: $F_{2,21} = 19590$, pseudo $R^2 = 0.81$, $p < 0.001$), even once the previous year's population abundance had been controlled for (mean slope ± S.E. = 0.81 ± 0.385, z = 2.117, p = 0.034), with 81 % of the variation in the subsequent year's population abundance being explained by the combination of current year's abundance and breeding productivity. Mean annual productivity itself explained 8 % of the variation in the subsequent year's population abundance (GLM: $F_{1,22}$ = 8250, pseudo R^2 = 0.08 $p < 0.001$). The interaction between population size and fledging success in the current year was not significantly associated (p = 0.829) with population size in the subsequent year, indicating that there was no significant density dependence influencing population change.

2.5 Discussion

2.5.1 Population change in a global, long-term & multi-species context

The present study identifies some demographic processes which contribute to the change in a Pied Flycatcher population and examines the role of weather conditions (temperature and rainfall) in driving the underlying demographic changes. Significant declines occurred over the 25-year study period, in both the numbers of breeding pairs of flycatchers at Cwm Clydach, and the proportion of nest boxes occupied by them. The decline in population size (66 %) in Cwm Clydach was greater than the UK average over the same period (38 %) (Woodward *et al.* 2018), but smaller than declines in other Welsh woodlands where Pied Flycatchers have recently become extinct. The population decline seen at Cwm Clydach over the period 1990 – 2015 is also steeper than has been reported among Pied Flycatcher populations across Europe over a similar period (1980-2016), which has been described as a ‘moderate’ decline (< 5 % per year) (PECBMS 2015). The mean population trends for Pied Flycatchers in the UK (1995 – 2016) and across western Europe (1980 – 2016) were both 38 %. The rate of population decline in Cwm Clydach is not, therefore, fully explained by the continental scale decline, but is likely to be more rapid due to more local factors.

The proportion of nest boxes occupied (10-50 %) by Pied Flycatchers was comparable with other UK studies where inter-specific competition was the most important factor which affected the proportion of nest boxes occupied (Burgess 2014). The lack of an increase in Pied Flycatcher abundance after the protracted decline implies that the population is continuing to be constrained by environmental factors such as inter-specific competition, food availability and weather. Lundberg *et al.* (1981) found no density dependent effects on clutch size or hatching success in years of good weather. In bad weather (heavy rain and near freezing temperatures), however, occurring near the time of hatching, nestlings growing in high density areas were more successful than those in low density areas (Lundberg *et al.* 1981b). Breeding densities were comparable between the present study and those in Lundberg *et al*. (1981) and were likely to be higher than those nesting in natural cavities which would therefore have reduced intra-specific competition for nest sites.

2.5.2 Inter-annual variation in weather conditions

At Cwm Clydach, weather conditions affected Pied Flycatchers throughout the breeding season. Those parents which were most able to adjust to variations, by being behaviourally plastic, maximised their lifetime reproductive fitness. Across the 25-year study period, mean monthly (April, May, June) temperatures fluctuated between 7 °C and 16 °C, and monthly mean rainfall fluctuated between 2.6 mm and 22 mm. Although there were substantial and statistically significant variations between years in weather conditions, as denoted by the five PCs, there were no significant long-term linear changes in any of the PCs across the study period. The large inter-annual variation in patterns in weather mean that long-term climate trends are not exhibited (IPCC 2014). A longer time series of weather data would permit understanding of the changes in weather at a decadal scale, providing clearer patterns in climate. Nevertheless, the substantial variation between years in weather conditions highlights the inter-annual behavioural plasticity required by the parents to time egg laying and incubation correctly, to result in high fledging success of their offspring.

2.5.3 Changes in the timing of breeding

Across the temperate zones, winter is becoming wetter and summer drier, with mean monthly temperatures increasing (IPCC 2014). Increased mean temperatures in April would advance both tree bud burst and caterpillar peak abundance. As the rate of change is consistent across the UK (Burgess *et al.* 2018), birds could compensate for the advancement by a shift in range to higher altitude or latitudes, or matching the advancement of the date of clutch initiation. Failure to do this has been shown to result in a mis-match between peak nesting demand and peak food availability (Burgess *et al.* 2018).

Laying dates were significantly negatively correlated with mean temperature in April which resulted in birds laying significantly earlier following warm Aprils. This behavioural plasticity reduced phenological mis-match. As Pied Flycatchers did not lay earlier after a drier than average April, April's temperature may be the cue for laying and not rainfall. Mean laying date varied by seven days across the range of temperatures experienced during the study, with a linear advancement of 1-2 days over the 25 years (Figure 2.4). This observed advance in mean laying date is in line with the rate of change reported in other studies of 0 - 0.6 days per decade (Croxton *et al.* 2006), in which similar rates of advancements have been reported over an even greater range of temperatures and laying dates (Both and Visser 2001). Not all Pied Flycatcher populations respond to the same degree to changes in temperature. In some populations there is no advancement in laying dates despite significantly increased spring temperatures (Sanz 2003; Goodenough *et al.* 2010).

The large intra-annual variation in laying dates, but minimal linear trend, suggests that variation in laying date is primarily due to phenotypic plasticity at an individual level, rather than being an evolutionary response to consistent directional selection at the population level.

2.5.4 Variation in clutch size

There was substantial inter- and intra-annual variation in clutch size, although again no long-term linear trend in clutch size across the 26-year study. The highly variable temperature observed during the study period may be associated with the variation in clutch size within and between seasons. The relationship between temperature and clutch size is, however, unclear; in the present study there was no long-term change in temperature and there was also no long-term change in clutch size. Previous studies have differed in their conclusions. Sanz (2003) reported a decrease in clutch size associated with increased spring temperatures, whereas Winkel and Hudde (1997) found an increase in clutch size at higher temperatures. Burgess (2014), on the other hand, found no biologically significant relationship between the two.

There is intra-annual variability in clutch size, specifically, a seasonal decline in clutch size of approximately three eggs between the beginning and the end of the breeding season. The magnitude of this seasonal decline is consistent with that described previously (Lundberg and Alatalo 2010). The seasonal decline in clutch size is correlated with a seasonal decline in the food availability in a territory; when the timing of parental food demand did not coincide with peak food availability (mis-match) a lower than average mean clutch size was observed (Arcese and Smith 1988). Temporal decrease in clutch size during the breeding season, combined with an increased proportion of birds laying later than the peak in food availability, would also result in a reduced mean population clutch size (Hamann and Cooke 1987; Stenning *et al.* 1988).

2.5.5 Variation in hatching success, brood size and number of fledged chicks

As with laying date and clutch size, hatching success varied substantially between years (range: 50 % - 87 %) but with no significant linear long-term trend. The maximum hatching success was comparable to previous studies (82.4 % (Stenning *et al.* 1988) and 86 % (Siikamäki 1995)). Individual brood size (population mean = 6.01) was driven primarily by hatching success (rather than clutch size) and varied more than was reported for Pied Flycatchers elsewhere in Wales by Wright (2004) (mean = 5.7 birds).

The number of chicks which hatched (brood size) varied significantly between years but there was no significant long-term change across the study, indicating that this aspect of demography is not affected by a constant and unidirectional selection pressure in the breeding season. The number of chicks which fledged per nest varied significantly between years and showed a long-term significant decline across the study. A small difference between the brood size and the number of nestlings at seven days is consistent with previous studies showing that chick mortality within the first seven days is low (Lundberg and Alatalo 2010), especially if the nest is in a nest box rather than in a natural cavity (Baillie and Peach 1992). Clutches which failed to produce any fledglings occurred in approximately one out of every six nests (14%) which is broadly comparable with similar studies in the UK (22 and 19%) (Lundberg and Alatalo 2010). The main cause of nestling mortality is starvation, driven by inclement weather reducing food availability and increasing interspecific competition, as shown by a density dependent response exhibited most strongly in bad weather (Baillie and Peach 1992).

2.5.6 Associations between weather and breeding parameters

Both temperature and rainfall had significant effects on fledging success at different times during the breeding season. Temperature and rainfall in months with peak nestling demand, and high rainfall in June, have previously been shown to affect nest productivity (Burgess 2014). The current study clarifies this relationship by describing the interaction between rainfall prior to laying and fledging, and incorporates the effect of temperature during incubation and chick rearing.

Fledging success declined significantly during the study period and varied significantly between years in relation to the variable weather conditions experienced in different years. Fledging success was high (near 100 %) at both extremes of rainfall in April, provided that the same conditions persisted into May. Conversely, the lowest mean fledging success (40 %) occurred when April had higher than average rainfall, and May was dry. In addition to the effect of rainfall throughout the breeding season, there was an additive effect of temperature in May and June, when warmer temperatures result in higher fledging success.

Even before passerine chicks achieve homeothermy at eight days (Bourret *et al.* 2017), they have a high tolerance for hypothermia (Blix 2016) which may explain why rainfall is a greater predictor of fledging success than temperature. Heavy rainfall events wash lepidopteran caterpillars off the oak leaves, decreasing the foraging efficiency of the parent birds (Burgess 2014). Reduced food availability for the growing chicks results in reduced fledging success from a nest. The ideal weather for high Pied Flycatcher fledging success is high rainfall in April and May (promoting leaf growth), with considerably less rainfall in June (improving caterpillar survival and hence Pied Flycatcher foraging efficiency), and warmer temperatures in May and June (promoting caterpillar development). As temperature in April also affects laying date, weather plays an important role in the timing of breeding, as well as the success or failure of a nest, and therefore population change.

2.5.7 Drivers of population change

The fledging success (% of eggs resulting in fledged chicks) in each year accounted for only 8 % of the variation in the population size in each following year, suggesting (i) that the observed changes in breeding productivity in the present study explain some – but not all - of the population change, and (ii) that factors other than breeding productivity, such as adult survival, are also important drivers of population change in Pied Flycatchers (see Chapter 4). As weather variables influence fledging success, and fledging success accounts for 8 % of the population change, this study provides evidence for a partially weather driven change in the abundance in this population of Pied Flycatchers.

As only approximately 3 % of Welsh Pied Flycatcher fledglings survive to return to their natal area (Kern *et al.* 2014), factors operating during the trans-Saharan migrations, and on the sub-Saharan wintering grounds, may be of greater importance than factors operating on the breeding grounds. This is not the case for all Afro-Palearctic migrants; breeding productivity in the Willow Warbler has been shown to have significant impacts upon the breeding population in subsequent years, such that high fledging success in one year can reverse the population decline in the next (Morrison *et al.* 2016).

The changes in fledging productivity observed in the present study appear to have a small (<10 %) but significant impact upon the subsequent year's population size. This is contrary to Wright *et al.* (2004) who found no link between population declines and changes in breeding parameters. Baillie and Peach (1992) proposed that it is not fledging success which drives population change in Pied Flycatchers and other long-distance migrants (e.g. Blackcap (*Silvia atricapilla*), but instead post-fledging mortality. In breeding seasons following a higher post-fledging survival, recruitment is high and therefore population declines are lower. Conversely, mass brood mortality, as observed in Spain, due to a spring cold snap, can lead to significant loss of recruitment and, therefore, negatively impact population size (Moreno *et al.* 2015). In addition to that accounted for by fledging success, in the present study 73 % of the subsequent population size was explained by the current year's population size. Therefore, reductions in the number of individuals returning from Africa in one year will significantly affect the subsequent year's population (Stenning *et al.* 1988). This highlights the importance of understanding the effects of adult survival across the non-breeding season, on population trends.

The trends in breeding population size are not the same for all UK breeding woodland species; this could lead to changes in community composition. Over the same period that Pied Flycatchers declined by 38 % (across western Europe), Blue Tit populations remained relatively stable (3 % decrease) and Great Tits increased by 30 % (Woodward *et al.* 2018). The inverse relationship between presence of Pied Flycatchers and the level of inter-specific competition from Blue and Great Tits was the main predictor for presence of Pied Flycatchers in Yarner Wood, Devon (Burgess 2014). It is possible, therefore, that the decline in Pied Flycatchers may, at least in part be due to greater interspecific competition (Amar *et al.* 2006). No such data were available for analysis in this study, however in each year there were multiple unoccupied nest boxes. As such, interspecific competition for breeding sites is unlikely to limit Pied Flycatcher population size although it is possible that competition for food is a limiting factor at Cwm Clydach. Blue Tits and Great Tits are known to have better over-winter survival when the weather is milder (warmer mean temp, reduced precipitation), allowing for better conditioned individuals to breed as soon as conditions allow in the Spring (Stowe 1987). Blue Tits are also known to track the changes in food availability, by altering laying dates, more effectively than Great Tits and Pied Flycatchers (Visser *et al.* 2004). They may, therefore, occupy nest boxes first in years during which the caterpillars emerge earlier (Visser *et al.* 2004), to the exclusion of Pied Flycatchers, whose laying date is constrained by the timing of arrival from their long-distance migration (Both and Visser 2001). By using long-term studies such as this to understand the climate-driven demographic changes underlying population trends in Pied Flycatchers it is possible to identify potential causes of decline (or even increases) in other species within the woodland community.

2.5.8 The value of long-term studies for understanding the climatic and demographic drivers of population change

Long-term studies of population changes, recording population size, demographic trends and relevant environmental data are essential for understanding the way in which animal populations vary (Baillie and Peach 1992). This long term approach is complementary to focused shorter term studies of mechanisms (Stenning *et al.* 1988). These concepts highlight the importance of comprehensive long-term studies such as the one analysed here, and recognises the bridge they form between understanding past patterns and predicting future trends.

Despite the extensive literature on Pied Flycatchers there are not many long-term datasets available from the UK. Vaugoyeau *et al.* (2016) analysed a total of 23 long-term studies of which only three were using UK datasets. The mean duration of these studies was 15 years and so one of the important contributions of this present study is the addition of a 25-year dataset. Short-term studies may be subject to bias, with conclusions not always being independent of the start and end time of the project (IPCC 2018). This is primarily due to any lag effect in a population (i.e. If there were a particularly bad breeding season then the population recovery may take multiple years to occur, not showing a representative general long-term trend). The lack of independence is particularly important when considering the need for forecasting potential trends under future climate scenarios, and for planning management practices and conservation strategies. The analyses of these studies therefore needs to be flexible so that any future predictions are not constrained to simplistic extrapolation of linear or similar mathematical functions (e.g. Wright *et al.* 2004).

The rapid decline in iconic species such as the Pied Flycatcher is of public concern, but there is only a limited understanding of what drives these declines. How they can be mitigated remains unclear. This study highlights how breeding conditions, demography and productivity could explain a small but significant proportion of the population change. The links between weather and demography may be direct, through incubation intensity and hypothermia, but links through trophic levels will also have sizeable indirect impacts. These effects include changing tree bud burst date and duration, time of caterpillar emergence, leaf death through frost, invertebrate activity and interspecific overwinter survival.

3 Phenology of invertebrate abundance and Pied Flycatcher breeding biology -causes and consequences of trophic mis-matches

3.1 Abstract

Studies of trophic cascades can provide a mechanistic understanding of climate-driven mis-matches between timing of food availability and seasonal food requirements of predators. Trophic mis-matches are implicated in the rapid declines of temperate woodland-breeding summer migrant bird species, such as the Pied Flycatcher. In this study, the trophic mechanisms linking weather conditions, invertebrate availability and Pied Flycatcher breeding biology were investigated, to understand the role of trophic mis-matches in driving this decline. Across three years (2016-2018) the direct and indirect impacts of temperature and rainfall on Pied Flycatcher breeding demographics were observed. Invertebrate activity density was monitored using frass and sticky traps, and flycatcher breeding productivity was monitored through nest box checks. Warmer spring conditions were associated with earlier abundance of flying invertebrates and caterpillars, and short-term temperature variations were associated with fluctuations in invertebrate abundance. In each of the three years, the seasonal peak in Pied Flycatcher nestling food demand dates did not closely match the peak in caterpillar availability. This indicates that flycatchers were not able to respond fully to adjust their timing of breeding to variation between years in spring weather conditions and hence the timing of peak food availability. The majority of Pied Flycatcher nesting attempts were timed in a way that allowed for successful fledging, but later nests tended to be less successful. This variation in fledging success appears to be linked to the timing of invertebrate availability, driven by differences in weather, leading to lower fledging success in circumstances of greater trophic mis-match. These results together show the importance of reproductive timing in Pied Flycatchers, and the impacts that fluctuations between years in weather conditions and food availability may have on the breeding productivity of insectivorous birds.

3.2 Introduction

Understanding the mechanisms driving population declines of migrant songbirds is essential to be able to predict accurately future population changes and potential conservation interventions (M ø ller *et al.* 2004). The interactions between global climate change, local weather variations, and the abundance and timing of availability of food for migrant birds on their breeding grounds have been shown to have significant impacts on migrant birds (Both and Visser 2001). Broad scale impacts of climate on birds include range shifts, changes in demography, and changes in the timing of breeding (Green and Pearce-Higgins 2014). Birds respond to the environmental conditions (e.g. weather, food supply) that they experience on a local scale, rather than directly responding to global climate (Walther *et al.* 2002). Different species may also respond to different weather variables (e.g. temperature or rainfall) as well as food availability (Green 2010).

Predominant local weather effects come from temperature and rain, the effects of which can be direct or indirect. These effects are frequently non-independent as they are to some degree correlated and may also be additive. Decreased overnight temperatures increase metabolic costs, requiring adult birds to retain larger fat reserves overnight and to replenish them during the day (Thomas and Cuthill 2002). For breeding birds this may involve trading-off self-maintenance against provisioning their young. For example, in Blue Tits an increase in ambient temperature during incubation allowed females to leave the nest for longer and the males to make fewer mate-provisioning visits (Amininasab *et al.* 2016). Although adult birds are directly affected by weather (Dybala *et al.* 2013), during the breeding season, the effects are most severely felt by nestlings (Ross *et al.* 2018). Rainfall and low temperatures can result in chicks getting wet and becoming hypothermic (Barrionuevo *et al.* 2018). Even if these impacts are non-lethal then the metabolic cost to the chick, of producing enough energy to raise its body temperature, will be higher.

Indirect effects of weather are mediated mainly through impacts upon food availability. Breeding birds need abundant food to provision their chicks during the period when the chicks are in the nest, and during this period nestlings need an abundant supply of food if they are to grow rapidly to fledging (Visser *et al.* 2006). Weather conditions such as temperature and rainfall may influence the abundance and activity of invertebrates (Pearce-Higgins *et al.* 2005), changing the availability of prey species to foraging birds (Vafidis *et al.* 2016). Numerical abundance of prey may not be the only important factor influencing chick growth; for example the combination of high temperatures and low rainfall can result in reduced water content in food items, and so the birds may become dehydrated (Catry *et al.* 2015).

Changes in Spring phenology may disrupt previously synchronous events (e.g. weather-dependent food availability and the timing of breeding of long-distance migrants) which result in negative effects on demography and population trends. Higher spring temperatures result in earlier emergence of invertebrates, and also result in earlier laying by many species of birds. Long distance migrant birds may, however, be constrained in the extent to which they can alter their laying date. More specifically, the extent to which trans-Saharan migrant birds breeding in NW Europe can adapt to phenological changes between years is limited by their arrival date on the breeding grounds. The arrival date is linked to the departure date from the wintering grounds, which is triggered by small day-length changes in Africa (Gwinner 1996). As day length is a climate-independent cue, there is little flexibility in departure date, leading to a constraint on arrival date. A knock-on effect of limited plasticity of arrival is that laying date is itself constrained by arrival date, although the duration of the gap between arrival and laying can vary (Both and Visser 2001). As invertebrate emergence is climate-driven but the laying date of migrant birds is constrained, in years when invertebrate emergence is earlier, the lack of plasticity in laying date can result in a mis-match in timing between peak food demand of bird nestlings and the availability of their invertebrate prey. With continued climate warming, the extent of this mis-match is predicted to increase, with negative consequences for breeding success, demographic trends and population trajectories of insectivorous migratory birds such as Pied Flycatchers.

Whilst the mis-match between food availability and peak requirements for breeding birds has been extensively described (Both *et al.* 2009; Burgess *et al.* 2018), the specific links between local and short-term weather conditions, invertebrate availability and bird breeding parameters, are still poorly understood. Although not all species and populations have responded (or failed to respond) to climate driven changes to the same degree, some of the clearest examples of trophic mis-match have been reported for Pied Flycatcher populations (Both and te Marvelde 2007).

Despite their name, Pied Flycatcher diet comprises a wide diversity of invertebrates across the breeding cycle, which they capture at a wide range of heights in the woodland habitat. Pied Flycatchers spend 30 - 40 % of their time taking prey from the field layer, and approximately 40 % taking prey in the canopy (Stowe 1987). Temporal variation in diet may result in Pied Flycatchers switching their diet between different taxa at different stages of the breeding cycle. On arrival in Spring, prior to breeding and during egg laying (April-May), caterpillars are usually still scarce and so diet may be more based on other invertebrates such as parasitoid wasps (Stowe 1987). Many parasitoid wasps belonging to the families *Ichneumonidae* and *Braconidae* parasitise Lepidopteran larvae (Wharton 1993) and are in flight in April and May, with some species (e.g. *Itoplectis maculator*) specialising on Tortrix moth larvae emerging in March (Fitton *et al.* 1988). The broad ecological niche of parasitoid wasps means that they parasitise many other orders as well as Lepidoptera, including Coleoptera and Diptera.

During the nestling period, in June, both adult and nesting diet is dominated by Lepidopteran caterpillars, but also is comprised of; Coleoptera, Hymenoptera, Aranea and Diptera (Bel'skii and Bel'skaya 2009). In many woodlands, this caterpillar biomass is itself dominated by caterpillars of the Winter Moth *Operophtera brumata* (Visser and Holleman 2001). Winter moths emerge in November/December and lay their eggs on or near Oak buds. These eggs develop through Winter and hatch in early Spring. Egg hatching is strongly temperature driven, and synchrony of hatching with Oak bud burst is essential to the survival and growth of 1st instars (Salis *et al.* 2016). Winter Moth caterpillars complete leaf feeding at the beginning of June, before they descend into the soil to pupate during June and July at which time they become unavailable as food for Pied Flycatchers.

Pied Flycatcher timing of arrival and breeding partially track local temperature trends (Ahola *et al.* 2004). Between 1974 and 2001 in Wales, Pied Flycatcher mean laying dates advanced by eight days (Wright *et al.* 2004). Temperatures at the time of arrival increased over the same period. In contrast, in parts of their breeding range where temperatures after arrival have not changed substantially, Pied Flycatcher breeding timing has not advanced. In other locations, Pied Flycatchers have advanced their laying days, but not enough to keep pace with the advance in caterpillar phenology. For example, in the Netherlands, increased Spring temperatures caused bud burst in Oak leaves to advance by 2.9 days between 1988 and 2005. The resultant advance in peak caterpillar abundance was 15 days, whereas the corresponding advance in the mean Pied Flycatcher laying date was only 7.2 (Both *et al.* 2009). These resulting phenological mis-matches between caterpillar emergence and Pied Flycatcher laying dates have resulted in lower food availability during peak nestling demand, leading to reduced fledging success (Burgess *et al.* 2018). Research on this classic case study of trophic mis-match has primarily focussed on the trophic interaction between Pied Flycatchers and Lepidopteran caterpillars, as the Flycatchers forage primarily on caterpillars during chick provisioning (Stowe 1987), whereas little is known about the role of other taxa in influencing the impact of the mis-match with caterpillar phenology. Nevertheless, caterpillars may be nutritionally important during chick rearing, and the positive association between the relative abundance of caterpillars in the diet, and

Pied Flycatcher fledging success suggests that caterpillar abundance is an important constraint on breeding productivity.

The overall hypothesis to be tested in this chapter is that Pied Flycatcher demography (specifically laying date and fledging success) is driven directly by variations in annual spring and summer weather patterns, and indirectly by the effects of weather variations on food availability. Variation in inter-annual and seasonal temperature and rainfall patterns will be examined, to identify a) their direct effects through a mechanism of reduced incubation stress in warm weather and wetting of incubating females during heavy rainfall events and b) their indirect effects on Pied Flycatchers through their impacts on the timing of invertebrate abundance as availability of food for Flycatchers. Pied Flycatcher breeding data will be used to investigate the phenology of flycatcher laying date and fledging success in relation to weather-dependent food availability. Specifically, higher temperatures in early Spring are predicted to lead to an earlier and higher availability of flying invertebrates, which in turn will lead to an earlier laying date in Pied Flycatchers. In addition, higher Spring temperatures are predicted to lead to an earlier peak in caterpillar abundance, which will lead to a greater mis-match in timing between nestling demand and caterpillar availability, reducing Pied Flycatcher fledging success.

3.3 Methods

3.3.1 *Study Site*

Tŷ Mawr woodland (52°12'23 N 3°29'06 W), is an unmanaged, privately-owned semi-natural broadleaf woodland in upland Mid-Wales. The woodland is dominated by Oak, and other tree species present consist of; Beech (*Fagus sylvatica*), Holly (*Ilex aquifolium*), Birch (*Betula pendula*) and Ash (*Fraxinus excelsior*). There is little understory with a ground flora comprised of Common Bluebell (*Hyacinthoides non-scripta*) and Bilberry (*Vaccinium myrtillus*). No active sheep grazing has occurred in recent decades. Predation at the study site was minimal, and so therefore not included in the present analyses. The site is split into three sub-units (Redwood, 6.25 ha, Ridge, 4.7 ha and Bank, 9.99 ha), two of which (Ridge and Bank) are contiguous, while the third (Redwood) is separated by approximately 150 m. Redwood has a south facing aspect and a gradient of approximately 20 %; Ridge and Bank are north-west facing with gradients of approximately 4 % and 10 %, respectively. The altitude range of the woodland spans 217-312 m a.s.l.

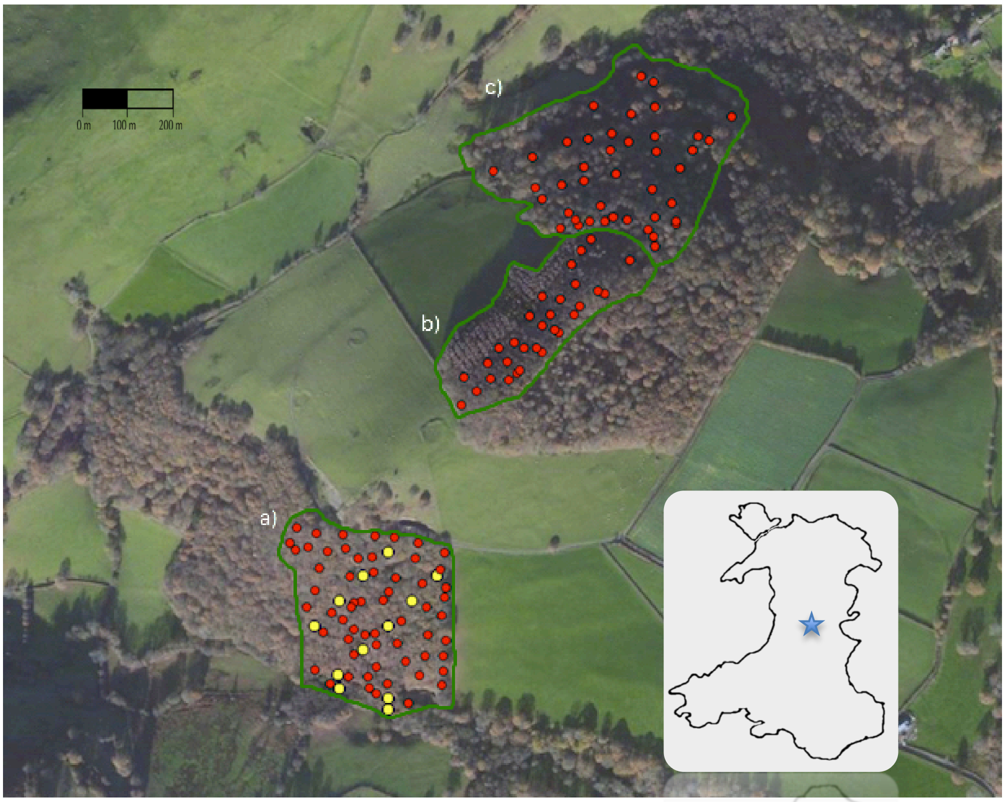

Figure 3.1 Tŷ Mawr farm near Llysdinam, Wales. a) Tŷ Mawr Redwood, b) Tŷ Mawr Ridge and c) Tŷ Mawr Bank. Red dots indicate nest box location and yellow dots indicate sticky trap and frass trap invertebrate-sampling locations.

3.3.2 Weather

Daily mean temperatures, total daily rainfall and the number of frost events per month were obtained from the Llysdinam Field Centre weather station (1.5 km away from Ty Mawr woodland).

Four iButton temperature loggers [Thermochron High Res, iButtonLink LLC] were deployed within the Tŷ Mawr woodland, between March and June, in 2017 and 2018. Due to incomplete data, temperature data for Tŷ Mawr were not available consistently throughout the three years. In order to validate the use of temperature data from a nearby weather station (Llysdinam), Temperatures recorded *in situ* at Tŷ Mawr were compared with daily mean temperatures from the Llysdinam weather station. I used GLMs to examine the difference in mean temperature between the two locations, and a linear regression to examine the association between temperatures at the two locations. As the temperatures at the two sites were strongly positively correlated (slope ± S.E. = 0.856 ± 0.037, t = 23.003, $p < 0.0001$), and as no significant differences in temperatures between Llysdinam and Tŷ Mawr were found (mean difference = 0.047 °C, $t_{423.93} = 1.285$, p = 0.1994), the temperatures recorded at Llysdinam were used in subsequent analyses.

Llysdinam temperature data from March 1st to June 30th in each year were included in the subsequent analyses. Integrative measures of temperature and rainfall across duration of each nest were calculated as i) cumulative rainfall (mm) and ii) cumulative daily temperature for the estimated life time of each chick. Life time was calculated as the Julian day of the first egg date, plus the clutch size, plus 14 days for incubation and 14 days for growth until fledging. For an average clutch of seven eggs this is a period of 35 days. Temperature (°C) was summed across the relevant period for each chick.

A Degree-Day is the number of degrees above a given threshold, e.g. 11°C for a 10°C threshold (the threshold for invertebrate development) equals 1 Degree-Day. All Degree-Day values were summed across the focal period (1st March-30th June), for minimum grass temperature and mean daily air temperature.

3.3.3 Invertebrates

Relative abundance of flying invertebrates was recorded using plastic sticky traps (100 mm x 55 mm) [Greenhouse sticky traps, Dragonfli Ltd., Michigan], placed inside wire mesh cages (mesh size = 10 x 10 mm) and attached to trees 1 m from the ground. Twelve traps were placed in pairs running perpendicular to the river in the Redwood section of Ty Mawr woodland. The traps were retrieved and replaced weekly, and stored inside transparent plastic wallets at room temperature. Invertebrates were identified to order level, separated into size classes and counted. Size classes were <2 mm (small), 2-5 mm (medium) and >5 mm (large). An index of cumulative fly abundance during the lifetime of the chick was calculated as the mean total number of small flies available, across all traps, for the 14-day window when the chick was in the nest.

Caterpillar faeces (hereafter referred to as "frass"), were used to calculate caterpillar biomass. Frass was collected in twelve frass traps (fabric squares suspended on square wooden frames measuring 50 cm x 50 cm) which were built using techniques adapted from Hinks *et al.* (2015). Frass traps were positioned at the same location as the sticky traps and suspended 1 - 1.5 m from the ground, with one side of the frame positioned against the tree which provided stability against wind. The centre of the muslin square was weighed down to prevent the muslin material from billowing and ejecting the frass. Each frass trap was emptied weekly, between April and July in all years, with all captured material being removed, stored in 25 ml Universal sample tubes [Sarstedt, Nümbrecht], and oven-dried for a minimum of 24 hours before being stored as per Hinks *et al*. (2015) to remove any non-frass material. Before processing, samples were re-dried for 24 hours, then sorted from debris and weighed to 0.01g. Weekly values were divided by seven to give daily masses. Frass mass was converted to caterpillar biomass using the equation presented by Tinbergen and Dietz (1994): biomass ($mg/m^2/day$) = 24.38 x F -0.767 x F x T, when F = frass ($mg\ m^{-2}$) and T = Temperature (°C). The frass traps used in Tinbergen and Dietz's calculation were placed 1m from the trunk of the tree. My data are therefore not completely comparable between studies, but they are comparable within my study (e.g. for examining seasonal changes across the same twelve traps). Caterpillar biomass has widely been used as an index of food availability in the study of timing of breeding in insectivorous birds (see (Visser *et al.* 2006; Scholl *et al.* 2016; Burgess *et al.* 2018). Caterpillar biomass was converted into caterpillar abundance by dividing biomass by the mean mass of a caterpillar (taken to be 45.94 mg, following (Tikkanen *et al.* 2000).

3.3.4 Birds

There were 153 nest boxes checked during the study with 63, 40 & 50 in Redwood, Ridge and Bank respectively, resulting in a density of 19, 23 and 15 boxes per hectare. Nest boxes had internal dimensions of 90 x 110 x 170 mm, and an entrance hole diameter of 32 mm. Those with damaged fronts increasing the size of the hole had a metal plate placed to restrict the hole diameter to 32 mm. Most boxes had been in place for >10 years prior to the start of the present study. Where necessary, boxes were replaced with new ones, but there was no difference in the frequency of use between new and old boxes (pers. obs.) as has been shown for other hole-nesting species of woodland birds (Hipkiss *et al.* 2013).

Nest checking protocols were in accordance with the BTO Nest Record Scheme (Crick *et al.* 2003) to minimise impact on the birds and the risk of increased predation (Arroyo *et al.* 2017). Boxes were visited twice per week, unless additional nest box visits were conducted in order to ring the adult females, and to ring the chicks when seven days old. A range of demographic parameters were recorded, including first egg date, clutch completion, hatching and fledging success, and clutch size and number of fledglings. From this dataset, survival of nests and breeding success could be calculated. Nests were considered to be occupied if egg laying was initiated and those nests from which a chick fledged were considered successful. If laying date was not recorded directly, then it was estimated based on an assumption of one egg laid per day, and incubation starting from the day of completion of the clutch (Yom-Tov *et al.* 2000; Slagsvold 2004). If a female was found to be brooding young and the laying date was unknown, then the calculation was based on an assumption of one egg per day plus 14 days for incubation, plus the apparent age of the chicks (Laaksonen *et al.* 2006). Maximum clutch and brood sizes were observed by nest box checks.

3.3.5 Statistical analysis

All analyses were conducted using R Statistical Software (R Core Team 2018) with additional packages lme4 (Bates *et al.* 2015) and mgcv (Wood 2011) being used for linear and non-linear models, respectively. The packages dplyr (Wickham *et al.* 2018) and tidyr (Wickham and Henry 2018) were used to handle data and ggplot2 (Wickham 2016), RColorBrewer (Neuwirth 2014) and gridExtra (Auguie 2017) were used to create graphics. Initial model error distribution and link functions were selected following methods in Thomas *et al.* (2017) with link function selection refined using comparisons of Akaike Information Criterion (AIC) values, with selection of the link function giving the lowest AIC.

3.3.5.1 Models of temperature and rainfall

Seasonal and yearly patterns in mean air temperature and total rainfall were each modelled as dependent variables using General Additive Models (GAMs) using Gaussian and Gamma error distributions respectively and log link transformations. Julian day, as an independent variable, was represented with a thin plate spline, with the degree of non-linearity selected using generalised cross validation (Wood 2006). Year was included as a categorical term, and the model included the 2-way interaction between year and Julian day. All terms were significant and so no model refinement was needed.

3.3.5.2 Calculating seasonal invertebrate abundance in relation to weather

Trends in invertebrate abundance collected by using frass and sticky traps were analysed using Generalised Additive Mixed Models (GAMMs). Abundance of small flies (dependent variable) caught on sticky traps were analysed using a negative binomial error distribution and log link function. Julian day (smoothed independent variable) was represented with a thin plate spline, with the degree of non-linearity selected using generalised cross validation (Wood 2006). Year was included as a independent categorical variable to explain inter-annual variation. The model included the 2-way interaction between year and Julian day. Mean weekly air temperature and mean weekly rainfall were included as fixed covariates, as well as the 2-way interaction between temperature and rainfall. The sampling location was included as a random term to control for any spatial variation across the woodlands and to account for the repeated measurements from each location. Traps were not positioned to sample individual bird territories, but rather to estimate the overall abundance of invertebrates across the sampling area. An ANOVA between models which included trap location and those which didn't showed no significant difference indicating that trap location was not a significant predictor of frass abundance. Spatial autocorrelation was therefore controlled for in the final model by inclusion of the trap location as a random term. Fixed term model selection and degree of smoothness were also refined based on lowest AIC.

The association between Pied Flycatcher laying date (dependent variable) and the seasonal abundance of small flies (smoothed independent term) was modelled using a GAMM (Poisson error family, log link function). In addition to fly abundance being used as a fixed effect, the sampling year, the 2-way interaction between fly abundance and year, clutch size, cumulative temperature of the 14 days prior to laying and quantity of rainfall for the same 14 days and the 2-way interaction between temperature and rainfall were all included as candidate fixed effects. Model refinement was based on lowest AIC. Residual deviance was calculated by comparing the final GAMM with the null model GAMM. The most parsimonious model after refinement resulted in laying date (dependent variable) being explained by the cumulative temperature (independent variable) and the year (categorical independent variable).

Caterpillar frass (dry weight) or biomass (dependent variable) were modelled using a Gamma error distribution and log link function. Caterpillar models were run first run using frass dry weight as the dependent variable and secondly using caterpillar biomass as the dependent variable (calculated from frass dry weight and temperature using the Tinbergen and Dietz (1994) equation in section 3.3.3). These models were qualitatively the same with regards to the direction and significance of the relationships described. Caterpillar biomass was used in subsequent models and graphics as a more ecologically relevant dependent variable. All independent variables used in the fly models, above, were incorporated into the final caterpillar biomass model.

The fledging success of Pied Flycatchers was calculated by creating a two-dimensional matrix of the number of chicks which fledged, in relation to the number of chicks which failed to fledge. This was then used as the dependent variable in a GLMM, with a binomial error family and a complementary log-log link function. Due to the synchrony of hatching and fledging of birds within a nest, each nest was treated as a single unit. The cumulative air temperature and the total quantity of rainfall which occurred during the life-time of chicks in each nest was calculated. Abundance of caterpillars and small flies available in the woodland were calculated as the cumulative caterpillar or fly abundance available over the lifetime of the chicks, given an estimated time to fledging of 14 days. This model tested the hypothesis that fledging success depended upon the cumulative seasonal abundance of caterpillars, flies, year, the 2-way interactions between prey and year, clutch size, life-time temperature, life-time rainfall and the two-way interaction between temperature and rainfall. The sampling location was included as a random term to control for any spatial variation across the woodlands and to account for the repeated measurements from each location. Data were excluded for individuals that fledged after the final day of invertebrate sampling. The GAMM output showed that the association between fledging success and Julian day was linear in all years. The AIC of the GAMM was compared with the AIC of a comparable Generalised Linear Mixed Models and the GAMM was shown to be more efficient and was therefore used.

3.4 Results

Mean air temperature varied significantly within and between the three years of the study (Table 3.1). Mean air temperature in March 2017 was significantly higher than that of 2016 or 2018 (Figure 3.2b) and the thermal threshold for degree-days occurred earlier in 2017 (4th May) than in 2016 and 2018 (5th May) (Figure 3.2). There was a sharp frost on 11th May 2017 (day 131) represented by a sharp drop in minimum grass temperature (Figure 3.2a) which occurred after the initial increase in caterpillar hatching (Figure 3.5b). Although frosts occurred later in 2016 and 2018 (Figure 3.2a), these occurred before the initiation of caterpillar increase and therefore did not have the same effect on caterpillar abundance (Figure 3.5b). The frost impacted caterpillars indirectly as many recently emerged Oak leaves were killed, which resulted in a shallow peak in caterpillar abundance (J Smith pers. obs.). Despite the initial steep increase in cumulative minimum temperature in 2018, there was a prolonged cold snap which returned the cumulative minimum temperature back to that of 2016 and 2017 by the beginning of May (Figure 3.2a).

Rainfall also varied significantly within and between years (Table 3.2). There was a significantly greater quantity of daily rainfall in 2016 than in 2017 but not significantly greater than in 2018 (Table 3.2).

Table 3.1 GAM to explain mean air temperature (dependent variable) in relation to the year (categorical term) and Julian day (modelled as non-linear relationship), and the 2-way interaction between year and Julian day. Deviance explained by the model = 77.9%

Independent variable	Parameter value	SE	d.f.	t	P
Year: (vs. 2016)					
2017	0.17154	0.04247	1	4.039	<0.0001
2018	-0.03174	0.05363	1	-0.592	0.554
			e.d.f.	**F**	**P**
Julian day (2016)			7.465	29.02	<0.0001
Julian day (2017)			**7.065**	34.05	<0.0001
Julian day (2018)			8.658	24.55	<0.0001

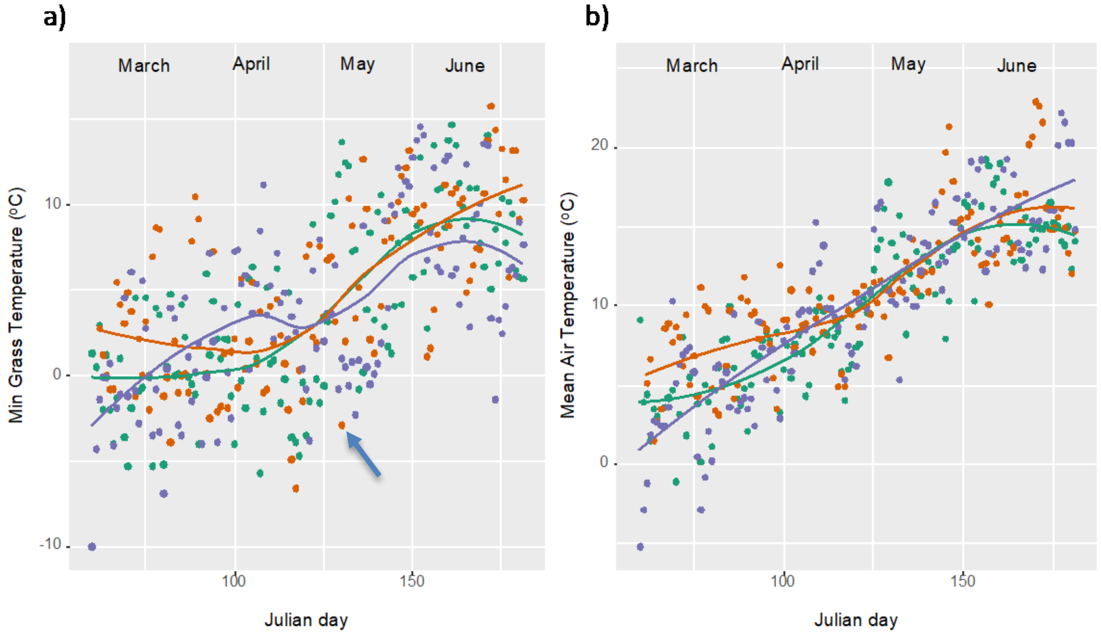

Figure 3.2 Trends in a) minimum grass and b) mean temperature change across three season. Date (1 = 1st January). Coloured lines represent modelled mean values and shaded areas represent 95% confidence intervals. Green = 2016, Orange = 2017 and Purple = 2018. Arrow indicates frost event occurring 11th May 2017.

Table 3.2 GAM to explain daily rainfall (dependent variable) in relation to the year (categorical term) and Julian day (modelled as non-linear relationships), and the 2-way interaction between year and Julian day. Deviance explained by the model = 25.0%

Independent variable	Parameter value	SE	d.f.	t	P
Year: (vs. 2016)					
2017	-1.1395	0.3244	1	-3.513	<0.0001
2018	-0.4256	0.3244	1	-1.312	0.191
			e.d.f.	**F**	**P**
Julian day (2016)			1.000	2.570	0.110
Julian day (2017)			5.781	19.638	<0.0001
Julian day (2018)			1.000	6.029	0.015

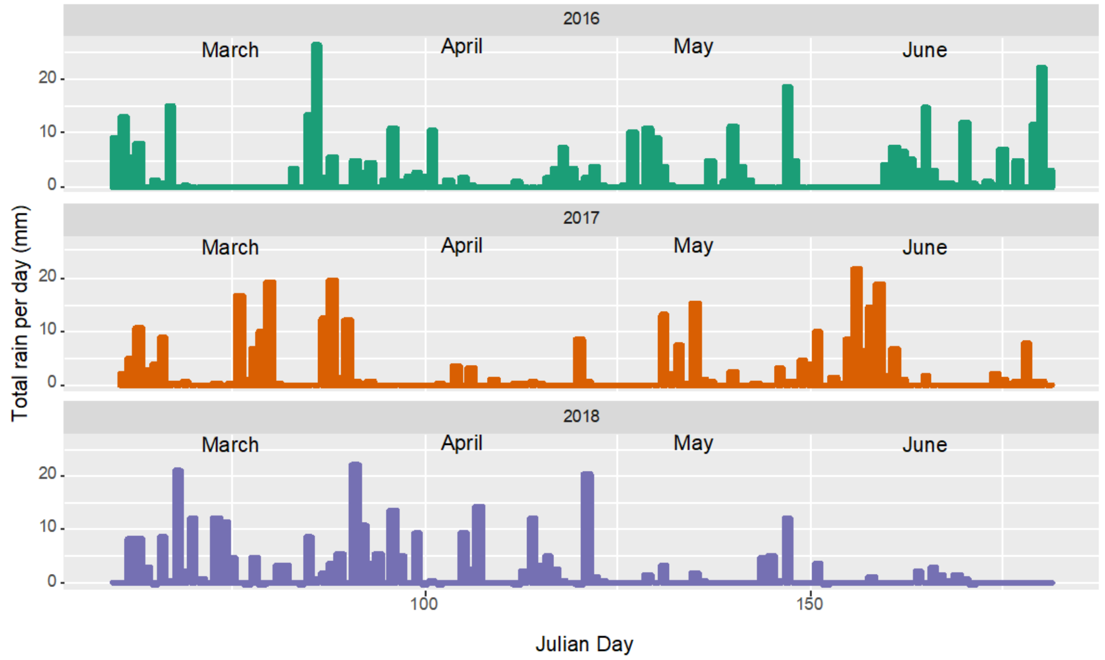

Figure 3.3 Seasonal changes in total daily rainfall across three seasons. Green = 2016, Orange = 2017 and Purple = 2018.

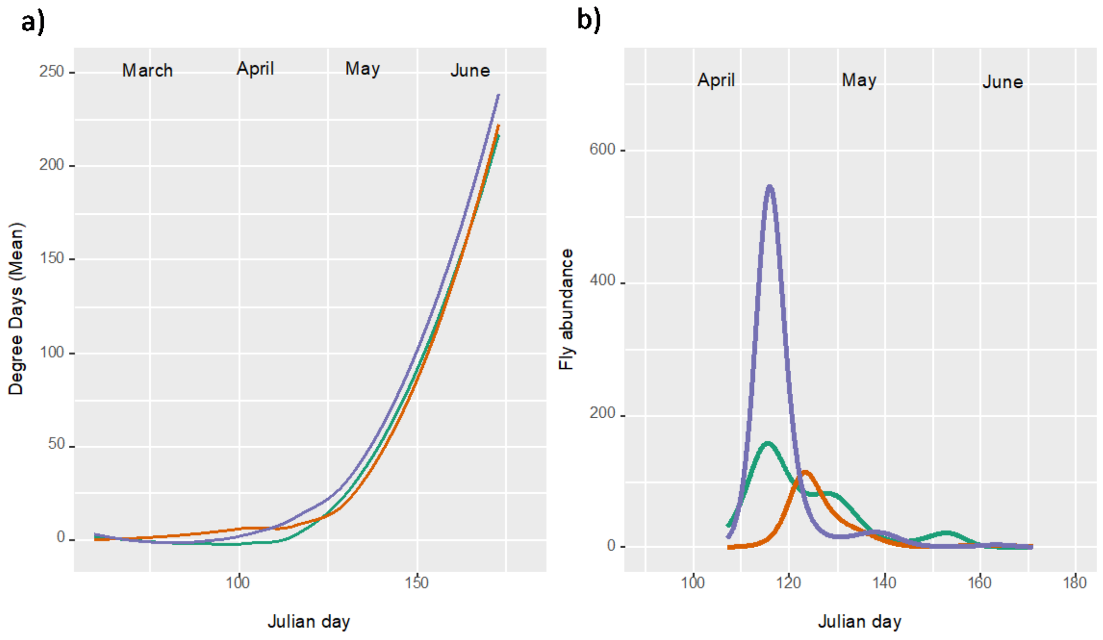

Figure 3.4 a) Seasonal accumulation of degree-days (i.e. days above 10°C), and b) Seasonal abundance of flies smaller than 2mm, across three seasons. Coloured lines represent modelled mean values and shaded areas represent 95% confidence intervals. Green = 2016, Orange = 2017 and Purple = 2018.

3.4.1 Weather and invertebrates

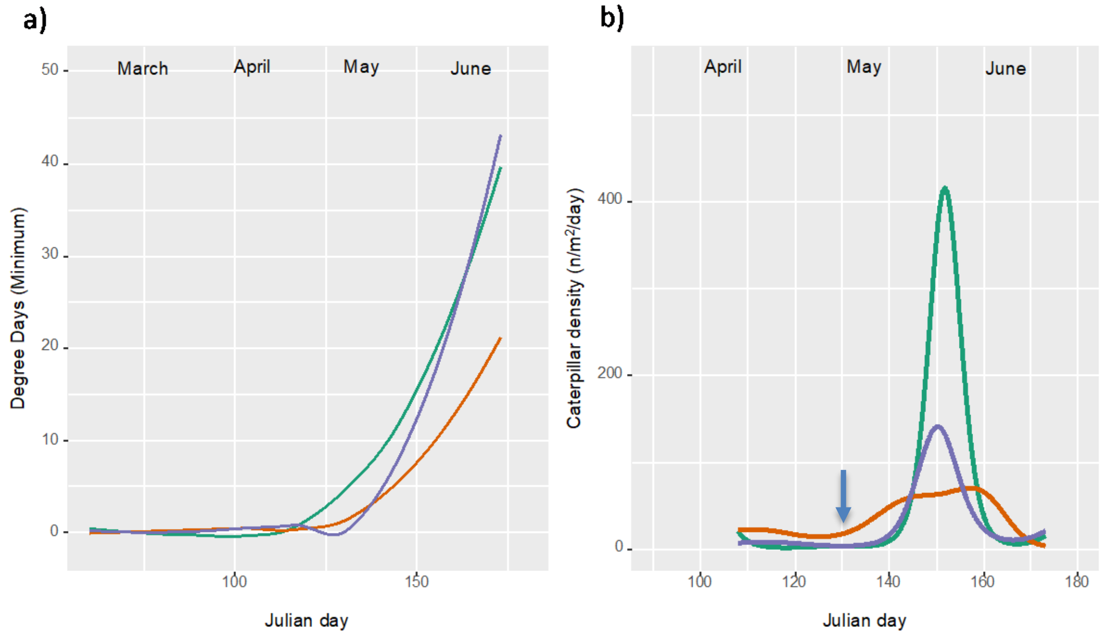

Figure 3.5 a) Minimum ground temperature measured in degree days (cumulative number of degrees above 10 °C, since Jan 1st) between March and June, across three seasons. b) Mean density of caterpillars (abundance per m^2 per day) across three seasons. Coloured lines represent modelled mean values and shaded areas represent 95% confidence intervals. Green = 2016, Orange = 2017 and Purple = 2018. Arrow indicates frost event occurring 11th May 2017.

By the end of June the mean air temperature in each year was similar, but through the breeding season the rate of increase differed (Figure 3.2). Temperatures in 2017 were higher initially but the rate of increase during the season was lower (Figure 3.2), associated with a lower abundance of caterpillars compared with the other two years (Figure 3.5b). Caterpillar abundance was significantly associated with the negative interaction between rainfall and temperature. In other words, the positive effect on caterpillar abundance of increased temperature was reduced under high rainfall and vice-versa (Table 3.3).

Table 3.3 GAMM to explain caterpillar abundance (dependent variable) in relation to the abundance of Julian day (modelled as non-linear relationships), daily mean air temperature and daily rainfall conditions, year (categorical term), the 2-way interaction between temperature and rainfall. Deviance explained by the model = 82.5%

Independent variable	Parameter value	SE	d.f.	t	P
Rainfall	0.480	0.241	1	1.992	0.047
Temperature	0.212	0.064	1	3.317	0.001
Rainfall:Temp	-0.054	0.018	1	-2.978	0.00313
Year: (vs. 2016)					
2017	0.632	0.104	1	6.068	<0.0001
2018	0.005	0.142	1	0.036	0.97144
			e.d.f.	**F**	**P**
Julian day:Year (2016)			5.900	61.77	<0.0001
Julian day:Year (2017)			5.153	23.98	<0.0001
Julian day:Year (2018)			5.749	26.45	<0.0001

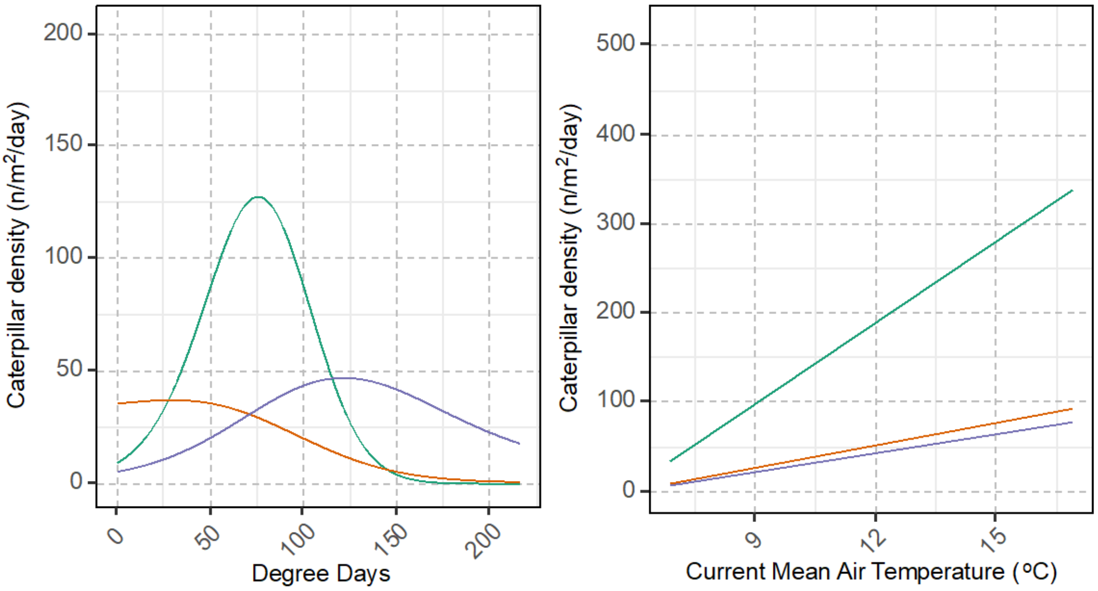

Figure 3.6 a) Changes in caterpillar density with degree days above 10°C. b) Changes in caterpillar density with observed tempartures, across three seasons. Coloured lines represent modelled mean values and shaded areas represent 95% confidence intervals. Green = 2016, Orange = 2017 and Purple = 2018.

3.4.2 Bird breeding parameters and phenology

The number of Pied Flycatcher nests within the 153 nest boxes in the woodland study area was 48 in both 2016 and 2017, and 53 in 2018 (Table 3.4). Pied Flycatcher first arrival dates in Ty Mawr woodland in 2016-2018 were April 13th, 4th and 9th respectively. First egg dates were 9th May, 28th April and 6th May, resulting in an interval of 34, 24 and 33 days in 2016-2018 respectively.

Table 3.4 Nest box occupancy and breeding demographics of Pied Flycatchers in Tŷ Mawr woodland, 2016-2018

Year	No. of Nests	Nest box Occupancy (%)	Mean Clutch size	Mean Brood size	Mean no. Fledglings	Fledging success (%)	Total number of fledglings from the population
2016	48	31.4	6.41	5.54	4.98	68.2	210
2017	48	31.4	7.12	6.43	5.04	70.4	241
2018	53	35.3	6.20	5.50	5.20	73.8	220

Mean laying date was earliest in 2017 and latest in 2016. A GLMM analysis (Table 3.5) showed that laying date was significantly associated with the cumulative temperature in the 14 days prior to laying and the year in which laying occurred but was not significantly associated with the seasonal variation in the abundance of small flies or the abundance of rainfall in the period prior to laying. Mean laying was ~5 days earlier in 2017 than 2016 and ~2 days earlier in 2018 than 2016 (Table 3.5). Timing of egg laying differed significantly between years, with laying occurring significantly earlier in 2017 (Table 3.5).

Table 3.5 GLMM to explain laying date (dependent variable) in relation to the cumulative temperature over the 14 days prior to laying and between-year differences across the three years of the study (2016-18). Cumulative abundance of flies, rainfall and clutch size, were not significant and so were not retained in the final model (P > 0.05). Deviance explained by the model = 11.5%.

Independent variable	Parameter value	SE	z	p
Temperature	+0.0007	0.0002	2.948	0.003 **
2017	-0.040	0.019	-2.080	0.038 *
2018	-0.021	0.018	-1.123	0.261

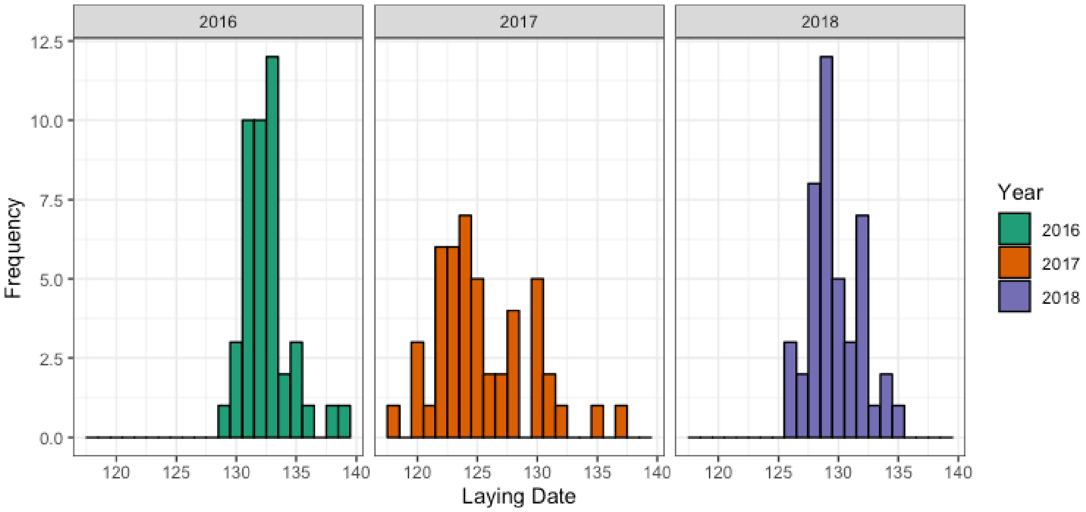

Figure 3.7 Timing of egg laying initiation. Date 1 = January 1st.

Laying dates were more variable in 2017 than in 2016 or 2018; they ranged from 9th May – 19th May (10 days) in 2016, 28th April – 17th May (19 days) in 2017, and 6th May – 15th May (9 days) in 2018 (Figure 3.7). The peak number of pairs laying on any one day was 12 in 2016 and 2018, and 7 in 2017. First egg date was 11 days earlier in 2017 than 2016 and 8 days earlier than in 2018. Earlier laying resulted in earlier hatching and earlier peak food-demand of chicks. A greater mis-match between peak chick food requirement and caterpillar availability was associated with lower fledging success (Table 3.6).

Table 3.6 Annual summary of temporal patterns of birds and caterpillars in nesting period. Dates are reported in Julian days. Mis-match is reported in days, demand is earlier (+) or later (-) than food availability.

Year	Laying date	Hatching date	Peak caterpillar date	Peak requirements	Mis-match (days)	Fledging Success (%)
2016	133	153/154	152	160	-8	68.2
2017	124	145	159	152	+7	70.4
2018	129	149	150	156	-6	73.8

3.4.3 Variation in Fledging success in relation to weather and caterpillar abundance

Chick fledging success was significantly associated with clutch size, temperature and rainfall and their interaction as well as caterpillar abundance and varied between years (Table 3.7). Fledging success was significantly higher in 2018 than in 2017 or 2016 (Table 3.7) and was highly positively correlated with the abundance of caterpillars available during the lifetime of the chick in the nest. This effect was stronger in 2017 than in 2016 or 2018. Chicks in larger broods had a higher probability of fledging. Fledging success was influenced by temperature and rainfall and their 2-way interaction.

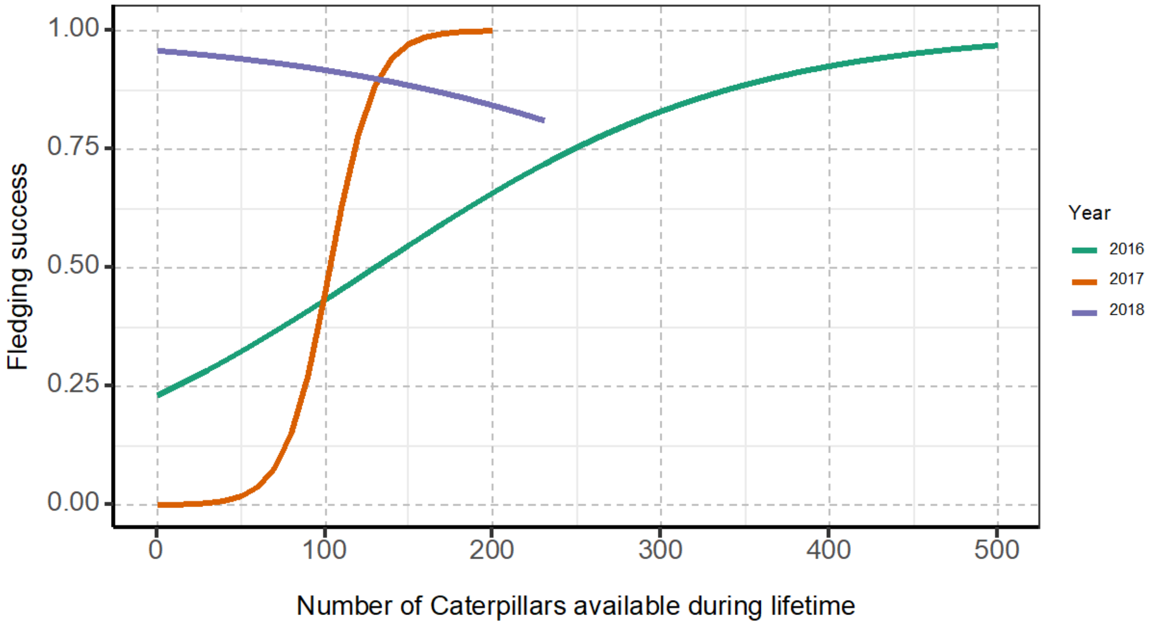

Figure 3.8 Proportional fledging success per nest in 2016 - 2018 in relation to caterpillar abundance. Coloured lines represent modelled mean values and grey areas represent 95% confidence intervals. Green = 2016, Red = 2017 and Blue = 2018.

There was a significant positive association between fledging success and caterpillar abundance, this association was strongest in 2017 (Figure 3.8). but there was a negative association between fledging success and rainfall but this was mediated by temperature (Table 3.7). As there was significantly less rainfall in 2018 the fledging success of the later birds was lower (Figure 3.8).

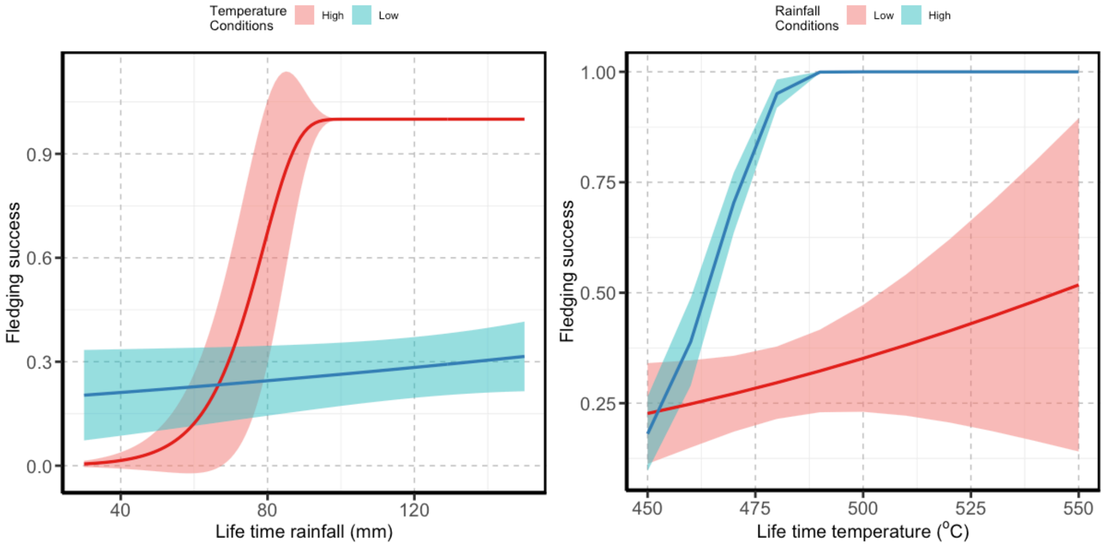

Figure 3.9 Fledging success at a) two different rainfall categories across a range of temperature measurements and b) two different temperature categories across a range of rainfall measurements.

If there is high rainfall in a year, then as long as a threshold lifetime cumulative thermal value of 490°C is reached then fledging success will be high. If there is low rainfall, then a cumulative temperature value of 100°C will increase the mean probability of fledging by 25% (Figure 3.9a).

The effect of rainfall on fledging success is highly dependent on temperature. If temperature is low then the effect on fledging success is minimal (10%) whereas if the temperature is high the difference in rainfall can result in a difference between complete failure (0%) and complete success (100%) (Figure 3.9b).

Table 3.7 GLMM to explain fledging success (dependent variable) in relation to caterpillar abundance, clutch size, temperature and rainfall conditions across the chick's lifetime, the interaction between temperature and rainfall and between-year differences across the three years of the study (2016-18). Delta marginal R^2 = 25.9%.

Independent variable	Parameter value	SE	d.f.	z	P
Caterpillars	0.009	0.002	1	3.931	<0.0001
Year: (vs. 2016)					
2017	-8.603	1.475	1	-5.833	<0.0001
2018	12.314	2.835	1	4.343	<0.0001
Clutch	1.006	0.147	1	6.848	<0.0001
Temperature	-0.165	0.050	1	-3.290	0.001
Rainfall	-1.110	0.226	1	-4.921	<0.0001
Rainfall: Temp	0.002	0.0004	1	5.070	<0.0001
Caterpillars: (vs. 2016)					
2017	0.065	0.010	1	6.471	<0.0001
2018	-0.017	0.011	1	-1.488	0.136

3.5 Discussion

The present study has shown the relationships between weather and food availability for Pied Flycatchers, and the relationships between food availability and Pied Flycatcher breeding parameters, ultimately influencing overall breeding productivity of the birds. These relationships are important for understanding the cascading impacts of climate variation across trophic levels in the woodland ecosystem.

3.5.1 Weather variation

There was substantial variation between years in progression of changes in weather variables between March and June, prior to arrival of Pied Flycatchers at the study site, until the majority of their chicks had fledged. Spring warming in 2017 was earlier than in 2016 and 2018, but included a sharp frost on 11th May, just as caterpillars were starting to increase in abundance (Figure 3.3). Rainfall also varied between years; 2016 was wettest, with rainfall distributed more evenly across the study period, whereas 2018 was driest, with most rainfall concentrated in March and early April (Figure 3.3).

3.5.2 Invertebrate abundance and phenology

The rate of accumulation of mean degree-days in April was highest in 2018, which coincided with a higher peak abundance of small flying invertebrates than in 2016 or 2017 (Figure 3.4). Recording of flying invertebrates only began after the Pied Flycatcher arrival on their breeding territories (day 110 onwards), and we cannot discount the possibility that an earlier peak in 2017 may have occurred prior to the start of sampling, given the relatively early increase in degree-days in March-April 2017 (Figure 3.4). This may be particularly likely for univoltine species of Hymenoptera and Diptera, which have a bimodal emergence; the first peak due to emergence of the males and the second peak for the females (Forbes *et al.* 2010).

The emergence of budding leaves, and the herbivorous invertebrates which feed on them (Blondel *et al.* 1993), is closely tied to local weather conditions (Meineke *et al.* 2018). Earlier increases in spring temperatures result in earlier Oak bud-burst, and emergence of leaf-feeding caterpillars (Visser and Holleman 2001). In the present study, mean degree-days accumulated slightly earlier in 2017 than in 2016 and 2018. Likewise, caterpillar emergence was earliest in 2017, but followed by the sharp frost in early May described above. A previous study in the Netherlands showed that a frost which occurred between 18 and 21st April damaged leaves and killed caterpillars (Both *et al.* 2009). Frost occurring during caterpillar growth therefore results in mortality of caterpillars (Abarca *et al.* 2018), and the frost in May 2017 was followed by a slower increase and a lower peak caterpillar abundance than in either 2016 or 2018. The timing of frost may be very important. If frost occurs, in early May, when the oak leaves are emerging and not frost resistant then they can freeze and wither as happened in 2017 (J Smith pers. obs.). The effect of this is that food availability for caterpillars is severely reduced reducing their ability to survive or grow (Both *et al.* 2009). The reduction in biomass of caterpillars can then have a direct impact on flycatcher productivity due to the reduction in food availability for chicks. In 2017 the frost occurred at a time when leaves were emerging and had ramifications on caterpillar biomass throughout the breeding season. All chicks in 2017 could have been affected. If the last frost occurred prior to the oak leaves emerging, as happened in 2016 and 2018, then there would have been little to no effect (indirect or direct) on the flycatcher breeding performance. Overall caterpillar abundance was highest in 2016, which notably had a much more rapid accumulation of minimum degree-days than occurred in 2017 and 2018.

Overall, both flies and caterpillars appeared to show between-year differences in seasonal abundance that were broadly associated with between-year differences in spring warming -particularly the rate of accumulation of degree-days (specifically regarding mean degree-days for flies, and minimum degree-days for caterpillars) and for caterpillars, an additional effect of current air temperature (Figure 3.5b). Although these associations do not demonstrate causation, it is striking that the observed differences in spring warming between the three years are consistent with the expected responses of invertebrates, given the previous literature on this subject. Differences between taxa in responses to weather are to be expected, given that temperature thresholds for development themselves differ between taxa (e.g. ~2°C for flies and ~10°C for caterpillars (Johansen 1990).

3.5.3 Pied Flycatcher breeding phenology

Prior to the chick-rearing phase, caterpillars are yet to have emerged. During this period, adult Pied Flycatchers have a much higher proportion of small flying invertebrates in their diet than during the chick-provisioning stage, when both adult and nestling diet is dominated by caterpillars (Stowe 1987). The nutrient content of these flying invertebrates provides high levels of calcium, good for egg deposition, leading to high hatching success (Bidwell and Dawson 2005) but was not shown to influence laying date.

The mean laying date of flycatchers was earlier in 2017, and laying dates were less synchronised, than in either 2016 or 2018 (Figure 3.7). This between-year variation in laying date appears to be linked to weather conditions and food availability in the pre-laying period, since 2017 was an earlier spring, with earlier caterpillar emergence (Figure 3.5). It is not clear, however, that the phenology of small flying invertebrates was earlier in 2017, as discussed above. Some of the flexibility in the timing of laying date relates to the time intervals between arrival, nest building, and egg laying. The variation in laying dates between years shows that Pied Flycatchers have some capacity for behavioural plasticity in the timing of laying. We did not measure the time between nests being built and laying in the present study, but in deciduous woodland in Sweden there was a mean interval of 6.1 days (Lundberg *et al.* 1981a), implying that birds could advance their egg laying by up to 6 days by reducing this interval.

The degree of mis-match experienced by the birds ranged from chick demand peaking on average seven days before the peak availability in caterpillar abundance in 2017, to eight days after the peak availability in 2016. The smaller the mis-match the greater the abundance of caterpillars in the diet of Pied Flycatcher nestlings (Sanz 1998), and in the present study a greater abundance of caterpillars was associated with a higher fledging success (Figure 3.8). Specifically, the smallest mis-match in 2018 (six days) was followed by the highest fledging success and the largest total number of fledglings produced from the study site (Table 3.6). Mis-match between migrant woodland species and peak availability of food has been demonstrated in the Netherlands (Both *et al.* 2009). Resident species accurately adjusted their timing of breeding to match peak food availability, whereas migrants failed to do so (Resident mis-match: 0 days (Great Tit), 2 days (Blue Tit) and 14 days (Pied Flycatcher)).

In the present study, mean annual hatching success remained relatively constant at between 86% and 90% across the three-year study period. Likewise, mean annual fledging success was relatively stable, at between 68.2% and 73.8% of eggs resulting in a fledged chick. However, mean annual clutch size varied between 6.2 and 7.1 eggs across the three years, so mean brood size was larger (by ~1 chick per brood) in 2017 than in 2018. Likewise, the number of occupied nests varied between 48 in 2016 and 2017, and 53 in 2018. The additive effect of these variations in the number of breeding attempts and demographic parameters together have implications for the total number of fledglings produced by the population of Pied Flycatchers within our study site. This varied between 226 and 250 fledglings across the three years. The highest number of fledglings was achieved in 2018, when clutch size was low but number of nests and fledging success were high, demonstrating that a higher number of nests and a higher fledging success were more important than higher clutch sizes in producing more fledglings for the population.

The interacting effects of temperature and rainfall are shown in Figure 3.9. Under high rainfall conditions, fledging success was highly temperature-dependent. At low cumulative temperatures and high rainfall, small increases in temperature significantly improved fledging probability, up to a threshold cumulative temperature of 490°C, above which, fledging success was 100% (Figure 3.9b). Under low rainfall conditions the effect of temperature on fledging success was much reduced (Figure 3.9b). Conversely, under high temperature conditions, high rainfall appears to be required for high fledging success (Figure 3.9a), whereas very dry conditions result in extremely low fledging success, irrespective of temperature (Figure 3.9a). Under high spring temperatures, the most significant change in fledging probability occurs between 40 and 90mm of rainfall over the chick's nestling period. During conditions of low temperature, fledging success was low and was largely unaffected by rainfall (Figure 3.9a).

Seasonal timing of breeding to coincide with abundances of prey species has been reported many times (Slagsvold 1975; Both *et al.* 2009). In 2017, when caterpillar density was lower but the peak was maintained for a longer period of time (Figure 3.5), Pied Flycatcher fledging success was positively associated with caterpillar abundance (Figure 3.9). This positive association was strongest in 2017 but was not evident in 2018. This lack of an effect of caterpillar density in 2018 may be due to the near ideal combination of weather conditions across the breeding season (wet April and May, dry and warm June, Chapter 2) combined with a low degree of mis-match between peak chick demand and peak caterpillar density (Table 3.6). These conditions potentially reduced the metabolic pressures on the nestlings, resulting in high fledging success despite the relatively low peak abundance of caterpillars in 2018. Relationships between Blue Tit fledging success and food abundance, using caterpillar frass as a proxy for caterpillar numbers, were identified by Tremblay *et al.* (2003), showing that a measure of 373 frass mg m^2 day^{-1} resulted in 100 % fledging success. If Pied Flycatchers have the same, relative to mass, requirements as Blue Tits then Pied Flycatchers would require 440 mg m^2 day^{-1} to successfully raise a chick. This equates to an available abundance of approximately 110 caterpillars m^2 day^{-1}.

This study has been conducted over a small spatial scale which required use of local temperature and rainfall measurement in contrast to broader spatial scale studies which have used patterns in the North Atlantic Oscillation (NAO) to study impacts of weather of flycatcher breeding success (Sanz 2003). Conclusions in this study show that the interaction between the weather in multiple months and not just singular months as has been reported previously (Burgess 2014) effect the timing and abundance of food availability for Pied Flycatcher breeding productivity. The interplay between temperature and rainfall also reported in Chapter 2 and reinforced here has resulted in the reporting of the overall weather in a season rather than separating out individual months.

Although the focus of this study was to identify trends between direct and indirect effects of local weather on Pied Flycatcher breeding productivity it must be noted that there are also potential carry over effects from the other aspects of the annual cycle, particularly weather on the wintering grounds (Saino *et al.* 2011). Brood size in Common Redstart, for example, has been shown to increase with increased rainfall in the Sahel, in comparison with no change in response to weather conditions during the breeding season (Finch *et al.* 2014).

The interconnected nature of woodland ecosystems means that demographic changes such as laying date not only have an impact on individuals and intraspecific interactions (Burgess *et al.* 2018) but also on interspecific relationships too (Both *et al.* 2009). Broadleaf upland woodlands contain a community of bird species whose energetic demands overlap temporally as well as spatially and so inter specific synchrony of breeding may contribute to variation in breeding success. The impacts of breeding synchrony and the additive effects of weather variables adds significant ecological stress in a habitat, such as woodlands, which has a short period of peak food abundance (Sheldon). In other habitats where food availability exists at a lower level but over a much broader peak these same constraints do not have such strong impacts (Seward *et al.* 2014; Vafidis *et al.* 2016).

3.5.4 Overall conclusions

This study has provided evidence that variation in Pied Flycatcher fledging success is both directly and indirectly (via food availability) effected by temperature and rainfall. It has also provided evidence that increased abundance of small flying invertebrates can advance egg laying date and increased Lepidopteran caterpillar abundance can increase fledging success. Overall, the smaller the phenological mis-match between peak chick food demand and caterpillar availability, the higher the fledging success, with an additive effect of temperature and rainfall.

4 Integral Projection Model (IPM) of Pied Flycatcher Demography and Population Dynamics

4.1 Abstract

Declines in Pied Flycatcher breeding populations have been well documented, but until now few attempts have been made to predict future population trends in response to changing environmental variables. Annual variation in food availability and weather conditions drive decisions about the timing of egg laying. Here I identify the demographic consequences that laying date can have on a focal Pied Flycatcher population in South Wales, using laying date to predict annual adult survival and recruitment, as well as examining changes in the timing of breeding from one year to the next and from generation to generation. Laying date had a significant effect on adult survival and fledging success, with early-laying birds having a higher probability of surviving, a longer life expectancy and higher fledging success. The ongoing population decline in the study population is predicted to continue; under current demographic parameters the study population is projected to go extinct within the next 15 years, but potentially in the next five years depending on inter-annual variation in breeding conditions. Sensitivity analysis of demographic processes revealed that increased inter-annual survival of early laying birds would result in potential population growth. Additionally, a greater consistency in laying dates between years of early laying individuals appears to be the strongest mechanisms by which this population could avoid extinction in the longer term.

4.2 Introduction

Monitoring of population trends of organisms is well established for a wide range of taxa (e.g. birds, butterflies, moths, some mammals), but most studies have focused on reporting the abundance of a species (Gross *et al.* 2007; Hayhow *et al.* 2015) and describing historic patterns of population change, rather than projecting future changes. These studies have been essential to record the decline of many species, leading to research addressing the causes of decline, and identifying potential conservation actions (Goodenough *et al.* 2009). An extension of these studies of abundance is to estimate the impacts of vital rates such as survival and reproduction in driving these trends. Combining patterns in abundance and changes in vital rates into a modelling framework provides greater insight into the causes of population trajectories. Using statistical modelling it is also possible to test the sensitivity of each of the parameters to predict responses in population trends to future conditions.

Studies of demographic parameters often overlook variation in these parameters when assessing population trajectories. Plasticity in behavioural traits such timing of breeding and variation in survival rates is important to quantify and incorporate into the modelling process. Such studies present the opportunity to construct population models, integrating population changes and the demographic parameters underlying them. Such models can be used (i) to understand past and current population trends, (ii) to forecast future trends, (iii) to identify the primary demographic drivers of these trends, (iv) to explore the sensitivity of different parameters to environmental change, in order to (v) design effective conservation strategies for declining populations in the face of ongoing environmental change.

Phenotypic plasticity in behaviour allows individuals to adapt instantaneously to changes in their local environment (Arroyo *et al.* 2017). The individuals who have the greatest plasticity will be able to adjust most effectively to environmental stressors, in order to survive and raise offspring (Clauser and McRae 2017). If the plasticity of a trait is itself heritable, then the offspring will themselves benefit from this flexibility (Serobyan and Sommer 2017). In the context of avian breeding biology, this means that a female’s ability to change the date on which egg-laying is initiated (hereafter “laying date”) to most closely match the changing climate conditions could be passed on to her offspring. Her offspring would therefore have a better chance of reproducing under variable environmental conditions than offspring who do not exhibit this plasticity. Combinations of individual behaviours result in variation in individual fitness and population-level effects with potentially large impacts. The effects of these individual behaviours can be investigated in a modelling framework.

Many different types of population models have been used to understand population trajectories, based on the traits of individuals (Individual Based Models; IBMs), or based on discrete (i.e. categorical) traits (Matrix Population Models; MPMs), and more recently using continuous labile traits (Integral Projection Models; IPMs). Individual Based Models use the properties and behaviours of individuals to answer questions which aid in determining the structure of the systems which they form (Grimm and Railsback 2005). Hundreds of studies have been published using MPMs on a diverse variety of taxa (Jones 2019) which are able to project future population sizes based upon categorical demographic classes, e.g. life-stage. Neither of these previous model structures incorporate information from individuals and population level demographics which the IPM does. The evolution of IPMs from MPMs means that by using a continuous trait (e.g. laying date), rather than a categorical trait (e.g. early/late laying) it is possible to identify the effects of variation in individual traits on population trends at a much finer resolution. One of the major novel aspects of my research is the use of IPMs for linking ecological and evolutionary processes in a declining population of birds; the Pied Flycatcher. Currently only three papers using IPMs on birds have been published, the first on resident Blue Tits (*Cyanistes caeruleus*) (Childs *et al.* 2016), the second on migrant Black-tailed Godwits (*Limosa limosa*) (Kentie *et al.* 2018) and most recently the European Hoopoe (*Upupa epops*) (Plard *et al.* 2018).

I shall be using laying date of the first egg as the continuous trait variable of interest. If earlier laying is beneficial, then eggs that are laid earlier will hatch to produce more chicks of higher quality than are produced from eggs that are laid later; this will be measured by quantifying the association between laying date and chick fledging success. Chicks which fledge first will generally have higher food availability (Visser *et al.* 2004), and so may be of higher quality than later-fledging birds, thereby increasing their survival. Fledglings which survive to the next year and reproduce successfully will provide chicks for recruitment into the population. By specifying survival rate and reproductive output *per capita*, we can estimate population growth rate. In this way, IPMs can be used to develop robust predictions of future population change, via a mechanistic (i.e. demographic) explanation of how that population change arises. Using this framework, I identify how laying date and other covariates influence survival, growth, reproduction, and how the changes in those demographic parameters affect the population size of a local population of Pied Flycatchers (Figure 4.1).

Pied Flycatchers are an important model study species because of their current decline and the abundance of published literature on them, including Chapters 2 & 3. The potential high breeding density in which Pied Flycatchers can nest provides an opportunity to acquire large sample sizes which are necessary for IPMs. In addition the medium sized clutches which are frequently laid allow for variation in success to be recorded compared to species with one offspring which either survives or doesn't (Ozgul *et al.* 2010). Pied Flycatcher breeding biology has been extensively documented, with many papers showing that breeding productivity has not declined over the past 30 years (Wright *et al.* 2004), leading to a current research focus on over-wintering survival in Africa (Ouwehand and Both 2017).

As shown in Chapter 3, there is evidence of a mis-match in timing between the maximum food requirements of the Pied Flycatcher chicks and peak food availability. How this affects the population as a whole, rather than one individual or one nest, requires a larger scale modelling approach - which I address using the IPM. I test whether the number of fledglings produced is significantly affected by the date on which the first egg was laid. I also test whether the effort expended by adults to raise young will affect their between-year survival; specifically predicting that earlier-laying birds (and their offspring) will have higher overwinter survival. The mis-match between timing of maximum prey availability and peak nestling food-demand would be smaller than for late-laying individuals, leading to less energetic stress on early-breeding parents. These pressures will impact any migrant passerine breeding in a habitat with an ephemeral timing of food availability.

In this Chapter, I combine the IPM approach of quantifying the effect that different variables (i.e. survival, growth, reproduction, inheritance) have on subsequent events (e.g. change in population size), with the General Linear Mixed Model (GLMM) approach of trying to explain what is causing variance in the variable of interest (laying date) in the first place. My aim is to identify whether there is an effect of laying date on survival through the overwintering phase and recruitment into the subsequent breeding season, with implications for population growth rate.

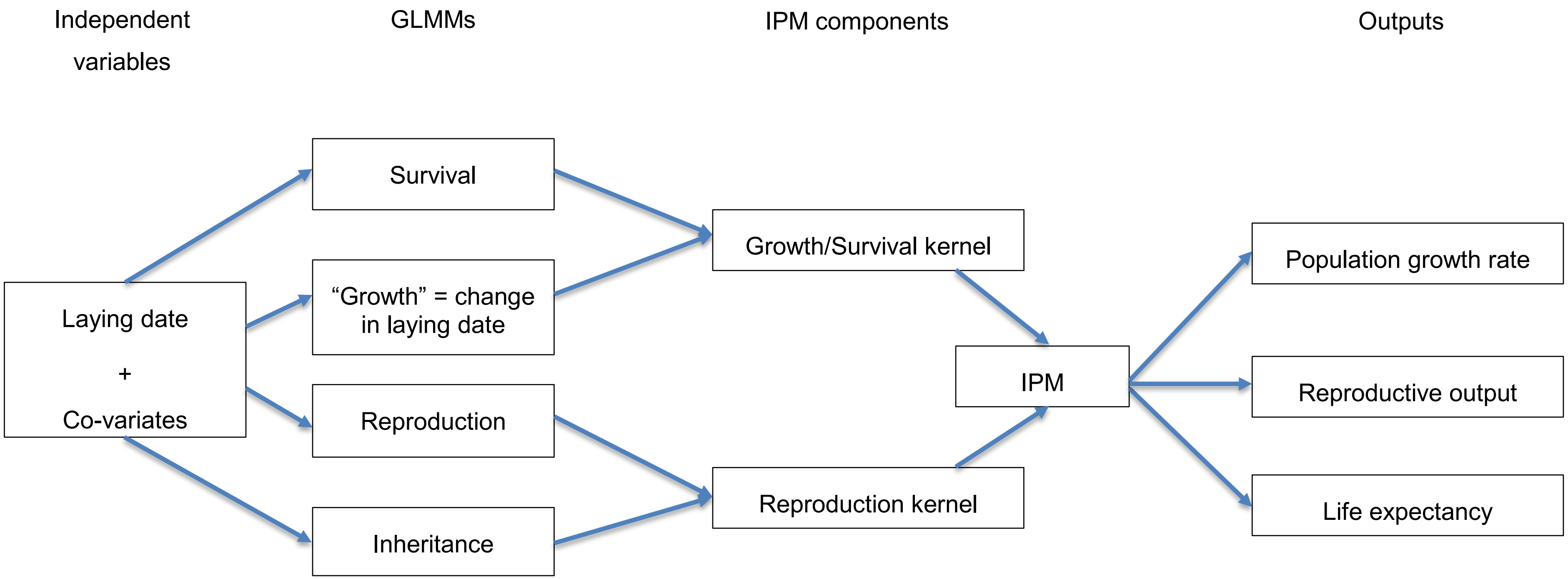

Figure 4.1 Flowchart of the structure of an IPM. The input variables include the main variable (laying date) as well as population annual mean laying date and clutch size. Intercepts and coefficients from four GLMMs are used as input variables for the IPM

4.3 Methods

4.3.1 Data set

The same dataset is used as for Chapter 2, namely variables of individual laying date, clutch size, year and female identity. In addition to the data collected, I have also calculated new variables for use in the present chapter; i) annual mean population laying date (year t), ii) individual laying date relative to the corresponding year's mean (year t), iii) annual mean population laying date (year t+1), iv) individual laying date relative to the corresponding year's mean (year t+1) and v) survival status (0 or 1). Offspring laying date was defined as the date on which they were laid as they cannot have a laying date until they have returned and recruited into the population. A study by Tomas (2015) has shown that hatching date better correlates with peak food demand in chicks. As hatching dates were not directly recorded in this citizen-science project, any attempt to calculate it would require addition of a fixed value and would therefore be nullify the purpose.

4.3.2 Overview of the IPM

The IPM is comprised of two major components, frequently described as "kernels" which are each in turn comprised of four Generalised Linear (Mixed) Models (GLMMs) (Figure 4.1). The four GLMMs represent key demographic processes influencing individual lifetime fitness and population change, namely; i) Survival, ii) Reproduction iii) "Growth" and iv) Inheritance. Each uses a labile (i.e. continuous) term as the independent trait variable. The premise is that a trait represented by a continuous variable (e.g. laying date) has a direct link to the survival of an individual, which in turn affects its reproductive output. Changes between years in an individual's expression of the trait (termed "growth") is examined in the Growth model of the IPM, and whether the trait itself, or the plasticity of the trait, is passed on between mother to daughter is investigated in the Inheritance part of the model. This variable is termed "growth" for historical reasons as the first IPMs to be developed used plant growth as the primary variable of interest. In this IPM the labile trait used is the laying date of each individual female in that year. All laying dates are reported in Julian days from January 1st, so that 1st May = day 121.

Each demographic process (e.g. Survival) was modelled using four different model structures. Model 1 contained the dependent variable (e.g. survival) and the sole independent variable of laying date. Model 2 contained laying date and mean population laying date, for survival, growth and inheritance models, and clutch size for the recruitment model. Model 3 contained the independent variables from model 2 plus the random term of "year". This controlled for inter-annual differences in environmental variables (e.g. weather).

Model 4 contained model 3 variables plus the addition of female identity as a random term. Any pseudo-replication from individuals laying in multiple years was controlled for. Appropriate error structures were used with link transformations selected based upon lowest AICs. Model 1 allowed for estimates of the impact of laying date on each function if not other variables had any affect. Inter-annual difference in environmental variables change the optimal laying date for the population. By inclusion of mean population laying date into model 2, inter-annual variation in optimum conditions was controlled for. In addition, any long-term changes in demographic parameters would be identified. The cause of this variation, however, was not completely controlled for by inclusion of mean population laying date, so remaining inter-annual variation was controlled for with the inclusion of year in model 3.

Each function identifies the impact that each individual's laying date had on demographic parameters between time t and t +1. The survival function describes the probability of an individual surviving from time t to time t +1 depending on its laying date. The recruitment function describes the number of offspring produced in year t that survive to year t + 1. The analysis focuses on identifying the expected number of offspring produced by a female having a given laying date. The laying date "growth" function describes how laying date changes among surviving individuals from year t to year t + 1. Not all surviving individuals that had the same laying date in year t will have had identical laying dates in year t + 1, meaning that for each laying date in year t there was a probability distribution of possible laying dates at time t + 1. The relationship between an individual parent's laying date and its offspring's laying date is identified using the inheritance function. The purpose with all of these functions is to calculate an estimate of the mean parameter value and variance around the mean, for each function, which can subsequently be inserted into the IPM framework.

Two different types of IPMs were run, deterministic and stochastic. The first contained only fixed terms (laying date, mean population laying date and/or clutch size) which provided instantaneous population growth estimates, without error, as they did not incorporate any variation observed between years. The second type of IPMs were stochastic models which incorporated inter-annual variation and resulted in a distribution of population trajectories. The comparisons between the deterministic and stochastic models were used to gain ecological and evolutionary insights in the population dynamics.

4.3.3 Statistical analysis

All analyses were conducted using R Statistical Software (R Core Team 2018) with the additional package lme4 (Bates *et al.* 2015) being used for generalised linear mixed models. LMERConvenienceFunctions (Tremblay and Ransijn 2015) and lmtest (Zeileis and Hothorn 2002) were used to validate GLMMs. The packages data.table (Dowle and Srinivasan 2018) and tidyverse (Wickham 2017) were used to handle data and ggplot2 (Wickham 2016), and RColorBrewer (Neuwirth 2014) and gridExtra (Auguie 2017) were used to create graphics. Code for parameterisation of the IPM has been modified from Coulson (2012) using the Matrix (Bates and Maechler 2018) package and the IPMpack package (Metcalf *et al.* 2012). Recapture and survival estimates were calculated in MARK (White and Burnham 1999) to ensure that recapture probabilities did not bias survival estimates.

4.3.3.1 Laying date – survival

In situations where not all living individuals are recorded then mark–recapture analysis has been widely used for cases (Lebreton *et al.* 1992). Annual recapture and survival probabilities were estimated using the program MARK. Mean recapture probability was 0.57 with an inter-annual range of 0.29 to 0.83, with mean survival probability (corrected for recapture probabilities) of 0.45 with a range of 0.21 to 0.94. The results obtained from MARK were very similar to those obtained from classical linearalised modelling, with regards to both survival and its relationship with laying date (Appendix 2). I, therefore, used a GLMM to identify the equation explaining individual survival. Individuals either survived or didn’t and so a binomial error structure was used.

4.3.3.2 Laying date – recruitment

Pied Flycatchers can fledge between zero and nine chicks with a maximum recorded in the Cwm Clydach dataset of nine fledglings therefore the models of reproductive success have a Poisson error structure. As chicks were hatched from one year but begin laying in the subsequent (at the earliest), a multiplication factor was used to represent an apparent survival of 0.03 or 3 % (Kern *et al.* 2014). I also ran a further two deterministic models using multiplication factor values of 0.05 and 0.07 to model the effect of higher apparent over-winter fledgling survival on population dynamics. Previous IPMs have specified whether or not an organism has bred and therefore requires an estimate of the proportion of reproductive adults in the population. In this study only reproductive females were recorded and so as the proportion of reproductive adults would be one, I have not included that element in the IPM structure.

4.3.3.3 Laying date – inter-annual change

To investigate how individuals changed their laying dates between years, I regressed laying date in year t with laying date in year t + 1. The change in laying date of an individual was calculated by squaring the residuals of the initial model (following Coulson 2012). Determining how the magnitude of this change varied with initial laying date was done by regressing the newly calculated change in laying date against the original laying date. This regression examined whether late or early laying birds who survived, advanced their laying dates more, or less, than those laying at the population mean laying date. As the change in laying dates formed a broadly normal distribution, a Gaussian error family was used. Stochastic models allowed me to examine the effect of inter-annual variation and individual level variation on the modelled parameter estimates.

4.3.3.4 Laying date – inheritance

To identify the strength of inheritance of laying dates between mothers and offspring, I regressed the laying date of offspring that recruited into the population at time t + 1 against that of their mothers at time t. As I dealt with only the female component of the population, I used maternal laying date at time t. This protocol excludes the effect of any polygamous males having multiple laying dates. Offspring inheritance was calculated by using only the subset of females who were born in Cwm Clydach, had subsequently been recruited back into the population and had laying dates recorded for subsequent years. Only the first year after hatching was used in order to remove any effect of breeding experience on laying date. Due to the small sample size available in these data, only four mother/daughter relationships were recorded, inheritance coefficients from these models were unreliable. To overcome this, values provided for an ecologically similar and closely related species, the Collard Flycatcher (*Ficedula albicollis*) from Sheldon et al. (2003) were used. As with the "growth" model, the distribution of laying dates formed a broadly normal distribution, hence a Gaussian error family was used.

4.3.3.5 IPMs

To identify how laying date affects each of the four processes above (Survival, Growth, Reproduction and Inheritance) a deterministic IPM was created. This used the intercept and laying date coefficients from model 1 from each model type to parameterize the IPM. As the breeding season for the flycatchers is between 110 to 150 days from January 1st (20th April to 30th June) this is the range of hypothetical laying dates on which I based my IPM. The first deterministic IPM (model1) allowed me to identify the direct effect of laying date on each demographic parameter, although any inter-annual variation of population mean laying date was not controlled for. This meant that effects on demographic parameters caused by variation between years in weather conditions, which resulted in “early” and “late” breeding seasons, were not accounted for. In order to do so, another deterministic IPM (model 2), which incorporated population mean laying dates and clutch size, was created. In this IPM (model 2) individual clutch size was included as an independent variable to control statistically for variation in clutch size. The two deterministic models only included fixed terms which resulted in single specific values for population growth rates. To include inter-annual variation in population projections, stochastic models were required.

Table 4.1 Fixed and random terms included in each demographic model.

Model	Fixed variable 1	Fixed variable 2	Random variable 1	Random variable 2
1	Laying date			
2	Laying date	Population mean laying date / Clutch*		
3	Laying date	Population mean laying date / Clutch*	Year	
4	Laying date	Population mean laying date / Clutch*	Year	Female ID

Two different stochastic models were created. The introduction of annual variations by inclusion of year as a random term (model 3) allowed me to identify population growth rates in hypothetically good, mean and poor years. The causes of these variations are not explicitly stated but will include direct and indirect effects of food availability and weather (Chapters 2 and 3). Including female identity into the stochastic model (model 4) allowed me to control for pseudo-replication caused by individual females laying in multiple years, as their laying dates are more likely to be similar to their previous laying dates than to the laying dates of others in the population. By perturbing stochastic models, the variation accounted for by these variables provided an opportunity to identify how population growth rate and other output variables change through time, including the probability of extinction.

Once the initial IPMs were created they could be used to identify the relative effects of changes in different demographic parameters on population level growth rates. For example, if adult over-winter survival was 1 % higher than the mean, how would this affect the population growth rate? Here I altered each input parameter by 1 % to identify the resulting change in reproductive output and population growth rate. The parameters

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* Clutch size used in recruitment model only. Population mean laying date used in other three models.

perturbed were; 1) the intercept of the model, 2) the slope of the relationship between the dependent variable and laying date and 3) the slope of the relationship between the dependent variable and the population mean. Perturbations of 1 % in parameters had different directional effects on the output depending on the individual parameter perturbed and whether it was positive or negative. The sensitivity of each parameter in the individual demographic models was assessed. A 1 % increase in the intercept, which was positive in all models, resulted in an increase in that demographic model's output e.g. a 1 % increase in the value of the intercept in the survival model would result in increased mean survival for all individuals irrespective of laying date. The relationship between survival and laying date, however, was negative, therefore an increase in the strength of that relationship of 1 % resulted in a more negative relationship. An increase in that relationship, therefore, would result in later laying birds having a lower probability of survival than before the perturbation. Population growth rates, stable population size distribution, reproductive values and life expectancy were calculated from these models.

4.4 Results

Over the 26-year time period over which the Pied Flycatcher population was surveyed at Cwm Clydach, 16 years had laying date recorded (Figure 4.2). The declining number of records across the study period reflected the decline in the number of Pied Flycatcher pairs breeding within the study site (see Chapter 2). Mean population laying date varied from 5th May to 13th May with the overall mean of 8th May (Julian day = 125-133).

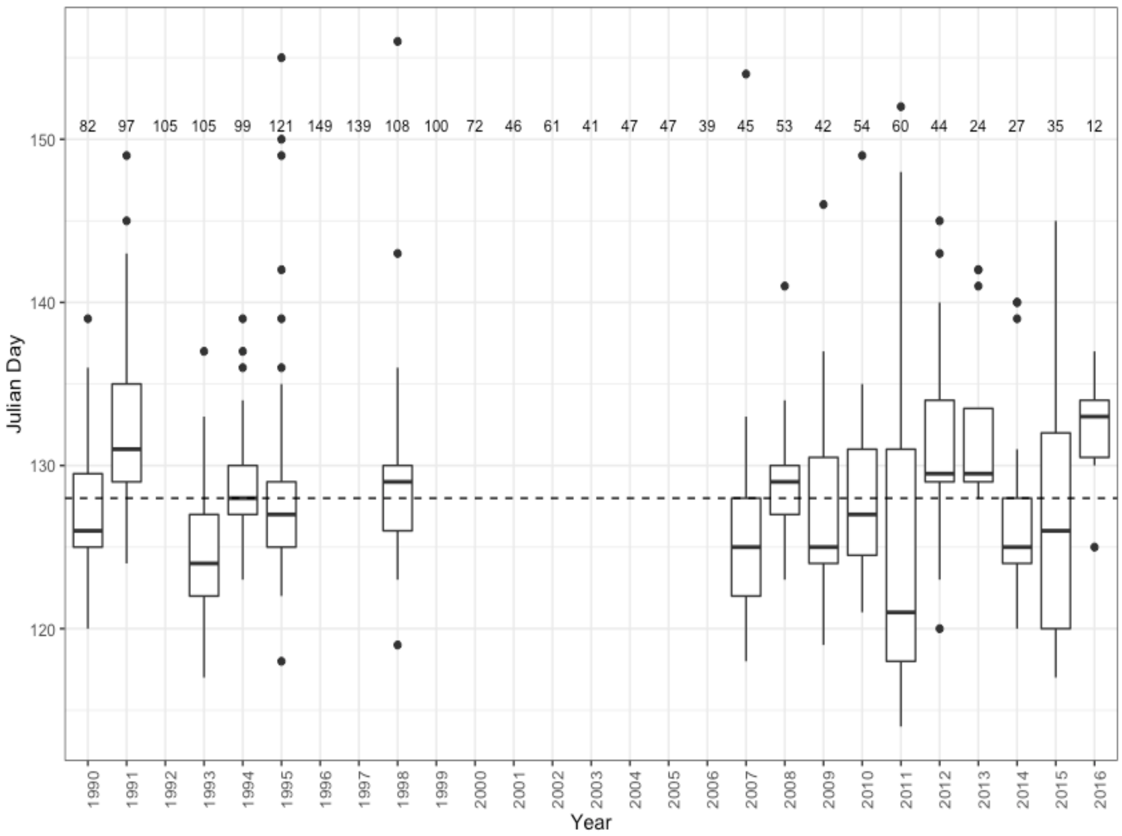

Figure 4.2: Annual variation in laying dates throughout the study period. Bold lines within each box represent the median values for each year. The population mean laying date across study period is shown as a dashed line. Annual sample size is shown above each year.

4.4.1 Laying date in relation to the demographic models (Survival, Reproduction, Growth & Inheritance)

4.4.1.1 Laying date vs. survival

The probability of female flycatchers surviving from one laying season to the next, declined with later laying dates (Figure 4.3a). Those laying at the beginning of the breeding season (25th April, Julian day 115) had twice the survival probability of those laying towards the end of the season (22nd May, Julian day 142) (GLM model 1; slope: -0.05, $F_{1,573} = 0.743$, $p = 0.0002$, pseudo-$R^2 = 0.018$). All models (1-4) had a similar slope for this relationship showing robustness of this result to the specific design of the model chosen (Figure 4.3a).

4.4.1.2 Laying date vs. reproduction

The number of chicks which fledged from a nest was significantly associated with laying date and clutch size (GLM model 2; $F_{1,450} = 594.8$, $p < 0.0001$, pseudo-$R^2 = 0.07$). Surviving females returning to breed produced an average of five fledged chicks per year (mean across all years = 5.18 chicks) but the number fledged varied in relation to laying date (GLM model 2; slope ± SE: -0.01 ± 0.003). For every 12 days later a bird laid, one fewer chick fledged (Figure 4.3b). There was a significant positive association of clutch size with fledging success; for every additional seven eggs that were laid, one more chick fledged (GLM model 2; slope ± SE: 0.13 ± 0.02).

4.4.1.3 Inter-annual variation in laying date i.e. "Growth"

Breeding females who survived between years and had a subsequent breeding attempt were not consistent in their timing of laying (GLMM model 4 $F_{1,129} = 0.260$, $p = 0.613$, $R^2 = 0.02$). In other words, those who laid late in one year did not necessarily have a late laying date in the next year (Figure 4.3c).

4.4.1.4 Inheritance of laying date

It was not possible to detect a significant effect of inheritance in laying date using the Cwm Clydach dataset, as there was no significant association between laying dates of mothers and their daughters (relative to the annual mean; GLM model 1, $F_{2,1} = 1948.0$, $p = 0.853$) (Figure 4.3d). The mother's laying date explained only 17.5% of the variance in the daughter's laying date (i.e. pseudo-$R^2 = 0.175$). This is likely due to the small sample size described in section 4.3.3.4. Therefore, the slope coefficient to be used in subsequent IPMs is +0.192 with a variance of 0.0016 extracted from Sheldon's *et al.* (2003) study of Collared Flycatchers.

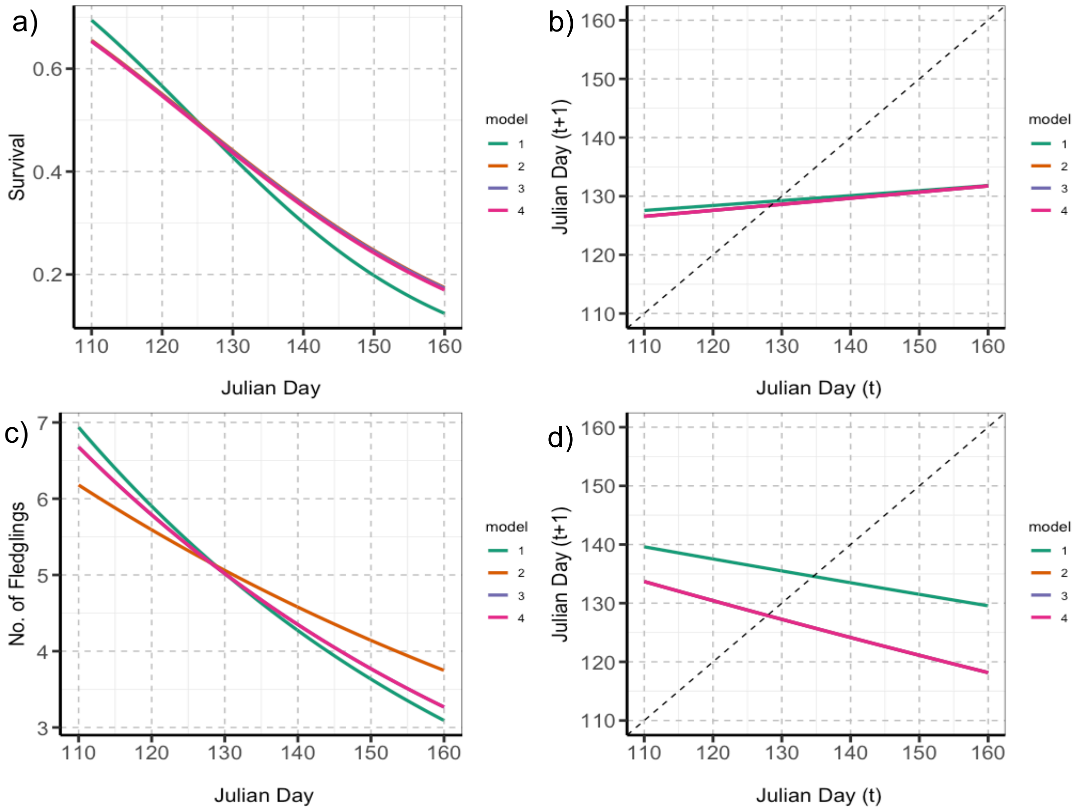

Figure 4.3 Relationships between demographic variables and laying date for each of the four model structures from the Cwm Clydach dataset. a) Survival, b) Growth, c) Reproduction and d) Inheritance. Dashed lines indicate a one-to-one relationship for graphs b & d.

Table 4.2: Parameter estimates from models 1- 4 of each demographic model structure (Survival, Reproduction, Growth and Inheritance).

	Survival Models				Reproduction models			
	1	2	3	4	1	2	3	4
Fixed effects								
Intercept	6.923	15.264	17.075	17.075	3.715	1.984	2.667	2.667
Laying date	-0.055	-0.044	-0.044	-0.044	-0.016	-0.010	-0.014	-0.014
Pop. mean laying date		-0.076	-0.090	-0.090				
Clutch size						0.134	0.115	0.115
Random effects								
Year			0.268	0.268			0.137	0.137
Female				0				0
	Mean growth models				**Mean inheritance models**			
	1	2	3	4	1	2	3	4
Fixed effects								
Intercept	4.777	4.026	-	4.026	5.103	3.382	3.382	-
Laying date	0.001	0.001	-	0.001	-0.001	-0.002	-0.002	-

Pop. mean laying date		0.006	-	0.006		0.014	0.014	-
Clutch size								
Random effects								
Year			-	0			0	-
Female				0				-

	Variance growth models				Variance inheritance models			
	1	2	3	4	1	2	3	4
Fixed effects								
Intercept	2.582	-105.021	-	57.917	0.902	-13.565	-13.565	-
Laying date	0.005	0.051	-	-0.125	-0.006	-0.015	-0.015	-
Pop. mean laying date		0.798	-	-0.353		0.118	0.118	-
Clutch size								
Random effects								
Year			-	0.934			0.098	-
Female				2.588				-

4.4.2 Results from the IPM

The IPM predicted a mean laying date of 8th May (Julian day ± SD = 128 ± 3). This mean is the same as the true population mean laying date over the study period. The standard deviation of three days represents a variation in predicted laying date between early and late years. The observed range in mean laying dates was between 5th and 12th May.

4.4.2.1 Results of the Deterministic IPM

Variation in laying date, when not controlling for mean population laying date and clutch size (model 1), predicted an annual population decline of 72 %. When both of these covariates were controlled for, however, by including them in the model (model 2), the mean population decline predicted was 52 % per year. The mean number of fledglings produced by an individual at mean laying date (day 128, 8th May) was 5.18 fledglings but this varied extensively depending on when the clutch was laid. The mean number of fledglings produced per female ranged from 6.9 to 3.2 for individuals which laid on 24th April and 9th June respectively, the earliest and latest observed laying dates in the study (Figure 4.3c). A breeding individual's life expectancy also depended upon their laying date. Those individuals which laid on or before 5th May had a mean future life expectancy of two years and therefore had an opportunity for two further breeding seasons, whereas those individuals who bred after 5th May, lived on average for only one further breeding season. The model suggests that hypothetically, if a bird were to lay before 23rd April then they could live for three further breeding seasons, and therefore potentially have three times the number of additional breeding seasons of an individual laying 20 days later (Figure 4.4b). The earliest observed laying date was the 27th April and therefore close to the 23rd April threshold.

Early laying individuals have a higher probability of surviving between one year and the next, and therefore have a longer life expectancy. This compounds the positive effect that these individuals would have on the population growth rate. The IPM quantifies this effect, showing that those individuals which lay early have the largest impact upon the population growth rate. Not only do the breeding individuals have a higher probability of survival to breed in subsequent years (Figure 4.4b), but their reproductive value is higher (Figure 4.4a), meaning that they contribute more recruits to the population as their chicks, which would have hatched earlier in the season, have had a higher probability of surviving until fledging (Figure 4.3c).

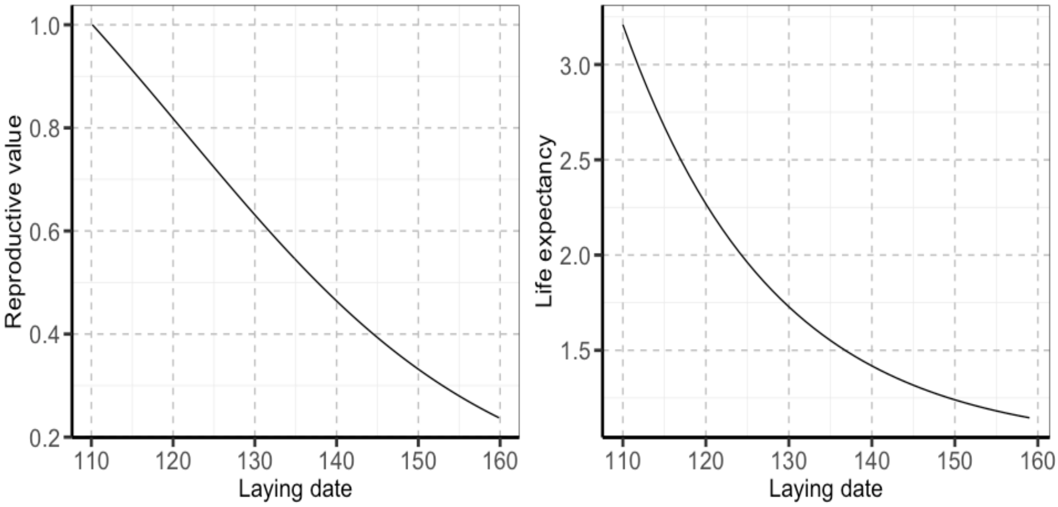

Figure 4.4 a) Reproductive output for individuals on different laying dates. Range 0-1, 0 = complete nest failure, 1 = complete success (i.e. 100% eggs result in fledging young), b) Life expectancy (post fledging) of individuals based on laying.

The distribution of laying dates needed to maintain a stable population (growth rate = 1) was predicted and visualised (Figure 4.5). When laying date was the only independent variable used in the IPM there was a bimodal distribution in the laying dates required to produce a stable population. This bi-modality arises due to the distribution of early and late population mean laying dates in the dataset (Figure 4.5a).

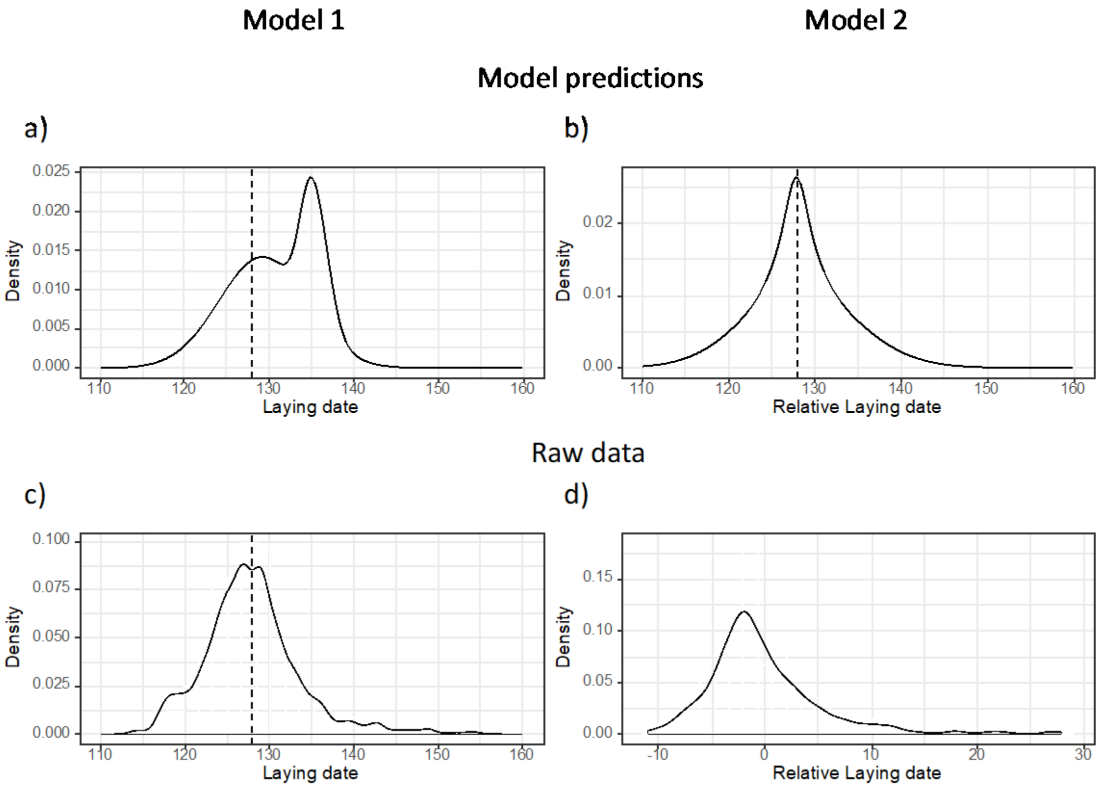

Figure 4.5 a) Distribution of laying dates required to maintain a stable population, peak density is at day 135 (15th May) using model 1. b) Distribution of laying, after controlling for annual mean laying date, required to maintain a stable population, peak density is at day 128 (8th May) using model 2. c) Observed distribution of laying dates in the Cwm Clydach Pied Flycatcher population using raw data. d) Observed distribution of relative laying dates in the Cwm Clydach population.

The observed distribution of laying dates (grey bars in Figure 4.5b) does not exhibit the second peak around day 135 (15th May) but is in fact close to a normal distribution peaking at day 128. Once shifts in mean annual laying date had been accounted for in model 2, the laying date distribution required to produce a stable population size was unimodal and predicted a peak laying date of 8th May (Figure 4.5c).

4.4.2.2 Investigation of changes in model parameters in the IPM

The effect of varying different demographic parameters on population growth rate and reproductive value was assessed by varying mean laying date and recruitment in the model.

4.4.3 Varying laying dates in the deterministic IPM

In order to examine the effect on breeding behaviour of population level variation in mean laying date the IPM was parametrised to represent different scenarios i.e. early at late laying dates. In a year when the mean laying date was early (5th May) (Figure 4.6a) then a relatively synchronous distribution of laying dates would be required in order to achieve a stable population. In contrast, in a year when the mean laying date was later (11th May) (Figure 4.6b) then a less synchronous distribution of laying dates would be required.

When a hypothetical population's mean laying date was advanced from the observed long-term mean of 8th May to 5th May, the annual population decline reduced from 52 % to 39 %. Conversely if the mean population laying date was delayed by from 8th May to 11th May, then the mean population decline increased to 68 %. The change in population decline due to a three day delay (-16 % change) is greater than the population decline due to a three day advance (+13 % change) shows the non-linear impact of laying date on the rate of population decline.

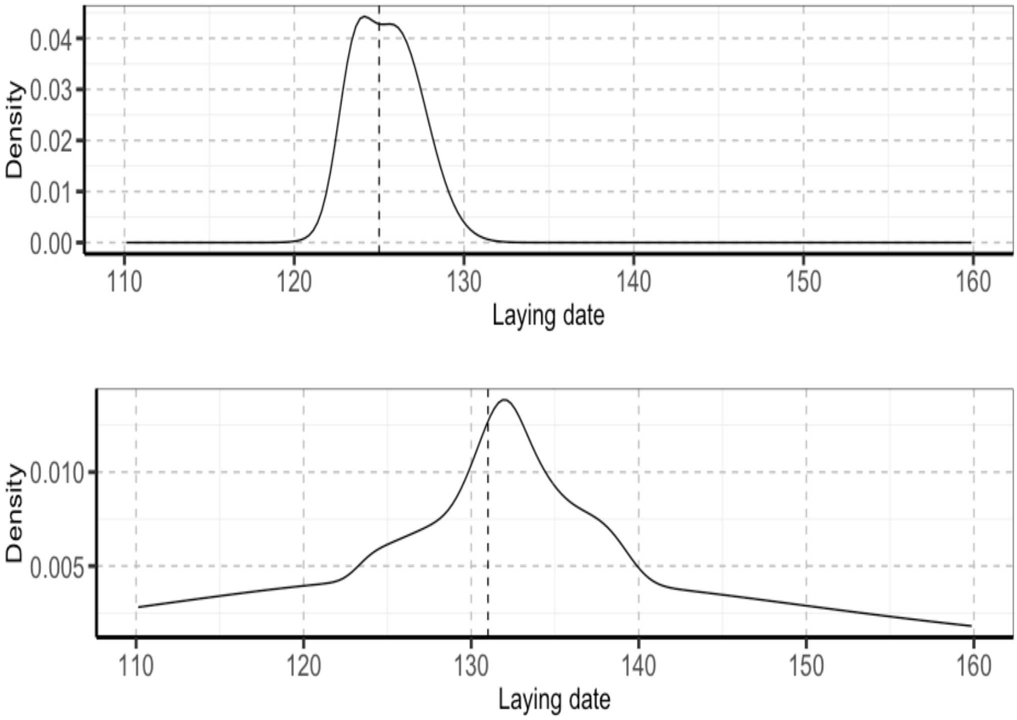

Figure 4.6 Distribution of laying dates required to achieve a stable population, for two hypothetical populations with a mean laying date of a) 5th May and b) 11th May, showing the very different variances in laying dates under the two scenarios. Bold dashed lines indicate the mean laying date.

4.4.4 Varying recruitment in the deterministic IPM

Increasing recruitment in the hypothetical population from 3 % to 5 % or 7 % had the effect of reducing the decline to 33 % or 19 % respectively. Increased post-fledging survival and recruitment to the breeding population is therefore predicted to have a large positive impact on the population trajectory.

As the distribution of laying date is so synchronous within real Pied Flycatcher populations, and because the effect of laying date on survival and recruitment is so strong, a small population level shift towards earlier laying will have a large impact on the population growth rate.

4.4.5 Stochastic IPMs

Stochastic changes between years in demographic parameters (e.g. caused by variation in weather conditions) were introduced into a stochastic IPM to examine the effect of this variability on population growth rates. The mean population growth rate was calculated, as -0.50, where 0 represented a stable population and -1 represented instantaneous extinction. This population was therefore predicted to halve each year. This stochastic model was run 500 times, in zero of these instances the population growth rate was above zero (population increase), and in 16 instances the population growth rate was -1 or below (instantaneous extinction) (Figure 4.7, Table 4.3).

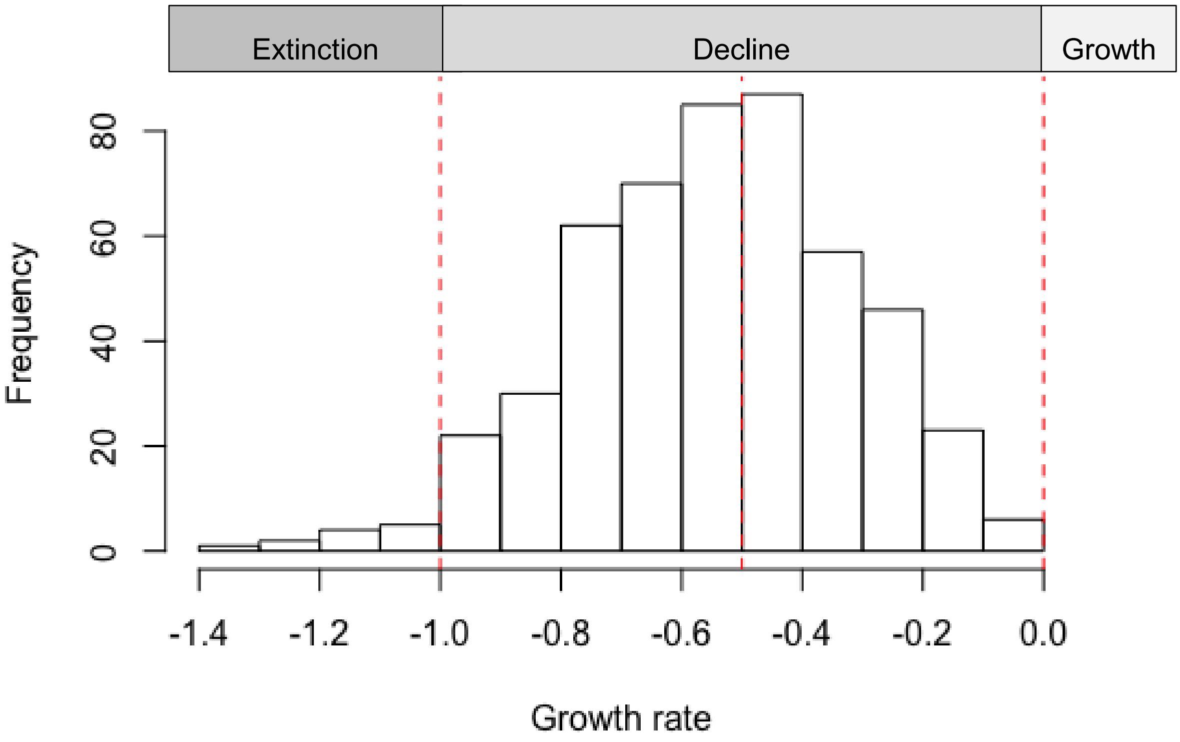

Figure 4.7 Long-run growth rate of population when annual variations are incorporated (model 3). A growth rate of 0 represents stable population growth and a growth rate of -1 or below represents instantaneous population extinction, as indicated by the red dashed lines.

Table 4.3 Stochastic simulation model outcomes based on 500 simulations, which compared baseline stochastic model parameters (model 3), with inter-annual variation increased by 50%

Parameter	Extinction events	Population Growth	Extinction : growth ratio
Baseline	16	0	16:0
Survival	12	0	12:0
Reproduction	15	1	15:1
Growth	18	1	18:1
Inheritance	18	0	18:0

4.4.5.1 Stochastic sensitivity analysis

A sensitivity analysis is a process of examining how model predictions change when an individual model parameter is slightly altered. To do this, model sensitivities were calculated by separately perturbing each model parameter by 1 %, describing the size and direction (positive or negative) of the effect on the model output.

When each of the four parameter values were increased by 1 %, in turn, then the number of extinction events changed relative to the number of growing populations (Table 4.3). The only positive effect on the population growth rate was when the reproductive parameter value was increased; the effect of increasing the other parameters was negative, i.e. they caused the population to decline more rapidly. An increase in the “growth” parameter (i.e. an increase in difference in laying date between two years) had a large impact on the population’s persistence, as 18 extinction events were observed from 500 simulations, but only one population growth event (Table 4.3). When the survival parameter value was increased (i.e. weakening the relationship between laying date and survival), the relative frequency of extinction events increased. When the inheritance parameter value was increased (i.e. weakening the negative relationship between laying date of mother and daughter), the relative frequency of extinction events slightly increased. In all of the population trajectory models the probability of extinction occurred before growth.

4.4.6 Relative importance of demographic parameters

4.4.6.1 Effects on population growth rate

Small perturbations (1 %) were added to the model parameters to identify the relative effect on population growth (Figure 4.8) and lifetime reproductive success (Figure 4.9). Overall, increasing mean survival had the largest positive impact upon the population growth rate

(Green line Figure 4.8a), and increasing the mean difference in laying date between years had the largest negative impact (green lines in Figure 4.8c). The specific effects of each perturbation are as follows:

A 1 % increase in mean survival had a positive effect (15 %) on population growth for early laying individuals, but little to no effect on late laying birds (Green line; Figure 4.8a). If the slope of the relationship between survival and laying date became greater by 1 %, such that early-laying populations experienced increased survival, then the population would decline by nearly 10 % (Purple line; Figure 4.8a). At an individual level, this effect is smaller; If the relationship between survival and laying date became stronger by 1 %, such that early-laying individuals experienced increased survival, then the population would decline by ~5 % (Orange line; Figure 4.8). Perturbations to mean and population level reproduction result in a higher population growth rate, however an increase in the individual laying date resulted in a small population decline (Figure 4.8), with little effect of clutch size (Purple line; Figure 4.8b).

Increased inter-annual difference between laying dates (“growth”) resulted in a considerable decrease in population growth rate of ~30%. As the earliest layers are disproportionately influential in the models, then a greater disparity between their laying dates, (i.e. from laying early and contributing positively to the population by surviving and producing more young to laying late and having a reduced survival and producing fewer young), had a large negative impact upon the population growth rate (Green line; Figure 4.8c). A decrease in the population level inter-annual difference in laying dates resulted in a small decrease in population growth rate for early laying populations, although this was not observed in late laying populations (Purple line; Figure 4.8c). There was no impact of individual-level changes in laying date on population growth (Orange line; Figure 4.8c). There was also no impact on population growth or declines of perturbing inheritance values (all lines; Figure 4.8d).

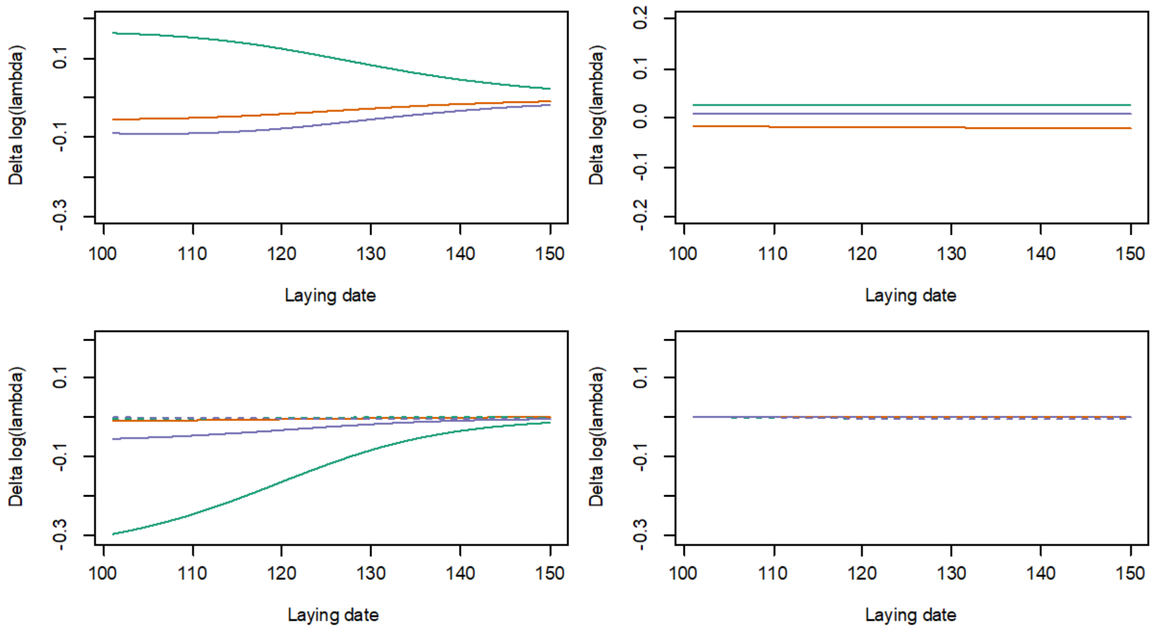

Figure 4.8 Modelled perturbations in a) Survival, b) Reproduction, c) Growth and d) Inheritance on population growth rates. 1 % increase in intercept (green), 1 % increase in individual laying date slope (orange) and 1 % increase in population laying date slope (a, c & d) / clutch size (b) (purple). In (c) and (d) solid lines represent perturbations to parameters in the mean functions and dashed lines represent perturbations to parameters in the variance functions.

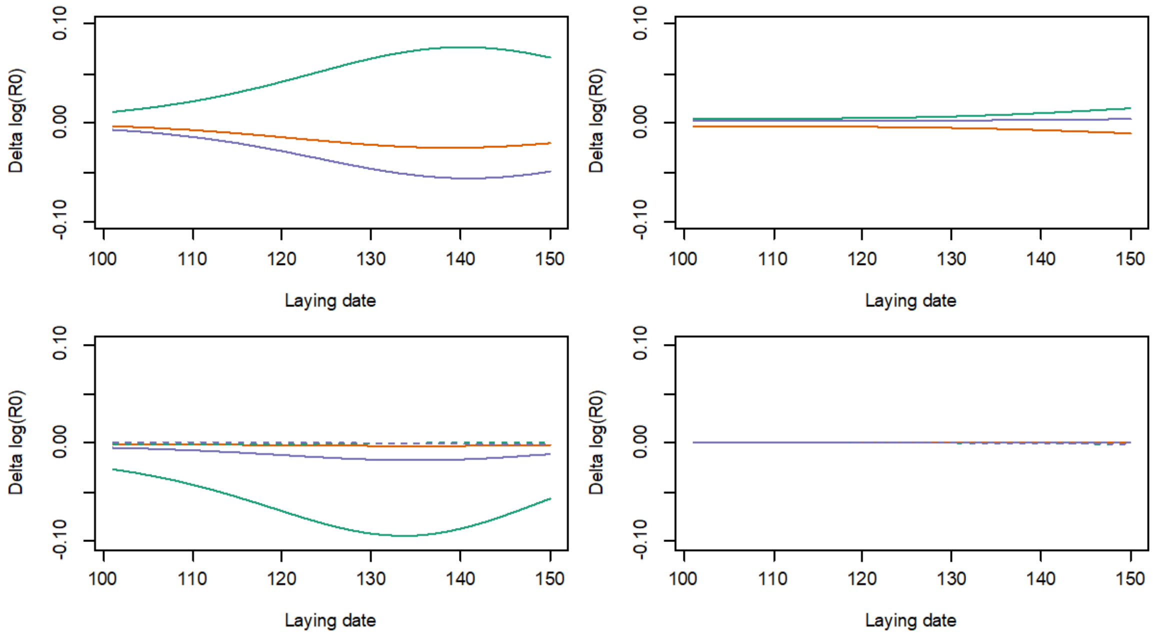

Figure 4.9 Modelled perturbations in a) Survival, b) Reproduction, c) Growth and d) Inheritance on lifetime reproductive growth rates (delta log(R0)). 1% increase in the intercept (orange), 1% increase in individual laying date (green) and 1% increase in population laying date (purple). In (c) and (d) solid lines represent perturbations to parameters in the mean functions and dashed lines represent perturbations to parameters in the variance functions.

4.4.6.2 Effects on reproductive output

Reproductive output was most strongly positively influenced by increased individual survival of later-laying birds (Green line; Figure 4.9a), as this provides an opportunity for a second breeding season. Reproductive output was negatively affected by larger disparity in laying dates between years (“growth”), for birds who laid in the middle of the season (Green line; Figure 4.9c). These individuals will be more likely to shift to a more detrimental laying date, which has a strong effect on reproductive output. As we have seen that a later laying date has more of an effect than earlier laying, the net result is a decrease in reproductive output. There was little impact of increases in clutch size, individual-level laying date changes, or mean number of fledglings, on reproductive output (Figure 4.9b). Stronger inheritance of laying date negatively impacted the reproductive output of individuals who laid at the end of the season (Figure 4.9d).

Overall, the most sensitive parameters to perturbation were survival and growth, with increases in mean survival and greater similarity of laying dates between years having the largest effects on the population growth rate and reproductive output.

4.5 Discussion

Pied Flycatchers represent a particularly useful model study system for exploring evolutionary and demographic processes. Extensive research has been conducted on many aspects of their vital rates which allows construction of population models to understand demographic processes (Hemborg and Lundberg 1998; Wright *et al.* 2004; Järvistö *et al.* 2016). This chapter takes advantage of the wealth of ecological and behavioural knowledge about this system, by combining statistical descriptions of demographic processes underlying population dynamics, into a series of IPMs. These models facilitate an understanding of future growth rates and identify the most sensitive parameters to perturbation.

4.5.1 Population decline

The global conservation status of the Pied Flycatcher is classified by the IUCN as Least Concern (BirdLife International 2018) but it has been reported as undergoing a moderate decline by PECBMS since 1980 (PECBMS 2015). The decline had not occurred prior to this in Wales, as Campbell (1965) reported that populations of flycatchers in numerous counties in Wales were increasing or remaining stable. Cwm Clydach is undergoing a steeper decline (Chapter 2) than the UK average between 1995 - 2016 (38 %; range = - 67 % to + 4 %) (Woodward *et al.* 2018).

The modelled population showed a population decline of between 53 and 72 % from the stochastic and deterministic models respectively. The deterministic model indicates a higher rate of decline than the overall observed rate of decline in Cwm Clydach (Chapter 2). The stochastic model indicates a lower but more variable rate of decline and shows sensitivity to random events as is to be expected with a small population. The likely difference between modelled and observed population declines is that not all of the potential influences on population size were incorporated in the IPM. For example, the population was assumed to be closed with no immigration or emigration whereas in reality there was some degree of mixing between local populations (G. Roberts *pers. comm.*). Cwm Clydach may be acting as a population sink with immigration exceeding emigration resulting in a slower decline in population size than predicted by the model. With the current demographic parameters and excluding any impact of immigration, the simulated population is unlikely to grow and could become extinct due to stochastic processes. By changing these parameters, we identified which of the vital rates are most sensitive to change and therefore changing population growth and reproductive success. Introducing inter-annual variation into the stochastic model does not significantly change the mean rate of decline but does highlight the variability between years and the higher likelihood of extinction than population growth (Table 4.2).

The conclusion of this study suggests that immigration to this site may be vital to the continuation of Pied Flycatchers at Cwm Clydach. Annual growth in this population, without immigration, is highly unlikely, and when it does occur it is unlikely to be sufficient to result in a long-term stable or increasing population. This is not unexpected as a population from north Cardiff (Coed-y-Bedw) has become extinct in the past five years (Wildlife Trust of South and West Wales 2012).

4.5.2 Demographic processes underlying population decline

To understand the mechanistic processes causing the decline of Pied Flycatchers in Cwm Clydach, IPMs were created to identify how each demographic process was influenced by the key behavioural trait of laying date. Of the four demographic models from which the IPM was comprised, laying date had a significant association with survival and the number of fledglings produced. It was not, however, as strongly associated with the change in laying date of an individual from one year to the next (“growth”). Neither was there a significant degree of inheritance of laying date between a mother and a recruited daughter.

4.5.2.1 Relationship between survival and laying date

A novel finding of the present study is that adult survival was associated with laying date at a fine scale; this finding was incorporated into the IPM in order to understand the ecological pressures acting on populations, and their impacts on population growth rates. Higher survival for early laying individuals resulted in longer life expectancy. Earlier laying birds would be able to obtain the highest quality territories which would result in reduced pressure due to increased foraging efficiency. This reduction in pressure, leading to increased fitness has a carry-over effect into the winter (Finch *et al.* 2014). The size of this effect is biologically important; early-breeding birds can live for twice as many further breeding seasons as late-breeding birds. With minimal extrapolation projected life expectancies for individuals laying on the 23rd April (3 years) could be twice that of those laying on the 18th May (1.5 years). Birds breeding at the mean laying date had a life expectancy of 1.75 years which is comparable to previous estimates of 1.6 (Artem'ev 1998; Lundberg and Alatalo 2010).

4.5.2.2 Relationship between fledging success and laying date

Eggs which were laid earlier had a higher probability of resulting in a fledged chick. This has been shown to be, in part, due to closer phenological matching of chick demand with food availability (Both *et al.* 2009). Higher chick provisioning resulted in faster fledging (Siikamäki 1998), which enabled parents to reach the end of the breeding season with a higher biological fitness and enabling the nestlings to fledge. Furthermore, these adults and fledglings may be ecologically fitter individuals for their migration to Africa with potential inter-annual carry over effects into the subsequent breeding season (Finch *et al.* 2014).

Birds laying earlier than the population mean of 8th May, not only had a higher probability of survival but also successfully fledged more offspring. As these offspring were more likely to survive and recruit, the population-level impact of an early laying mother was large. The mechanisms underlying the association between laying date and survival are not directly addressed in the present study but may involve a greater level of physiological and energetic stress on later-breeding parent birds that are temporally mis-matched with their invertebrate food supply (Chapter 3). Conversely, early-breeding birds may be of higher biological fitness, and therefore are able both to breed earlier and to survive, in contrast to lower quality individuals. Regardless of the mechanism(s) and direction of cause and effect, this relationship is revealed by the IPM to have important population-level consequences.

4.5.2.3 Relationship between mean population laying date and laying date synchrony

When temperatures increase earlier, than the average in Spring, there is a greater pressure on all potential breeders to breeds as quickly as possible to not miss the peak availability of food. This means that irrespective of when a bird arrives back on the breeding territory, they will lay as soon as possible, resulting in a relatively synchronous distribution of laying dates. Conversely when the temperature in spring increases more slowly or later in the year then mean laying dates are later. This is due to the reduced pressure on individuals to breed as soon as they can as the peak abundance in food availability may be later. As some birds arrived earlier than others, they may be in breeding condition and be ready to occupy territories. These individuals would lay early. The birds who arrived a few days later may have taken the same time to achieve the same level of condition and may lay later. The later the peak in food availability is the more spread the distribution of laying dates.

4.5.3 Sensitivity Analysis

The population-level consequences of associations between laying date and demographic parameters were experimentally tested *in silico.* These sensitivity analyses conducted on the IPM determined which model parameters had the greatest effect on population growth rate. The most sensitive parameters to perturbation were survival and inter-annual change in adult laying date, whereas inheritance and reproductive success had only small effects on the population growth rate predicted by the IPM. The high overall mean reproductive success of the population could explain the lack of sensitivity of reproductive success to perturbations, as there is little capacity to increase fledging success which is already close to the upper limit of 100 %.

The earliest-breeding birds contribute the most to the population growth rate. However, the birds which have the greatest potential to change the population growth rate are those birds that breed immediately either side of the population mean (8th May). The sensitivity analysis shows that these birds could have a large impact on the population growth rate by laying on or before the population mean laying date. Specifically, if those birds who previously bred just after the mean, were to breed just before the mean in the following year, their impact on population growth rate would be positive. As the standard deviation of laying dates is 5.7 days, only individuals who laid on or before the 14th May are likely to be able to advance their laying date sufficiently to lay on or before the mean laying date. These individuals would potentially have a substantial impact on the population growth rate. If a previously early breeder subsequently laid after the mean laying date in the following year, then the effect on the population growth rate would be negative. This is in part due to the low survival of individuals with a late laying date, who therefore do not have an opportunity to advance their laying date in subsequent years.

Increasing the difference between laying dates in consecutive years by 1 % has a negative effect on population growth rates, as there is a disproportionately large disadvantage of early birds becoming late. Late breeders contribute fewer recruited offspring into the population, in subsequent years, which has a negligible effect on population growth rate. As late breeding birds have low survival, they more rarely have the opportunity to lay early in a subsequent year. The number of days by which a bird could advance its laying date was not dependent on its original laying date (Figure 4.3b). This suggests that individual late-laying birds are not consistently advancing their laying date more than early laying birds, as would be expected if laying date were responding to selection pressure. Instead the difference in laying dates between years suggests an individual-level of plasticity whereby an individual could adjust its timing in response to current conditions.

Changes by 1 % in modelled reproduction and inheritance parameter values have only small effects on population growth. It is likely for reproduction that this is because an increase of 1 % of 7 eggs laid (0.07 eggs) is not a biologically meaningful change. The increased difference in a population's laying date between successive years results in a negative effect on population growth rate of mid-season laying birds, as those birds would become more mis-matched with food availability, and therefore produce fewer offspring and have a lower lifetime expectancy. The lack of consistency in laying dates between mothers and daughters (inheritance) indicated the plasticity in laying date which the birds exhibit. This plasticity enables them to respond to local conditions within a breeding season (Both and Visser 2001; Childs *et al.* 2016)

4.5.4 Future advancements of the IPM

To increase the explanatory power of this model, the model structure could be extended to include other variables such as the age or life-stage (e.g. number of prior breeding attempts) of each individual. This information was not available for most of the birds in the present dataset but would be possible to obtain from a more comprehensively marked population.

Inclusion of additional independent variables in the model would have been possible if we had those data for the same location and time frame as for the nest box dataset; specifically, weather variables and food availability in terms of temperature, rainfall, phenology and abundance of different invertebrate taxa from the same woodland (see Chapter 3). This would allow the model to be parameterised to examine the role of phenological matching in driving the processes described by the current model.

For Pied Flycatchers I would like to be able to identify what drives productivity in a population within a woodland, but also affects their dynamics on a landscape scale. The current IPM assumes a closed population with no immigration or emigration, and future extensions would incorporate these dynamics into a wider meta-population model. The lack of inclusion of emigration and immigration is one possible cause of disparity between the modelled and realised population decline. In addition to this the large variability in the population decline observed in the stochastic model indicates the possible range of growth outcomes for the Pied Flycatchers given the changing environmental conditions. A meta-population scale model would therefore incorporate philopatry, as a covariate, to understand the role of dispersal mechanisms in driving declines across multiple populations. This approach is illustrated by Howell *et al.* (2018), who designed a new spatially explicit model which incorporates both landscape heterogeneity and metapopulation dynamics of colonisation and extinction.

Two of the novel results from this study may have substantial implications for understanding the decline in Pied Flycatcher populations. Firstly, the positive effect of an early laying date on inter-annual survival of breeding individuals suggests that there may a selection pressure towards earlier laying. Any population with a large proportion of late-laying individuals would be expected to undergo a steep population decline. Secondly, these non-linear increases in survival associated with early laying dates result in individuals with a longer life expectancy and more breeding seasons, contributing disproportionately and positively to a population’s growth rate. A large proportion of early-laying individuals in a population could facilitate a positive population growth rate.

5 General Discussion

5.1 The novel contribution of this study

Breeding populations of Pied Flycatchers have been studied for many years (see Lundberg & Alatalo 2010) and more recently this model system has been incorporated into a tri-trophic framework for understanding cascading impacts of climate change across trophic levels, from trees to caterpillars to birds (Burgess *et al.* 2018). For the first time, this thesis integrates a long-term observational study of breeding biology, with a short-term intense study of the tri-trophic system, to specify an Integral Projection Model (IPM) of a Pied Flycatcher population. IPMs have been used to understand demographic trends in species across many taxa, including plants and mammals (Adler *et al.* 2010; Ozgul *et al.* 2010), however to date only four IPMs have been created for birds (Childs *et al.* 2016; Kentie *et al.* 2018; Plard *et al.* 2018; Plard *et al.* 2019). Until now, short-lived long-distance woodland migrants have not been represented in any IPMs, and so this study presents the first such IPM to be developed for this ecological guild (Figure 5.1).

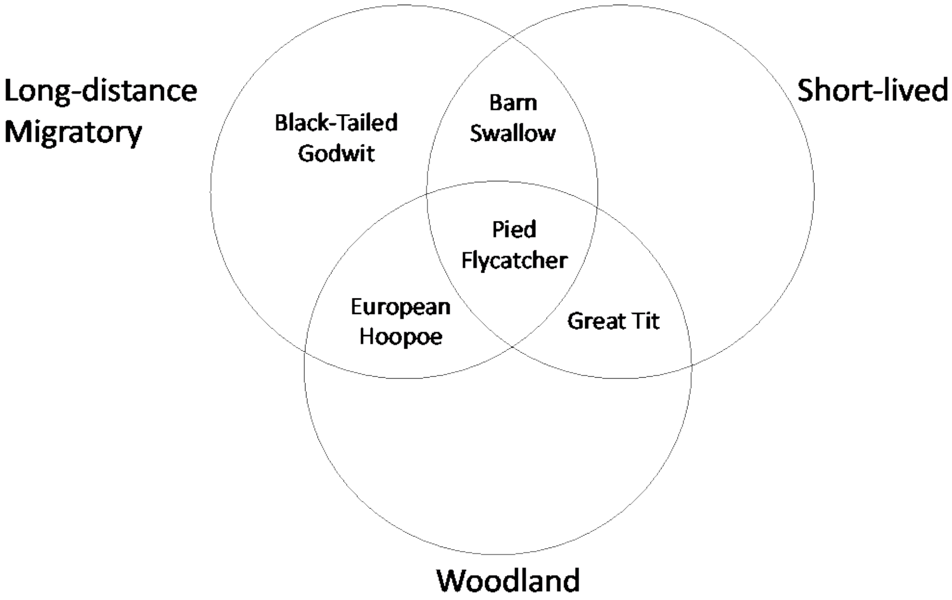

Figure 5.1 Venn diagram of existing bird IPMs, showing Pied Flycatcher to be the only short-lived, woodland-breeding, long-distance migratory species to be examined with an IPM.

Table 5.1 Previously published Integral Population Models of bird populations.

Study	Species	Focal trait(s) and other traits considered	Age-structured model?	2-sex model?	Integrated with population model (IPM²)?
Present study	Pied Flycatcher *Ficedula hypoleuca*	**Laying date**	N	N	N
Childs *et al.* 2016	Great Tit *Parus major*	**Laying date (synchrony),** sex, age	Y	Y	N
Plard *et al.* 2018	Eurasian Hoopoe *Upupa epops*	**Fixed morphology, body condition,** sex, age	Y	Y	N
Kentie *et al.* 2018	Black-tailed Godwit *Limosa limosa*	**Laying date**	N	N	N
Plard *et al.* 2019	Barn Swallow *Hirundo rustica*	**Laying date** Breeding attempt	N	N	Y

Statistical modelling in general, and IPMs in particular, allow questions to be asked about the demography of birds of conservation concern, and to model the potential population-level outcomes of different ecological, demographic or conservation-focused changes. In this way, monitoring and modelling of a study population feeds into actionable responses, rather than just recording the decline of bird populations to extinction. Short-lived bird species provide a greater opportunity for rapid evolutionary change than long-lived species, due to their faster maturation and shorter generation times. As such, shorter time frames (e.g. the 26 years examined in Chapters 2 & 4) can provide an opportunity to study potential evolutionary changes as well as phenotypic changes in behavioural traits across multiple generations. Species living in habitats with seasonally ephemeral food resources (e.g. Oak woodlands, see Chapter 3) may undergo stronger selection pressures than those occupying habitats with long-lasting peaks in food supplies (e.g. agricultural landscapes, Plard 2019). More extended food peaks can allow multi-brooding in bird species breeding in such habitats, which reduces the impact of a single unsuccessful nesting attempt. The evolutionary pressure on woodland long-distance migrants, such as the Pied Flycatcher, provides another reason why Pied Flycatchers are a good candidate system for this approach.

Trans-equatorial long-distance migrants are undergoing some of the steepest population declines among avian taxa (Green and Pearce-Higgins 2014) and so understanding the causes of decline is both essential and time-limited. As these individuals are vulnerable to the sum of all impacts of environmental changes along the migratory route, and therefore across the annual cycle, an in-depth understanding of each stage is important. The combination of these life-history traits (short-lived), behavioural traits (long-distance migratory) and habitat traits (woodland-breeding) results in the Pied Flycatcher IPM being an important case-study in modelling the decline of a species decline. Insights gained from the IPM result in an integrated view of the species' ecology, and help both to identify the primary causes of decline and mechanisms by which extinction might be averted.

5.2 The novel contribution of Chapter 2

The breeding status and population size of many species of conservation concern (Eaton *et al.* 2015) are recorded by citizen scientists, which provides a wealth of data. Unfortunately, many of these datasets are not brought into the public domain through appropriate analysis and publishing. The dataset from Cwm Clydach used in this study has been collected for 30 years and yet has not previously been analysed or published (H Coats pers. comm.). As conservation interventions also often lack formal evaluation, few management protocols have been enacted to help with conservation of migratory woodland birds. Recent local population extinctions at the edges of the Pied Flycatcher's core range in Wales (e.g. at Coed-y-Bedw near the south Wales coast, WTSWW 2012), and the rapid decline in Cwm Clydach (greater than national average, see Figure 5.2), have highlighted the need for urgent conservation management for this species. The work in this thesis has highlighted the importance of such management plans taking into account future variation in weather associated with climate change (IPCC 2014). Chapter 2 showed how weather variables may have interactive effects on nest productivity and so should be considered in a holistic view and not as single terms in isolation, as has frequently been the case in previous studies (Artem'ev 2002). Combinations of multiple weather variables also have temporally differing effects on various prey taxa, and so should be considered during a species-specific timeframe (e.g. incubation period, chick lifetime etc.) and not just as monthly data (cf. Burgess 2014). Ignoring these interactive effects and predicted changes in future weather may result in underestimating rates of population declines.

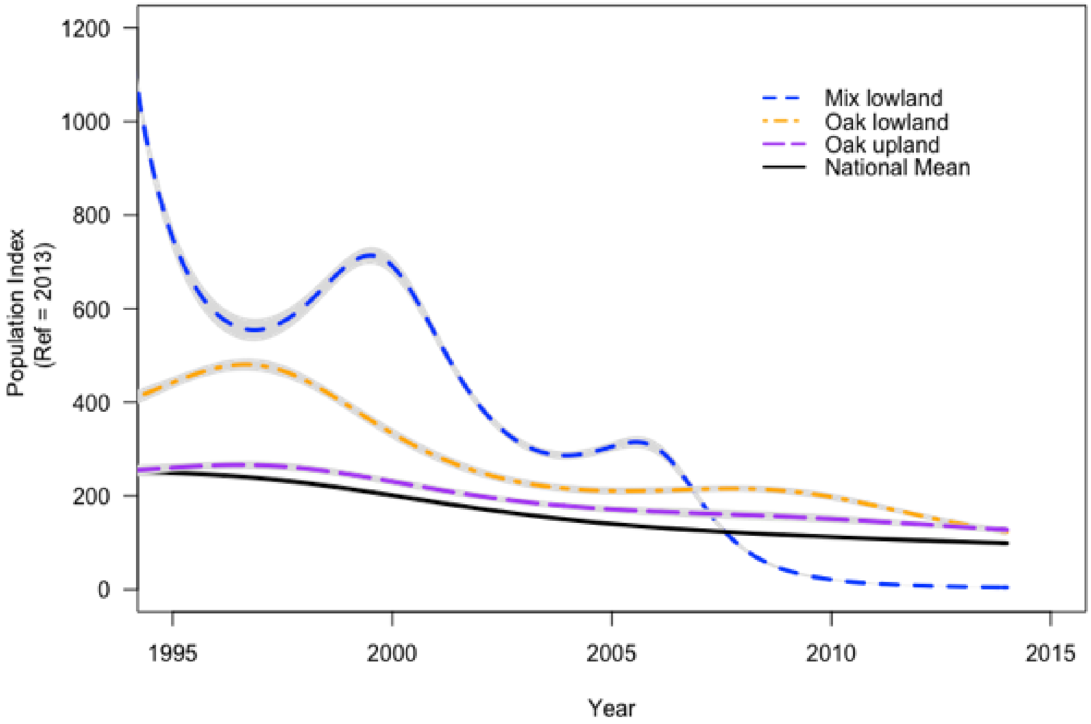

Figure 5.2 Population trajectories of different Pied Flycatcher populations in the UK, complied from data presented in Chapter 2 and previously published studies. A) Cwm Clydach, south Wales (Chapter 2), B) Coed y Bedw, south Wales (Wildlife Trust of South and West Wales 2012), C) Llanwrthwl, mid-Wales (Kern *et al.* 2014), and D) the UK national population estimate (Robinson 2018).

5.3 The novel contribution of Chapter 3

The prey of Pied Flycatchers has been identified by hard parts analysis (Stowe 1987), camera trapping (Sanz 1998) and molecular analysis (Tyrrell 2017), but the present study is the first to model the effects of food availability (in the form of both caterpillars and small flying invertebrates) for Pied Flycatcher chicks in the UK over multiple years. I extended this approach by identifying the impacts of temperature and precipitation on timing and abundance of prey items and subsequent effects on Pied Flycatcher fledging success. This led to the quantification of the temporal mis-match between peak caterpillar availability and peak nestling demand (considered to be 7-10 days after hatching) and demonstrated the high sensitivity of Pied Flycatchers to phenological mis-match.

5.4 The novel contribution of Chapter 4

IPMs made it possible for the first time to identify the impacts of individual laying date on population demographics and population growth rate. The link between early laying date and individual life expectancy, reproductive success and population growth have extended our knowledge of Pied Flycatcher breeding biology. The variation around these estimates, provided by the inclusion of annual variation in stochastic models, provides estimates of population change under the observed inter-annual variability of recent weather conditions. Longer life expectancy has been reported to be important in population persistence and growth (Lundberg and Alatalo 2010), as has a reduction in phenological mis-match between peak food demand and availability, mitigated through advancing laying date (Both *et al.* 2006). The present study is the first study on Pied Flycatchers to link early individual laying date to increased life expectancy. The results add support to previous research into Pied Flycatcher breeding biology which has noted no long-term change in the number of fledglings produced or population breeding success ((Woodward *et al.* 2018). Chapter 4 shows, however, that due to decreased life expectancy of late laying birds, the consequent reduced life-time reproductive success may indeed be a driver of population decline.

Several recent studies on Pied Flycatcher breeding biology have highlighted the importance of overwinter conditions as drivers of population change, leading to a great research focus on the overwintering ecology of Pied Flycatchers in sub-Saharan Africa during the Palearctic wintering period (Mallord *et al.* 2016; Ouwehand and Both 2017). The results of these studies reported that the rainfall in the Sahel was a driver in population declines on the breeding grounds, but here I reveal a potentially more complex story, involving carry over effects from breeding into over-wintering survival, and from the over-wintering period to breeding, with the probability that there will be additional stressors at the staging grounds *en route*. These ecological pressures on long-distance migrants represent an important distinction from resident species, which are subject to different overwinter pressures, and are much less constrained in their decisions about laying date. As a result, resident bird species have generally tracked phenological changes in their prey more closely than have long-distance migrants.

Many woodland-breeding long-distance migrant birds (e.g. Common Redstart (*Phoenicurus phoenicurus*), Wood Warbler (*Phylloscopus sibilatrix*), Tree Pipit (*Anthus trivialis*), and Ovenbird (*Seiurus aurocapilla*)) share a similar ecology to Pied Flycatchers; laying a single clutch in broadleaf deciduous woodlands between April and July, feeding their nestlings on invertebrates and migrating to trans-equatorial regions to over-winter. As such, these species all experience similar conditions on both the breeding and wintering grounds with regards to food availability and weather conditions, and therefore experience similar ecological pressures. It is therefore unsurprising that like Pied Flycatchers, they have all declined significantly during the same period. Many of these species are more difficult to monitor extensively due to their nests being more difficult to find, or due to low breeding densities, and therefore have had considerably less research conducted on them. Due to the similarities in ecology between these species it may be possible to extend the IPM framework developed here to compare drivers of population declines amongst this wider guild of woodland migrants. In order to make the models as relevant as possible, data which have been collected on these species could replace the parameter estimates for individual functions wherever these data are available. By doing so we could create the most robust models for these species that is possible with current data. To then identify how the parameters for which we do not have directly observed values influence the population growth rate, we can use sensitivity analysis as has been demonstrated here using the Pied Flycatcher IPM. This may allow us not only to understand what elements of a species' demography are contributing to the observed decline but may also lead us to understand what research questions need to be addressed in order to mitigate these drivers of decline. Until these extensions to -and applications of- the present IPM are conducted, it is important to acknowledge the large step forward that single species IPMs can and are contributing to our understanding of the drivers of population declines. Here we have shown that an individual's laying date has a significant effect on its survival and lifetime reproductive success, which in turn has an important effect on the population growth rate.

The heritability parameter estimated from the very limited data available from the Cwm Clydach dataset (only four mother-daughter pairs) was not significantly different from zero, and yet laying date must show some degree of heritability (for example because there are consistent between species differences). Sensitivity analysis showed how the impact of heritability on population growth rate changed with altered levels of inheritance (Chapter 4). Two methods to improve this estimate would be to i) increase the number of years over which this population was studied to increase the probability of an increase in recruited individuals being present or ii) use estimates from other populations to create a more robust estimate for use in the IPM. An extension to the inheritance model has already been developed by Childs *et al.* (2016) by explicitly incorporating genetic components into the model which address the impact of phenotype on the inheritance of the focal trait.

5.5 Future developments

Often it is not possible to obtain data on individual level survival, reproduction and laying dates from the same location. Designed for these situations, Integrated Population Models (IPMpop) were developed (Schaub and Abadi 2011), which use population estimates of these demographic parameters from geographically distinct studies to build a population model. The strength of this was combined with the strength of the IPM to form an "IPM^2", where individual level values (IPM) are used from multiple distinct populations (IPMpop), to form a robust geographically structured model. Given the different population trajectories exhibited by Pied Flycatchers in the UK (Figure 5.2) it is important to extend the framework of the IPM constructed in this study to understand population trajectories across the UK and

Europe. This would integrate parameter estimates across the broad geographic range of the Pied Flycatcher and enable widely applicable conservation strategies to be created.

To increase the explanatory power of these models it would be beneficial to add other co-variates which have been shown to be of importance for Pied Flycatcher demographic processes (e.g. between-year variation in caterpillar abundance and phenology, and weather). Incorporating these into the already powerful IPM framework would increase our mechanistic understanding of this ecosystem. Explicitly modelling the spatial resolution of food availability and phenology could further increase the power of this analysis (Cole and Sheldon 2017). In this study, the spatial variation within the Tŷ Mawr woodland was statistically controlled for, to enable a population-wide understanding of the effects of mean food availability, and increasing the number of nests which could be included in the analyses.

I have interpreted the association between laying date and survival as implying that earlier laying facilitates individuals surviving for longer, however it is possible that ecologically fitter individuals may be able to breed earlier than less fit individuals, and subsequently have higher survival. To be able to address the causal mechanism underlying this association we would need to artificially advance or delay the laying dates of multiple individuals, and identify the subsequent change in survival and reproductive output. This raises both ethical and logistical concerns.

5.6 Selection pressure and adaptation.

The increased survival and life expectancy associated with early laying in the IPM, shows that there is likely to be strong selection pressure towards earlier laying. Despite departure date from Africa being independent of environmental conditions (Gwinner 1996), flexibility in departure date from Africa provides a mechanism for birds to advance their arrival dates (Ouwehand and Both 2017). There was little variation in migration duration between individuals (2.9 days) but large variation in departure date (five weeks). As the study conducted by Ouwehand and Both (2017) analysed a single year of migration it is not possible to identify whether this is an example of behavioural plasticity or individual differences.

The model estimates of individual phenotypic plasticity both within and between seasons and generations (5.7 days) is marginally more than the overall advancement in laying date (five days in 20 years) exhibited by a Pied Flycatcher population in the Netherlands (Both *et al.* 2009). The advancement in laying date in the UK, 10 days in 51 years, (Woodward *et al.* 2018) also exceeds the phenotypic plasticity demonstrated by individuals, which indicates that long-term adaptation has occurred. Selection pressure only produces evolutionary change if the response needed is greater than that which can be provided by phenotypic plasticity. Provided that the selection for earlier breeding is more beneficial to the overall lifetime reproductive success than it is detrimental to any other aspects of the annual cycle there will be an evolutionary response towards earlier laying.

5.7 Conclusion

The well-known quote from statistical modelling holds: “All models are wrong, but some are useful” (Box 1976). However, the more that we are able to accurately model the variation within a natural system, the more useful the models can be. This is particularly important in aiding the framing of conservation questions. Understanding what causes a species and ecosystem to change over a short- or long-timescale facilitates the development of effective conservation management strategies. These conservation management schemes are often enacted or monitored by members of the public conducting citizen science, yet the data collected are frequently underused. The interrogation of one such dataset in the present study, combined with new detailed observations of food availability and the combined effects of weather, have provided new insights into Pied Flycatcher breeding ecology in Cwm Clydach which can potentially be more widely applicable to other locations and other species. The combination of these results with the current literature emerging from research on wintering ecology in Africa will greatly increase the knowledge of Pied Flycatcher ecology and demographic trends.

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6 Appendix

6.1 Appendix 1

Table A1.1 Contrast of annual mean clutch size with population mean clutch size (represented by data from 1990)

Year	Mean	S.E.	z- score	p
Intercept	1.910	0.041	46.823	<0.001
1991	0.023	0.059	0.397	0.692
1992	0.038	0.058	0.646	0.518
1993	0.034	0.057	0.608	0.543
1994	0.000	0.057	-0.007	0.994
1995	0.025	0.056	0.445	0.657
1996	-0.026	0.058	-0.443	0.658
1997	0.035	0.055	0.630	0.529
1998	-0.037	0.057	-0.647	0.517
1999	-0.019	0.057	-0.336	0.737
2000	0.019	0.062	0.303	0.762
2002	-0.010	0.071	-0.135	0.893
2005	0.010	0.067	0.155	0.877
2006	0.042	0.069	0.611	0.541
2007	-0.056	0.072	-0.772	0.440
2008	-0.052	0.071	-0.726	0.468
2009	0.024	0.076	0.310	0.756
2010	0.024	0.076	0.310	0.756
2011	0.050	0.067	0.749	0.454
2012	0.022	0.071	0.311	0.756
2013	-0.167	0.100	-1.670	0.095
2014	0.042	0.089	0.476	0.634
2015	0.036	0.083	0.431	0.666

Table A1.2 Contrast of annual mean brood size with population mean brood size (represented by data from 1993)

Year	Mean	S.E.	z value	p	
Intercept	1.790	0.044	40.618	<0.0001	
1990	-0.084	0.064	-1.307	0.191	
1991	0.023	0.064	0.363	0.716	
1992	0.173	0.087	1.991	0.047	*
1994	-0.139	0.065	-2.157	0.031	*
1995	0.027	0.060	0.452	0.651	
1996	0.088	0.072	1.234	0.217	
1997	0.167	0.075	2.239	0.025	*
1998	-0.095	0.062	-1.519	0.129	
1999	0.110	0.099	1.110	0.267	
2000	0.156	0.083	1.884	0.060	.
2002	0.139	0.102	1.359	0.174	
2005	0.156	0.110	1.416	0.157	
2006	0.170	0.093	1.823	0.068	*
2007	-0.116	0.078	-1.482	0.138	
2008	-0.142	0.078	-1.814	0.070	.
2009	-0.052	0.083	-0.621	0.534	
2010	0.058	0.080	0.716	0.474	
2011	0.032	0.072	0.438	0.662	
2012	-0.034	0.078	-0.442	0.658	
2013	-0.080	0.107	-0.750	0.453	
2014	0.208	0.137	1.515	0.130	
2015	0.047	0.104	0.454	0.650	

Table A1.3 Contrast of annual mean fledgling number with population mean fledging number (represented by data from 1990)

Year	Mean	S.E.	z value	p	
Intercept	1.621	0.048	33.617	<0.0001	***
1991	0.151	0.067	2.242	0.025	*
1992	0.182	0.068	2.681	0.007	**
1993	0.083	0.066	1.249	0.212	
1994	-0.140	0.070	-2.003	0.045	*
1995	0.071	0.064	1.106	0.269	
1996	0.085	0.065	1.293	0.196	
1997	0.048	0.064	0.747	0.455	
1998	-0.399	0.073	-5.482	<0.0001	***
1999	-0.251	0.071	-3.539	0.000	***
2000	0.068	0.070	0.964	0.335	
2002	0.009	0.081	0.116	0.908	
2003	-0.065	0.096	-0.677	0.498	
2004	0.247	0.080	3.085	0.002	**
2005	-0.132	0.082	-1.612	0.107	
2006	0.156	0.077	2.014	0.044	*
2007	-0.229	0.089	-2.588	0.010	**
2008	-0.251	0.089	-2.836	0.005	**
2009	-0.140	0.094	-1.486	0.137	
2010	0.097	0.086	1.118	0.264	
2011	-0.075	0.082	-0.917	0.359	
2012	-0.127	0.093	-1.355	0.175	
2013	-0.051	0.111	-0.457	0.648	
2014	0.031	0.103	0.299	0.765	
2015	-0.083	0.103	-0.811	0.417	

Table A1.4 Contrast of annual mean nest productivity with population mean nest productivity (represented by data from 2002)

Year	Mean	S.E.	z value	p	
Intercept	1.179	0.052	22.582	<0.0001	***
1990	-0.102	0.064	-1.608	0.108	
1991	0.557	0.069	8.066	<0.0001	***
1992	0.623	0.071	8.776	<0.0001	***
1993	0.178	0.064	2.782	0.005	**
1994	-0.483	0.061	-7.862	<0.0001	***
1995	0.127	0.063	2.021	0.043	*
1996	0.495	0.068	7.287	<0.0001	***
1997	-0.039	0.062	-0.637	0.524	
1998	-1.073	0.061	-17.730	<0.0001	***
1999	-0.829	0.061	-13.651	<0.0001	***
2000	0.060	0.067	0.899	0.369	
2005	-0.534	0.068	-7.909	<0.0001	***
2006	0.471	0.077	6.143	<0.0001	***
2007	-0.550	0.071	-7.770	<0.0001	***
2008	-0.659	0.070	-9.429	<0.0001	***
2009	-0.600	0.073	-8.255	<0.0001	***
2010	0.305	0.082	3.742	<0.0001	***
2011	-0.477	0.067	-7.097	<0.0001	***
2012	-0.584	0.073	-8.024	<0.0001	***
2013	0.764	0.123	6.208	<0.0001	***
2014	-0.085	0.085	-0.991	0.322	
2015	-0.502	0.079	-6.373	<0.0001	***

6.2 Appendix 2

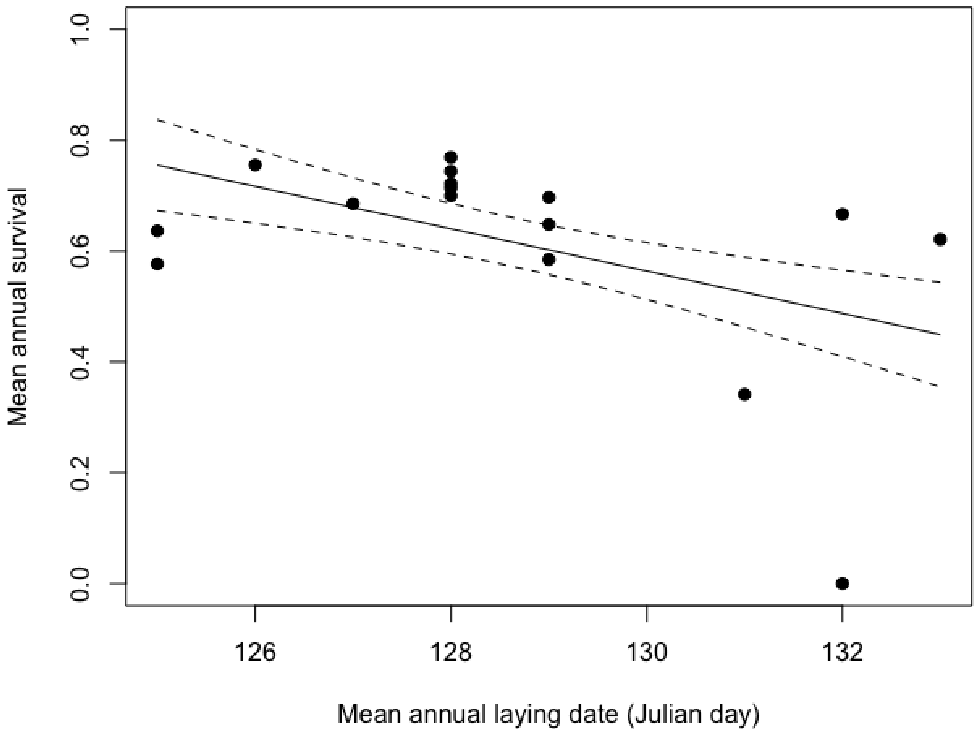

Figure A2.1 Linear relationship between mean annual survival and mean annual laying date