The breeding ecology of the blue tit in relation to temperature microclimate

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Declaration

I declare that this thesis is entirely my own work. Any other material is accordingly referenced and people who provided help and advice are listed in the acknowledgements.

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Sophie Bell
Abstract

With warmer springs we observe earlier Spring phenologies. Long-term trends for earlier phenologies in warmer years have been demonstrated using population mean responses against temporal, altitudinal and latitudinal gradients. Temperature driven changes in phenology are measurable in a model system such as the oak-caterpillar-blue tit and the degree of change from one trophic level to the next can be compared across the network. The majority of studies on such a system focus on population mean trends. In this study I construct a geospatial model of temperature microclimates and test if variation in the phenologies of the simple oak, caterpillar, blue tit ecological network corresponds to variation in temperature across a single study site. Temperature traces are predicted with relative ease to a robust degree using the statistical modelling approach and given the known environmental, seasonal and synoptic weather trends for the location and time of interest. A microclimate modelling approach removes the constraint of a restricted temperature data-collection period and data is not limited to the site or position of the logger. This enables the comparison of behavioural responses amongst individuals as well as within individuals.

I demonstrate that similar patterns of phenology are observed across the microclimates of a single study system as are observed for the same study system over time. More importantly by creating individual-specific temperature profiles I am able to compare the phenologies at each stage of the network to different temperature regimes as they occur under natural conditions. I find that not only do the three trophic levels differ in their periods of sensitivity to temperature change, but also that within these time-windows the phenologies of the tree, herbivore and bird are associated with differing temperature parameters. In addition to an effect on the timing of breeding, I also find an effect of microclimate temperature on incubation behaviour and female condition across the breeding effort.

Climate change can lead to the uncoupling of links within ecological networks, known as trophic mismatch, as the environment of cue perception becomes disassociated from the
environment of peak energy demand and selection. Given that the different trophic levels are sensitive to temperature change during different phases of Spring, I explicitly test whether temperature regimes are consistent across the Spring season and what impact differing temperatures between phases has on the breeding success of the apex predator. I find that not only are different temperature parameters not collinear, but that temperature changes are not concomitant across the Spring season. I therefore find support for the theory that trophic mismatch and blue tit nesting success is not just driven by warming temperatures, but by when temperature change occurs.
Acknowledgements

“It’s all part of life’s rich tapestry”
Dad (when things have gone wrong)

“Success is what you make of the failures”
Dad (when things have really gone wrong)

Though in the spirit of accurate referencing I think Winston Churchill got there first:

“Success is going from failure to failure without loss of enthusiasm”

Ian, I hope I’ve successfully fulfilled the brief with no dint to my enthusiasm! Thank you for your insight, humour, reassurance and the subtle nudges when I’ve wanted to go a bit jazz. I’ve learnt a lot. I am grateful to Alex Lord for introducing me to the Silwood Park study system and the many students, research assistants and volunteers who’ve helped with data collection during my tenure at the helm: Jack, Chris, Lucy, Stella, Giulia, Emma, Ryan, Michael, Alistair, Laura, Lavrentios, Lowri, Charlotte, Paul and the legend that is Audrey Detouef-Boulade-Wallace. Throughout my five years at Silwood I’ve enjoyed being a part of the Runnymede/Silwood ringing community and on the many cold and early mornings have been grateful for the good company, instruction and camping chairs of Phil, Carl, Andrew, Gary, Marion and Helen. This PhD would not be what it is or even have got off the ground, let alone into the canopy without the encouragement (and catapult) of Charlie Marsh, Ally Phillimore and the Jedi-master GIS teachings of Igor Lysenko and pragmatism of Tim Barraclough. Not forgetting Paul Beasley, Paul Nicholas, Jim, Taru, Christine and Anthony. Lastly big thanks go to Malc Burgess. You’ve been an unwitting mentor: a consistent source of good advice and opportunity over the last 5 years.

(Some days are born ugly)

John Steinbeck, Sweet Thursday

On those days I have counted myself very lucky to have in my corner my Wifey, Dorsy-bundle-poodle-pudding-of-joy, Channie, CT, Diane, Gio and Will. Will and Gio, my buddies across the corridor! Thank
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Lastly my thanks go to my husband Rob. Two weeks into our acquaintance I came upon you sitting glum under a tree and tried to cheer you up with some of my bad jokes: you told me I was your rock. From bobbing about trying to get the outboard motor started in Mauritius (not a euphemism) to our lighthouse in the North Sea, you are my port in every storm and home is whenever I’m with you.
Contents

1  General Introduction........................................................................................................... 18
   1.1  A model system........................................................................................................... 21
   1.2  Assessing temperature .............................................................................................. 23
   1.3  Study organisms.......................................................................................................... 25
   1.4  Study site.................................................................................................................... 30
   1.5  Research aims and thesis outline............................................................................... 34

2  A geospatial model of temperature that predicts phenology in wild populations of birds and trees ........................................................................................................................................................................................................................................... 37
   2.1  Introduction ................................................................................................................ 38
   2.2  Methods....................................................................................................................... 41
      2.2.1  Study area and data collection ........................................................................... 41
      2.2.2  Temperature recording ...................................................................................... 41
      2.2.3  Temperature prediction ...................................................................................... 45
      2.2.4  ‘Time window’ analysis and annual trends ....................................................... 48
      2.2.5  Testing for an association between phenology and microclimate ................. 49
   2.3  Results........................................................................................................................ 49
      2.3.1  Temperature mapping ....................................................................................... 49
      2.3.2  ‘Time window’ analysis and annual trends ....................................................... 54
      2.3.3  Association between phenology and microclimate ........................................ 56
   2.4  Discussion..................................................................................................................... 58

3  Does budburst predict Spring phenology of oak trees? ..................................................... 64
<table>
<thead>
<tr>
<th>Section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.1</td>
<td>Introduction</td>
<td>65</td>
</tr>
<tr>
<td>3.2</td>
<td>Methods</td>
<td>67</td>
</tr>
<tr>
<td>3.2.1</td>
<td>Study site</td>
<td>67</td>
</tr>
<tr>
<td>3.2.2</td>
<td>Oak phenology</td>
<td>68</td>
</tr>
<tr>
<td>3.2.3</td>
<td>Herbivore phenology</td>
<td>69</td>
</tr>
<tr>
<td>3.2.4</td>
<td>Temperature data</td>
<td>70</td>
</tr>
<tr>
<td>3.2.5</td>
<td>Data analysis</td>
<td>71</td>
</tr>
<tr>
<td>3.3</td>
<td>Results</td>
<td>72</td>
</tr>
<tr>
<td>3.4</td>
<td>Discussion</td>
<td>77</td>
</tr>
<tr>
<td>4</td>
<td>Incubation activity and female condition are predicted by microclimate temperature</td>
<td>82</td>
</tr>
<tr>
<td>4.1</td>
<td>Introduction</td>
<td>82</td>
</tr>
<tr>
<td>4.2</td>
<td>Methods</td>
<td>85</td>
</tr>
<tr>
<td>4.2.1</td>
<td>Study system</td>
<td>85</td>
</tr>
<tr>
<td>4.2.2</td>
<td>Incubation data</td>
<td>85</td>
</tr>
<tr>
<td>4.2.3</td>
<td>Temperature and rain data</td>
<td>86</td>
</tr>
<tr>
<td>4.2.4</td>
<td>Statistical analyses</td>
<td>86</td>
</tr>
<tr>
<td>4.3</td>
<td>Results</td>
<td>87</td>
</tr>
<tr>
<td>4.4</td>
<td>Discussion</td>
<td>92</td>
</tr>
<tr>
<td>5</td>
<td>The nesting success of a free-living bird is predicted by unequal Spring temperature change</td>
<td>95</td>
</tr>
<tr>
<td>5.1</td>
<td>Introduction</td>
<td>95</td>
</tr>
<tr>
<td>5.2</td>
<td>Methods</td>
<td>97</td>
</tr>
<tr>
<td>5.2.1</td>
<td>Study system</td>
<td>97</td>
</tr>
</tbody>
</table>
6 Quality of breeding territory mediates the relationship between paternal quality and sex ratio bias in a free-living bird population. ........................................................................................................... 108

6.1.1 Introduction .................................................................................................................. Error! Bookmark not defined.

6.1.2 Methods .......................................................................................................................... Error! Bookmark not defined.

6.1.3 Results .............................................................................................................................. Error! Bookmark not defined.

6.1.4 Discussion ......................................................................................................................... Error! Bookmark not defined.

7 General discussion .................................................................................................................. 108

8 Appendix .................................................................................................................................. 116

8.1 Temperature recording ....................................................................................................... 116

8.2 Temperature prediction ....................................................................................................... 120

8.3 Phenological trends ............................................................................................................. 124

9 References ............................................................................................................................... 126
List of Figures

Figure 1.1: Illustration of different temperature parameters recorded in April 2012 at two logger locations.

Maximum daily temperatures are shown in red (average maximum temperature: plot a=18.12 (+/-0.87); plot b = 11.82 (+/-0.37)). Minimum daily temperatures are given in blue (average minimum temperature: plot a=1.58 (+/-0.55); plot b = 3.01 (+/-0.49)). The overall mean temperature is marked by the green line (plot a = 7.54°C (+/-0.30); plot b = 7.34°C (+/-0.29)).

Figure 1.2: Map of Silwood Park study site. Oak trees are shown as green spots, nest boxes as red spots.

Figure 1.3: Silwood Park weather station records and breeding chronology of blue tit population. Plots from 1st January to 21st June in Julian days of mean temperature (black points), total rainfall (dashed blue vertical lines) and mean first egg lay date (solid red line; dashed red lines denote the first egg lay dates of the first and last nest for that year), for each year from 2002 - 13.

Figure 2.1: Maps of logger positions relative to geographical predictors used in the geospatial model of temperature prediction (map a: gradient or slope (°); map b: height above sea level (m); map c: predominant aspect (°); map d: density of oak trees – number of oak trees within a 50m radius).

Figure 2.2: Comparison of March, April and May 2013 temperatures recorded within the canopy and at nest heights (~1.8 m) of 32 trees (March: minimum: int. = -0.41, est. = 1, $r^2 = 0.90$; mean: int. = -0.01, est. = 0.93, $r^2 = 0.87$; maximum: int. = 0.48, est. = 0.92, $r^2 = 0.77$; range: int. = 0.30, est. = 0.99, $r^2 = 0.85$; p<0.0001, n=835. April: min: int. = -0.33, est. = 1.05, $r^2 = 0.95$; mean: int. = -0.15, est. = 1.01, $r^2 = 0.97$; max: int. = 0.98, est. = 0.90, $r^2 = 0.79$; range: int. = 0.99, est. = 0.90, $r^2 = 0.68$; p<0.0001, n=691. May: min: int. = -0.43, est. = 1.03, $r^2 = 0.92$; mean: int. = 0.01, est. = 1.02, $r^2 = 0.92$; max: int. = 2.90, est. = 0.88, $r^2 = 0.70$; range: int. = 1.35, est. = 0.97, $r^2 = 0.80$; p<0.0001, n=456).

Figure 2.3: Linear regressions of predicted and recorded temperatures for the month of April in 2012 and 2013. Predictions are derived from the georeferenced models of temperature and plotted against data collected by loggers at those locations. Summary statistics of the regressions are given in Table 2.2.

Figure 2.4: Linear regression of (a) the mean first egg lay date of each year from 2002 to 2013 against mean temperature for Julian day 48 – 102 of the respective year ($R^2 = 0.83$, 1 and 10 d.f., p<0.0001) and (b) mean oak budburst of each year from 2007 to 2013 against the mean temperature of that year for Julian day 88 – 107 ($R^2 = 0.97$, 1 and 5 d.f., p<0.0001).
Figure 3.1: Map of oak trees (*Quercus robur*) across the Silwood park study site (n=3215) with the subset of oaks for which phenology is recorded in each year 2010-2013 shown in dark green (focal oaks, n=370) and oaks for which heights have been measured in red (n=32). Histograms of oak circumference (n=3176) and height (n=32) are also shown.

Figure 3.2: Oak leafing phenology following a seven-point scale: 0 = dormant, woody buds; 1 = bud growth, starting to appear green; 2 = bud extension; 3 = budburst; 4 = full leaf extension; 5 = anthesis, pollen appears golden yellow; 6 = tanninisation: leaves dark green, thick and waxy. Adapted from Crawley and Akhteruzzaman (1988).

Figure 3.3: Barplot of the annual frequency of peak defoliation scores, given as the percentage of total leaf eaten below the bar, for the 370 trees monitored in each year 2010 – 2013 (2010 = 17.92 +/- 1.01, 367 trees; 2011 = 5.82 +/- 0.51, 367; 2012 = 11.08 +/- 0.36, 368; 2013 = 4.69 +/- 0.15, 366).

Figure 3.4: The number of days between budburst and tanninisation predicted by individual tree budburst relative to the annual mean budburst (2010: int=33.61, est.=-0.71, s.e.=0.02, $r^2$=0.48, p<0.0001; 2011: int=24.13, est.=-0.51, s.e.=0.02, $r^2$=0.25, p<0.0001; 2012: int=45.70, est.=-0.80, s.e.=0.01, $r^2$=0.72, p<0.0001; 2013: int=33.31, est.=-0.58, s.e.=0.02, $r^2$=0.28, p<0.0001) and an illustration of the duration of edible leaf predicted from the regressions, showing the mean budburst (black dotted lines) and mean tanninisation date (coloured dotted line) for the respective year.

Figure 4.1 Regressions of the number of offbouts recorded in 4 hours of incubation activity against the mean offbout length in minutes (2012: $r^2$=0.34, intercept = 23.53, estimate = -1.50, d.f. = 1 and 36, p < 0.0001; 2013: $r^2$=0.34, int. = 13.37, est. = -0.60, d.f. = 1 and 64, p<0.0001) and the total time spent incubating (cumulative onbout duration, 2012: $r^2$= 0.14, int. = 29.11, est. = -0.09, d.f. = 1 and 36, p=0.01; 2013: $r^2$= 0.23, int. = 21.84, est. = -0.08, d.f. = 1 and 64, p<0.0001). Data collected in 2012 is illustrated by the dashed blue regression line and filled blue circles. Data collected in 2013 is illustrated by the solid green regression line and green filled triangles.

Figure 4.2: Trends for 2013 data. The association of offbout number (a) and onbout duration (b) with mean ambient microclimate temperature at different oak densities (observed range = 0-183; plot a: $r^2$ = 0.29, d.f.=3 and 46, intercept = -0.97, estimate= -0.008, p < 0.02; plot b: $r^2$ = 0.28, d.f.=3 and 46, intercept = 45.15, estimate= 0.03, p<0.002). Plots of the decline in female condition against the number of offbouts
Figure 5.1: Schematic illustrating the time-windows in Julian days across which mean temperature most significantly predicts phenology. The phenologies are blue tit first egg lay date (uppermost horizontal blue bar), 7.5% defoliation of oak trees by chewing defoliants (middle light green horizontal bar) and oak budburst (bottom dark green horizontal bar). The time-windows are split into 3 phases: A, B and C.

Figure 5.2: The null expectation is that the rank of temperature in phase A is equal to that of phase C, a 1:1 line. Years that fall above the line are where the rank of temperature in phase A is higher than the rank of temperature in phase C which would predict an earlier blue tit phenology relative to caterpillar phenology. Years that fall below the line are where the rank of temperature in phase C is higher than the rank of temperature in phase A, predicting earlier caterpillar phenology relative to blue tit phenology.

Figure 5.3: Regression of ranked annual temperatures for phase A (Julian day 48 -88) against phase C (Julian day 107 – 121) for the parameters of mean temperature (a), average maximum temperature in phase A compared to mean temperature in phase C (b) and average maximum temperature (c). The solid line illustrates the 1:1 slope. The dashed line illustrates the linear regression of phase A versus phase C ranks (a: intercept [int.] = 4.18, estimate [est.] = 0.36, \(r^2 = 0.13\), p=0.26; b: int. = 4.09, est. = 0.37, \(r^2 = 0.14\), p=0.24; c: int. = 4.72, est. = 0.27, \(r^2 = 0.07\), p=0.39.

Figure 5.4: Regressions of ranked nest temperatures for phase A (Julian day 48 -88) against phase C (Julian day 107 – 121) for 2007 and 2013 for the parameters of average mean temperature (a, b), average maximum temperature (phase A) and mean temperature (phase C) (c, d), average maximum temperature (e, f). The solid red line illustrates the 1:1 slope. The dashed red line illustrates the linear regression and these are given in Table 5.2.

Figure 6.1: Relationship between sex ratio and male mate quality (male condition) across different territory qualities for different counts of oak within a 50 m radius of a nest box (n=0, 40, 80, 120, 156, observed range = 0-156) as predicted by the model: “sex ratio ~MQ+TQ+MQ:TQ” (binomial glm: AIC = 300.62, n=78, intercept = 2.54, estimate= 0.005, p <0.006). Filled circles represent territories with 27 or more oaks within a 50m radius of the nest box. Unfilled circles represent territories with less than 27 oaks within a 50m radius of the nest box.

Figure 8.1: Tinytag data logger field setup. Exposure to ambient air flow is indicated by the blue arrow.
Figure 8.2: i-button data logger field set up. Exposure to ambient air flow is indicated by the blue arrow.

Figure 8.3: Plots of logger recordings of mean temperature per day of data series (21st March, Julian day 82, of 2012 until 26th May, Julian day 148, of 2013). Plots a and c illustrate all recorded data (n = 27524). Plots b and d are of the data set with outliers removed (n=23866).

Figure 8.4: Plots of significant parametric terms in the georeferenced models of minimum, mean and maximum temperature; A=Autumn, S=Spring, Su=Summer, W=Winter.

Figure 8.5: Response shapes of smoothed terms in the georeferenced models of minimum, mean and maximum temperature. The trend is shown by the smooth curve, dashed curves indicate standard error bounds and dashed lines inside of the x axis show the distribution of data points.

Figure 8.6: Illustration of temperatures predicted by the interaction of aspect (degrees from 200°) and sunlight (MJ/m²) given a near flat (1°) and steep (12°) gradient.

Figure 8.7: Illustrations of interactions from the generalised additive models of temperature prediction. All other terms in the models are held at their mean value.

Figure 8.8: The correlation of mean temperature with mean oak bud burst date (plot a: Julian days 88 – 107, Intercept= 33.90, estimate= -0.22, s.e. = 0.03, d.f. = 1 and 5, r²=0.92, p<0.0005) and 7.5% defoliation (plot b: Julian days 96 – 121, Intercept= 47.07, estimate= -0.26, s.e. = 0.0006, d.f. = 1 and 2, r²=0.1, p<0.0001).

Figure 8.9: Plot of annual mean defoliation rate, derived as the number of days between 3 and 7.5% defoliation, and the annual mean peak defoliation score (percentage of canopy eaten) for 2010-2013.
List of Tables

Table 2.1: Topographic, geographic, seasonal and synoptic variables used to predict temperature variation across Silwood Park. ..................................................................................................................................................................................47

Table 2.2: Coefficients of the linear regressions of predicted and observed temperatures for April 2012 and April 2013 plotted in Figure 2.3. All regressions are highly significant (p<0.0001). 2012: 1 and 53 d.f.; 2013: 1 and 54 d.f. ........................................................................................................................................................................................................................................................................50

Table 2.3: Predictive models of daily temperature. Parameters with a p<0.05 are highlighted by t-values given in bold. ........................................................................................................................................................................................................................................................................52

Table 2.4: Results of linear mixed effects models of first egg date predicted by year’s average temperature and location-specific temperature of the nest box for the blue tit and oak time-windows; n=1881, groups = 12 years. The intercept is given in Julian days. ........................................................................................................................................................................................................................................57

Table 2.5: Results of linear mixed effects models of oak leaf budburst predicted by year’s average temperature and location-specific temperature of the oak tree for the blue tit and oak time-windows; n=1302, groups = 4 years. The intercept is given in Julian days. ........................................................................................................................................................................................................................................57

Table 3.1: Results of linear mixed effects models of leaf growth predicted by the year’s average temperature and the location-specific temperature of individual oak trees; groups=4 (2010-2013), n=1226. Significant results are shown in bold (p<0.05). ........................................................................................................................................................................................................................................73

Table 3.2: Results of linear mixed effects models of leaf defoliation predicted by the year’s average temperature and the location-specific temperature of individual oak trees with random effect structure of budburst date nested within year (2010-2013); budburst-first defoliation: n = 924, groups=97 budburst days across 4 years; defoliation rate: n = 455, groups = 4/82; 7.5% defoliation date: n= 746, groups = 4/107; peak defoliation score: n = 1302, groups = 4/121. Significant results are shown in bold (p<0.05). ........................................74

Table 3.3: Results of linear mixed effects models of leaf growth and defoliation predicted by the year’s mean budburst date and the relative budburst of individual oak trees. The number of years (groups) and number of oaks sampled (n) are given. Significant results are shown in bold (p<0.05). ..........................................................................................................................................................................................76

Table 4.1: Linear mixed effects models of incubation pattern, predicted by the interaction of ambient microclimate temperature and territory quality [TQ] and ambient microclimate temperature and summed rainfall and the change in female condition from egg stage to chick stage [FCC] as predicted by incubation
pattern. Julian day of recording nested within year was specified as the random effect in each model. Models were tested on a single year’s worth of data and the year given in brackets, where the model of both 2012 and 2013 was insignificant.

Table 5.1: Results of generalised linear models of chick survival probability tested against predicted temperature asynchrony for phases that predict blue tit phenology and caterpillar abundance, using a binomial error structure.

Table 5.2: Linear regressions of ranked microclimate temperatures for phase A (Julian day 48 - 88) against phase C (Julian day 107 – 121) in the years 2007 and 2013.

Table 6.1: The results after model averaging of the global model of sex ratio tested against pair-wise interactions of territory quality (TQ) with male mate quality (MQ), female mate quality (FQ), clutch size (Clutch), first egg lay date (Lay date), and year as a single term, using MuMin.

Table 6.2: Models of variation in sex ratio ranked according to AICc values, AICc differences and AICc weights after model averaging of the global model of sex ratio tested against the pair-wise interactions of territory quality (TQ) with male mate quality (MQ), female mate quality (FQ), clutch size (Clutch), first egg lay date (Lay date), and year as a single term, using MuMin.

Table 6.3: Correlation matrix of explanatory variables tested in the global model of primary sex ratio bias: territory quality (TQ), male mate quality (MQ), female mate quality (FQ), clutch size (Clutch), first egg lay date (Lay date), and year. Values are for the estimate in the first instance and $r^2$ in the second instance. Asterisks denote significant correlations: *indicates p<0.05, **indicates p<0.01, ***indicates<0.001.

Table 8.1: Correlation matrix of Pearson’s pairwise correlation coefficients of temperature parameters derived from hourly temperatures recorded by loggers (n=56) from March 2012 – May 2013. Collinear terms, with a correlation coefficient $|r^2| >0.70$ are given in bold.

Table 8.2: Descriptive statistics of temperature parameters recorded at nest box height across the site. The correlation coefficients of estimate and $r^2$ for April averages of minimum, mean and maximum temperature and the ranges in temperature recorded across the site, with day of recording, are presented. Asterisks denote statistical significance (*=p<0.05, **=p<0.01, ***=p<0.001).
Table 8.3: Predictive generalised additive model of hourly mean temperature at a height of 1.8 m, for Silwood Park from 21st March 2012 until 26th May 2013. Deviance explained = 97.7%, n = 619728, scale estimate = 0.82.

Table 8.4: Slopes of linear models of first egg lay date predicted by location-specific temperatures of nest boxes in each year (2002-2013). The sample size of nests in each year is given (n). Asterisks denote statistical significance (.=p<0.1, *=p<0.05, **=p<0.01, ***=p<0.001). The slope of the regression in each year, for either of the 3 temperature parameters was not predicted by the sample size of nests (p>0.69).

Table 8.5: Slopes of linear models of oak bud burst predicted by location-specific temperatures of each tree in each year (2002-2013 n=370). Asterisks denote statistical significance (.=p<0.1, *=p<0.05, **=p<0.01, ***=p<0.001).
1 General Introduction

The thermal experience and seasonal timing

At a global scale, temperature distribution is determined by solar radiation. The rotation of the earth on its axis causes seasonal variation in temperature toward the poles, while equatorial regions have a near constant temporal temperature experience. At a smaller scale the incidence of solar radiation can be interrupted by cloud cover, the daily rotation of the earth, topography, and vegetation, such that temperature varies within a season with synoptic weather conditions, across a day and across a habitat from a landscape to micro scale (Barry and Chorley, 1998). The temperature experience determines the rate of chemical reactions, meaning that an organism either experiences temperature-induced changes in metabolic rate or if endothermic, must expend energy to maintain a constant internal temperature despite the temperature fluctuations of the external environment. This can result in seasonal or diurnal patterns of activity, or microhabitat preference (Brown et al., 2004).

Plants and invertebrates show a direct dependence on temperature for growth and in turn fecundity, as reproduction requires significant energy expenditure (Martin, 1987). For endotherms it is not only less costly to breed when temps are nearer the internal optimum (Stevenson and Bryant, 2000), but also when food availability is at its peak. Plants and arthropods form the base of most networks (Fontaine et al., 2006, Mulder et al., 1999) and at higher latitudes, seasonal warming results in a concomitant period of growth and fecundity, synonymous with Spring and the focus of this thesis (Schwartz et al., 2006). Predictable annual temperature regimes have led to the evolution of seasonally recurring life cycle events referred to as an organism’s phenology (Helm et al., 2013, Visser et al., 2010). Daylength is a principle causal mechanism of seasonal behaviour in vertebrates, triggering a cascade of endocrine and physiological responses (Dawson et al., 2001, Hahn and Ball, 1995), but daylength is fixed from one year to the next. The annual variation in phenologies is the result of the organism’s energy budget at that time (Wikelski et al., 2008).
In Britain, Spring is a period of highly variable temperature. Even within the season, temperatures are highly variable, with long periods of constant weather trends very rare (Barry and Chorley, 1998). The Spring phenologies of organisms vary from year to year accordingly (Crick et al., 1997, Dhondt and Eyckerman, 1979, Spano et al., 1999, Sparks et al., 2000, Menzel et al., 2001). Since the 1970s there has however been a trend of rising temperatures year on year indicative of climate change (Houghton et al., 1996) and this has been matched by a trend for earlier Spring phenologies in Northern latitudes (Menzel et al., 2006, Parmesan and Yohe, 2003, Walther et al., 2002).

**Climate change and species responses**

In the last 100 years our planet has warmed by 0.75°C. The ten warmest years have all occurred from 1998 onwards only, since records began in 1850 (MetOffice, 2014). Across the current century temperatures in Northern Europe are predicted to increase from 1 to 3°C by 2080, with dryer summers and wetter winters and a greater frequency of extreme weather events (IPCC, 2013).

Climate change has already impacted on the ecology of the world’s flora and fauna, an impact that can only be expected to be exacerbated given projections of further temperature increase (Hughes, 2000, Walther et al., 2002). With respect to their geographical distribution, organisms must adapt to changes in their thermal environment or face extinction. They can respond in one of two ways (i) spatial migration and dispersal to more favourable conditions (Thomas et al., 2001a), or (ii) temporal migration, tracking temperature change and exhibiting earlier phenologies (Sparks and Carey, 1995). Both of these ‘climate driven shifts’ in range and phenology have been observed in line with predictions in response to climate change (Parmesan and Yohe, 2003, Walther et al., 2005, Parmesan, 2006).

There are numerous examples of climate driven shifts in phenology (e.g. meta-analyses: Menzel et al., 2006, Primack et al., 2009, Thackeray et al., 2010). These changes have been most pronounced in the Spring of temperate latitudes (Menzel, 2000, Root et al., 2003): earlier flowering dates (Fitter and Fitter, 2002), egg-laying of avian species (Crick et al., 1997), spawning of amphibian
species (Beebee, 1995), and general ‘greening up’ (Cleland et al., 2007). Tracking of temperature change is most dramatically observed in plant species, given that temperature is a proximate cue for plants (Lenoir et al., 2008, Lesica and McCune, 2004, Menzel et al., 2006, Walther et al., 2005).

Temperature is not necessarily the proximate cue for other species or functional groups within an ecological network. If all organisms within the ecological network track the changing climate in concert, there will be no discernible impact other than the temporal change (or perhaps competition as the network overlaps with the previously antecedent phenologies of another network). If they do not show congruent changes, trophic interactions and network links may become uncoupled (Edwards and Richardson, 2004, Liu et al., 2011, Memmott et al., 2007, Thackeray et al., 2010). This is coined as the match/mismatch hypothesis (Stenseth and Mysterud, 2002). The degree of mismatch is evaluated by comparing the phenology of the dependent organisms to the phenology of their food resource, with the lower trophic level acting as a ‘yardstick’ (Walther, 2010, Visser and Both, 2005) and quantifying the breeding success, survival and fitness of the dependent organisms as predicted by their degree of overlap (Cushing, 1990, Durant et al., 2007, Edwards and Richardson, 2004, Liu et al., 2011, Miller-Rushing et al., 2010, Post and Forchhammer, 2008, Thomas et al., 2001b, Winder and Schindler, 2004).

In this way, the novel thermal environments resulting from climate change have led to a selection pressure for adaptation (Brommer et al., 2005, Gienapp et al., 2010, Nager and Vannoordwijk, 1995, Ozgul et al., 2009). These can take the form of micro-evolution if there is a long-term directional change in the temperature gradient (Husby et al., 2011) or phenotypic plasticity, whereby organisms may change the phenotype given the environmental conditions (Nussey et al., 2007). In Spring, where there is a high variability in temperature from one year to the next, a phenological response in one year may not be adaptive in the next (Nager and Vannoordwijk, 1995). A heterogeneous or highly variable environment will favour different phenotypes given the conditions prevailing at that time. It is therefore adaptive for organisms breeding in more than one year, or where there is a high probability of progeny breeding in an environment different to that
experienced by the parent, to be labile in the trait and for the range in reaction norm to be heritable (Nussey et al., 2005). The success of phenotypic plasticity in mediating climate change does not just depend on the phenotypic range of an organism, but also the presence of reliable environmental cues (Valtonen et al.), demonstrated by migrant species, not able to track changing temperatures in preferred breeding areas due to their pre-breeding geographical remove (Both et al., 2010).

1.1 A model system

The model tri-trophic system of oaks, caterpillars and passerine birds has been studied intensively as a model system by which to observe the impacts of climate change on an ecological network (Perrins, 1979, Visser and Holleman, 2001, Visser et al., 2003a, Both, 2010). It is a relatively simple food-chain which is highly temporally constrained, limited by the abundance of the caterpillar, a major food source of the tit, which feeds on the new young oak leaves of Spring until they become unpalatable and dark green (Tikkanen and Julkunen-Titto, 2003). It enables study of the selection pressure of trophic mismatch through the easy quantification of breeding parameters of the avian apex predator, for example: onset of breeding activity, number of eggs laid, number of chicks fledged (Both and Visser, 2005, Lambrechts et al., 2004, Lambrechts et al., 1996, Norris, 1993, Perrins and Mc Cleery, 1989) and whether the individual returns to breed in the following year and progeny recruit into the breeding population (Both et al., 1999, Verboven and Visser, 1998, Verhulst and Tinbergen, 1991). The three links in the food chain are expected to differ in their responses to temperature change resulting in a decoupling of the network (Both et al., 2009, Dewar and Watt, 1992). An outline of the ecology of the oak, caterpillar and blue tit and their associations with temperature are given in section 1.3.

The simplicity of this network and its study means there is a large number of study populations, providing gradients of population mean responses and rates of change as a result of altitude or latitude, and the influence of vegetation type (Blondel et al., 1993, Both et al., 2004, Banbura et al., 1994, Lambrechts et al., 2004, Tremblay et al., 2003, Visser et al., 2003a), and find the
different phenologies between populations to be predicted to by their differing temperature experience (Sanz, 1998, Both et al., 2004). An example comparison is of the two long-running study populations of Whytham woods near Oxford (1947 to present day) and the Hoge Veluwe in the Netherlands (1973 to present day), which use the summed maximum temperature and mean daily temperature respectively. Both populations have seen an increase in Spring temperatures. Their tit phenologies are predicted by temperature variation over different phases of Spring, however: 1st March – 25th April at Whytham, 16th March to 20th April at the Hoge Veluwe. The Hoge Veluwe population shows a high degree of trophic mismatch with caterpillars showing an accelerated phenology three times that of the great tit exploiter (Visser 2006), while the Oxford population shows a maintained synchrony and a thriving population density (Charmantier et al., 2008). A comparison of just these two population responses, shows that populations differ not only in their rate of change, but in their period of temperature association, the temperature parameters used to draw comparisons, or even more local temperature differences (Stewart and Lister, 2001, Visser et al., 2003a).

Greater differences in phenology have been observed between populations only 50km apart within a country, than differences between countries across continents (Visser et al., 2003a). Given that mechanistic aviary studies show there to be a causal link with temperature and responses to be heritable (Nussey et al., 2005, Schaper et al., 2012, Visser et al., 2009) this suggests that responses of a Spring network to climate change may be population specific and that population responses may differ more than those of the individuals within them. Some studies have sought to compare lay date phenologies to temperatures at smaller scales such as meta-populations, referring to this as micro-geographic variation in first egg lay date, but habitat differences, such as coniferous versus deciduous woodland, have meant that temperature trends are obfuscated by the plant phenology (Moller, 2008, Thomas et al., 2010). The vegetation type and trends may themselves convey information on microclimate temperature though (Bourgault et al., 2010, Cole et al., 2015).
Within populations there is variation in phenology from which the mean is drawn. This variation is often largely ignored, but may be the product of temperature variation within the study system and microclimates across a habitat (Chen et al., 1999, Dobrowski, 2010, Scherrer and Körner, 2010, Suggitt et al., 2011). Within a population one temperature measure is typically used to compare against hundreds of nesting attempts (Grosbois et al., 2006, Matthysen et al., 2011, Vatka et al., 2011) and it is not straightforward to distinguish how individuals respond to different temperature regimes across the breeding habitat (Gienapp et al., 2005). Aviary studies enable the researcher to test different temperature regimes explicitly and gain a mechanistic understanding of the role of temperature (Schaper et al., 2012, Silverin et al., 2008), but removes the organism from the natural breeding environment with a logistical limit to sample sizes and regimes to be tested. An alternative is to monitor temperature across a study site and assess the response of the individual against their thermal experience.

1.2 Assessing temperature

Data-loggers can be deployed to record temperature across habitat gradients (Suggitt et al., 2011), changes in vegetation structure (Chen et al., 1999, Coulson et al., 1993, Saunders et al., 1998, Saunders et al., 1999) or even within a single tree (Serio-Silva and Rico-Gray, 2002) characterizing the temperature environment of a single leaf (Pincebourde et al., 2007). By distributing data-loggers across an area, temperature data is not isolated to the single recording location, but can be interpolated between points, for example by distance-weighting interpolation or krigging (Hengl et al., 2007, Jeffrey et al., 2001). As temperature is determined by the strength of sunlight and this is influenced by the incidence of sunlight, temperatures change with varying geographical characteristics of the land, such as gradient, aspect and landuse. Geographical and topographical characteristics can be employed to further enhance the mapping of temperatures and rainfall, and have been used extensively in climate studies and to predict microrefugia with climate change (Ashcroft and Gollan, 2012, Bennie et al., 2008, Dobrowski, 2010, Fridley, 2009, Jeffrey et al., 2001,
Lenoir et al., 2008, Scherrer and Körner, 2010). For a U.K. study system, such geographical and topographical information is readily available via the Ordnance Survey and British Geographic Survey (digimap.edina.ac.uk).

By recording temperatures at specific locations one can see that far from one measure of temperature being equal to all, two nests could have similar overall mean temperatures, but differ in their temperature extent (Illustrated in Figure 1.1). This is perhaps not surprising when one considers for example, that high daily temperatures are associated with clear skies, but a clear night sky is typically associated with the lowest minimum temperatures (Barry and Chorley, 1998). By mapping temperature across a study site, the thermal environment may be characterised and a better understanding gained of the biological significance of differing temperature regimes to organisms and their interactions within a network. Different characteristics of the thermal environment may act on the bird, caterpillar or tree. An increase in minimum temperature will alleviate basal metabolic costs (Silverin and Viebke, 1994, Bonhomme, 2000), while accelerating maximum temperatures may act as a cue for a fast approaching peak in invertebrate abundance (Schaper et al., 2012, Smith et al., 2011).

When comparing phenologies to temperature change, it is important not to confound temperatures with time, for example a ‘month before first egg lay date’ would vary each year with interannual variation in lay date. This means that when comparing temperatures, the period of temperature comparison should be fixed for a particularly timeframe from one year to the next. Studies either use temperatures of specific months or may identify a ‘time-window’ across which temperature variation best predicts interannual variation in phenology across their dataset (Phillimore et al., 2013, Roy and Sparks, 2000, Sparks and Carey, 1995, Sparks et al., 2000). Both are linear regression approaches of temperature predicting phenology. Another approach is to use a temperature summation referred to as the ‘summed degree days’, whereby the time taken to attain a temperature threshold is instead compared from year to year (Phillimore et al., 2013). This is a common approach in vegetation/forestry studies (Cannell and Smith, 1983a, Garcia-Mozo et al., 2002, Kramer, 1994, Kramer, 1995).
Figure 1.1: Illustration of different temperature parameters recorded in April 2012 at two logger locations. Maximum daily temperatures are shown in red (average maximum temperature: plot a=18.12 (+/-0.87); plot b = 11.82 (+/-0.37)). Minimum daily temperatures are given in blue (average minimum temperature: plot a=1.58 (+/-0.55); plot b = 3.01 (+/-0.49)). The overall mean temperature is marked by the green line (plot a = 7.54°C (+/-0.30); plot b= 7.34°C (+/-0.29)).

1.3 Study organisms

The oak

The oak (Quercus spp.) stretches from cool to tropical latitudes and includes 600 deciduous and evergreen species (Mabberley, 2008). Quercus robur, otherwise known as English oak or pedunculate oak, is a deciduous tree ubiquitous with the English countryside, but also native to most of Europe, extending through to the Caucuses and North Africa. Trees are dioecious, can grow to a diameter of 4m supporting a large crown and live to over a thousand years old. They support the greatest number of herbivore species in the UK at over 400 species (Kennedy and Southwood, 1984), commonly Lepidoptera, such as the oak processional, Thaumetopoea processionea, and gypsy moth, Lymantria dispar, but in turn insectivores such as the blue tit and pied flycatcher and mammal species such as...
squirrels that feed on the acorn fruit of the tree in Autumn. A similar species that inhabits the same range is the sessile oak, *Quercus patraea* (Scotti-Saintagne et al., 2004).

Dormant buds break into leaf in early Spring, from late March onwards. The small young oak leaves have a high nitrogen content which falls from 5 to 2% between first emergence and leaf expansion when the lamina of the leaf is fully extended (Buse et al., 1999). The young leaves are vulnerable to defoliants, but with increasing Spring temperatures the tannin content of the leaves increases making them highly resistant to damage by defoliants and fungi (Tikkanen and Julkunen-Tiitto, 2003). By the end of June the leaves have turned dark green and developed a waxy upper cuticle to limit water loss by evapotranspiration. Leaf abscission occurs in Autumn and prevents frost damage and further water-loss to the plant (Estrelle and Menzel ref 2006).

Individual trees show a consistent phenological rank across years, with the first trees to exhibit budburst in one year, among the first in the following year (Crawley and Akhteruzzaman, 1988). There is also a repeatable rank in tanninisation and though trees that come into leaf earlier typically show earlier leaf senescence, trees that come into leaf earlier are not necessarily those that go through tanninisation earlier (highly significant, but not collinear: $r^2=0.4$, 1 and 32 d.f. p<0.001).

The benefit of early budburst relative to the wider population of conspecifics is not just a longer growing season, but also means young vulnerable leaves emerge and develop before the peak in caterpillar abundance concomitant with the greater overlap in tree phenology (Crawley and Akhteruzzaman, 1988, Visser and Holleman, 2001). The trade-off is that early flushing trees are vulnerable to Spring frosts, which would kill young leaves, considerably affecting a tree’s yearly growth and instead shortening the overall growing season (Lechowicz, 1984). A longer growing season results in greater growth with a greater height increment (Vitasse et al., 2009a).

Oaks are highly sensitive to temperature in comparison to other temperate species, such as beech trees, showing both earlier budburst and later leaf senescence per degree increase when comparing populations across altitudes (Vitasse et al., 2009b). Comparisons across latitudes through transplant experiments show this to be a plastic response, rather than the result of high local
adaptation within a long-lived plant (Kramer, 1995). While the response to temperature as in other plants, is linear, this is given certain caveats: typically once temperatures have exceeded an initial threshold of 4-5°C (Cannell and Smith, 1983b, Garcia-Mozo et al., 2002) and also, as in other tree species, dependent on an initial chilling period from November onwards, which promotes the Winter dormancy (Cannell and Smith, 1983b), with colder Autumn temperatures resulting in less warmth needed in Spring to facilitate budburst (Murray et al., 1989, Sparks and Carey, 1995).

**The caterpillar**

The oak winter moth caterpillar, *Oberophthera brumata*, is abundant on pedunculate oak trees (Crawley and Akhteruzzaman, 1988). Though it feeds on a range of deciduous trees and shrubs and is even found on sitka spruce and heather, it feeds primarily on oaks of the genus *Quercus robur* (Kerslake and Hartley, 1997, Vanbergen et al., 2003, Wint, 1983). Eggs hatch in April or May. The head capsule of the first instar larvae is only 0.25mm in diameter and so is capable of feeding on only very young oak leaves (Buse and Good, 1996). The size of the caterpillar prior to pupation is strongly determined by the nitrogen content of the oak leaf and hatching on very young leaves results in pupae with the highest fat percentage which go on to become the longest lived females with greatest fecundity (Wint, 1983, Feeny, 1970). Caterpillars drop from the tree once leaves have become inedible and pupate in the soil beneath (Feeny, 1970). Eclosion from the pupa occurs in the Autumn and while the male can fly, the flightless female climbs the natal tree to mate and lay eggs in the crown, beginning the cycle for another year (Buse and Good, 1996, Feeny, 1970).

An individual is typically monophagous as the larva will feed on the tree on which it was hatched and emerge onto as an adult in turn, resulting in local adaptation to the individual oak (Wint, 1983, VanDongen et al., 1996). This is because migration, the alternative, is costly (Holliday 1977). There can therefore be greater variation in herbivore density between trees than between stands of trees (Zehnder et al., 2010). The oak wintermoth show greater inter-tree variation than another oak herbivore, the green oak leaf roller moth, *Tortrix viridana* (Hunter et al., 1997). This is ascribed to the
selection pressure of a lower starvation tolerance. Like other caterpillars they can survive some
degree of starvation (Leather, 1986): up to 4 days comfortably (Wint, 1983), 4-10 days according to
Tikkanen et al. (2003). Despite such high local adaptation and heritability of egg hatch date, there is
surprisingly large variance in egg hatch: 28 days within a sample when grown in constant conditions
(Buse and Good, 1996, van Asch et al., 2007, Merila et al., 2001).

There is a trade-off for the caterpillar (Singer and Parmesan, 2010). If they hatch early, they
risk starvation and massive mortality is observed (Hunter et al., 1997), but if they match they can hit
the jack-pot of increased fecundity. Despite the oak wintermoth coinciding egg hatch with budburst
(van Asch et al., 2007), they cannot directly detect budburst (Buse and Good, 1996) and yet when
caterpillars are reared with the trees at experimentally elevated temperature, the pupal mass was
not detrimentally affected and instead the caterpillars pupated earlier, suggesting that they could
anticipate the effects of climate change on foliar quality (Buse et al., 1998). Increasing temperatures
are predicted to benefit invertebrates (Thomas, 1993, Roy et al., 2001, Bale et al., 2002). The oak
wintermoth caterpillar has demonstrated the capacity for a rapid response to increasing
temperatures, able to accelerate development from 50 days to 20 days in an experimental
temperature increase (Buse et al., 1999). Earlier Springs, resulting in longer Spring/Summers are
expected to afford invertebrates a longer growing period, resulting in greater fecundity (Bale et al.,

The blue tit
The blue tit is a cavity nester and readily breeds in nest boxes, robust to disturbance and
manipulation (Perrins, 1979). As such it is a model species used for studies of sexual selection
(Andersson et al., 1998, Kempenaers et al., 1992) and sex ratios (Bell et al., 2014, Sheldon et al.,
1999), individual optimisation (Nur, 1988, Svensson et al., 1998, Arnold et al., 2010), habitat use
(Banbura et al., 1999, Dhondt et al., 2010) and life-history trade-offs (Svensson and Nilsson, 1997,
Woodburn and Perrins, 1997). Clutch sizes range from 8 to 14 eggs, though even 19 on one very rare
occasion (pers. obs.; Perrins, 1979). Adults and chicks can be caught on the nest for individual marking by metal identity rings enabling the collection of data such as overall breeding success and survival across an individual’s lifetime (Redfern and Clark, 2001). In turn the success of the current reproductive effort can be measured against the quality of the individual’s breeding environment and previous experience (Wilkin et al., 2007, Wilkin and Sheldon, 2009).

Blue tits are income breeders, depending on food resources available at the time of reproduction to support the breeding effort (Houston et al., 2007). As in most bird species reproduction is split into three phases of investment: egg production, incubation and chick provisioning. All three are energetically costly, and involve a trade-off between parental effort and maintenance of parental condition, common to the trade-off between current and future reproduction (Bryant, 1979, Daan et al., 1989, Drent and Daan, 1980, Stearns, 1989). The level of investment at incubation can impact on life-history events downstream, such as hatching date (Matthysen et al., 2011, Vedder, 2012) and future fecundity (Hanssen et al., 2005, Nilsson et al., 2008, Nord and Nilsson, 2011). Territory and individual quality can mediate investment in the current breeding effort and impact on individual fitness (Bell et al., 2014).

Blue tits are food specialists in the breeding season, taking advantage of a restricted period of peak caterpillar abundance in the Spring of higher latitudes (Gibb, 1954, Perrins, 1979). The caterpillar offers a high nutritional content at a reduced handling time compared to other invertebrates (Banbura et al., 1999). Where the peak in food demand of the nest coincides with the peak in caterpillar abundance chicks are more likely to fledge and in better condition (Tremblay et al., 2003). In turn, heavier chicks have a better survival probability with chicks laid earlier in the Spring showing greater recruitment (Tinbergen and Boerlijst, 1990, Verboven and Visser, 1998, Verhulst and Tinbergen, 1991). With a greater abundance of prey at the time of ultimate necessity, the breeding bird also gains from reduced foraging costs and time spent away from the nest (Tremblay et al., 2005). Miss-timed reproduction relative to such a vital food source, referred to as trophic mismatch, can have catastrophic consequences for the breeding attempt of that year (Visser et al., 2006, Visser
et al., 1998). Consequently blue tits are a model species for exploring the associations of food availability and breeding success (Lack, 1968, Banbura et al., 1994, Lambrechts et al., 2004, Tremblay et al., 2005, Tremblay et al., 2003).

1.4 Study site

Silwood Park

This study was carried out at Imperial College’s Silwood Park campus, a post-graduate campus specialising in ecology located approximately 40km west of London (51.25°N 0.4°W, ordnance survey grid reference SU 946 686). The 110 ha is typical of lowland England, classified as a NVC W10 community, dominated by oak woodland with acid grasslands (Crawley, 2005) and has a long history of ecological research (Crawley and Akhteruzzaman, 1988, Jones et al., 1993, Lawton, 1996).

Nest boxes for blue tits were distributed across this oak-rich woodland in 2002 and have been monitored for occupancy and breeding activity in each consecutive Spring. The nest boxes have a hole diameter of 28 mm, making them ideal for use by blue tits, the focus of the original research aim to explore the heritability of plumage colouration (Hadfield and Owens, 2006, Hadfield et al., 2006). A further 50 nest boxes with a diameter of 32mm, permitting both great tit and blue tit use, were added in 2009, bringing the total number to 275.

The phenology of 3215 individual Quercus robur oak trees have been monitored across the site since 2007 beginning with an initial sample of 347 trees and reaching a maximum of 1848 in 2013 (2010 = 1470, 2011 = 1819, 2012 = 1773, 2013 = 1848). From 2009 trees were monitored in a biennial rotation, with half monitored one year and the other half the next year, but a core subset of approximately 370 trees monitored every year from 2010 – 2013. Further to this defoliation activity has also been recorded.

Each oak and nest box has been mapped by geographical positioning system (Figure 1.1; Bell et al., 2014). A digital elevation model for the site (spatial resolution of 10m, available from Edina, 2012) provides data on elevation, aspect and slope and is complemented by an aerial photo captured...
for the site in 2008 (resolution of 0.125m pixel size, captured on 8th October 2008 by UKAerialPhotos, Brightmaster Ltd © 2012). The Silwood Park boundary was mapped in 2009 by Gary Powney.

The Silwood Park weather station has been recording temperature since 1987. Since 2009 it has recorded wind speed and wind direction, average ambient temperature and humidity (CS215 probe) and rainfall (CS500H tipping rain gauge) on an automatic hourly basis (Campbell Scientific CR100). Since 2002 the temperature has ranged from a minimum of -14 on 20th December 2010 to a maximum of 36.8 on 11th August 2003. Annual temperatures from 1st January until the end of June for each year from 2002, with daily summed rainfall and the annual distribution of first egg lay dates are illustrated in Figure 1.3.
Figure 1.2: Map of Silwood Park study site. Oak trees are shown as green spots, nest boxes as red spots.
Figure 1.3: Silwood Park weather station records and breeding chronology of blue tit population. Plots from 1st January to 21st June in Julian days of mean temperature (black points), total rainfall (dashed blue vertical lines) and mean first egg lay date (solid red line; dashed red lines denote the first egg lay dates of the first and last nest for that year), for each year from 2002 - 13.
1.5 Research aims and thesis outline

The aim of this thesis is to test whether variation in oak, caterpillar and bird phenology is associated with spatial variation in temperature across a single study site. To do this I constructed a robust geospatial model of temperature microclimates, providing information on the thermal environment at the metre-scale. The model is based on known topography, synoptic weather conditions, and seasonal trends and informed by over a year’s worth of temperature data recorded across the study site (Chapter 2).

Numerous studies test the reaction norms of spring-breeding passerines against a temperature gradient using long term datasets of breeding activity over multiple years (Nussey et al., 2007, Gienapp et al., 2005) or across different populations against their associated local temperatures (Both et al., 2004, Dunn, 2004). Such methods do not account for variation in phenology within the population. An alternative approach is to explicitly explore how an individual responds to characteristics of its thermal environment. The impact of temperature may be more subtle than warm versus cold. Organisms may respond to temperature extents or rates of change. Minimum temperatures may act as a limiting factor in a system limited by energy resources, while maximum temperatures may accelerate biochemical reactions and growth. By recording hourly temperatures, daily averages, but also the daily extremes in temperature can be mapped and predicted across the study site and the impact of different temperature regimes under natural conditions assessed (Chapters 2).

This tri-trophic network rests on the phenology of oak budburst, but though budburst determines the point at which caterpillars may feed on the oak tree, it is the date of tanninisation which dictates when caterpillars pupate and the limit of the food source for the breeding blue tit. I test if there is an association of oak leaf growth rate with temperature and assess how tanninisation varies with temperature across years and from tree to tree within a year. I also assess how the date of budburst itself may determine the dependent leaf and caterpillar phenologies downstream, with implications for the magnitude of defoliation (Chapter 3).
Microclimate temperature is also predicted to directly influence incubation behaviour as successful egg development is highly temperature dependent. A further application of mapping individual-specific temperature microclimates is to test associations of incubation behaviour with environmental cues. Not only daily, but hourly temperatures can be predicted. The influence of ambient temperature and territory quality information on incubation behaviour can be tested and the incubation behaviour adopted can then be used to predict changes in female condition accounting for the temperature microclimate of the nest location (Chapter 4).

Changing temperature environments that arise from a changing climate are predicted to impact on the cohesion of ecological networks as organisms at different trophic levels may show differing responses to temperature change. Different responses across a network may result when organisms differ in when they are sensitive to temperature change and which temperature parameter they are sensitive to if temperature parameters are not collinear. Throughout this thesis I identify the time-windows of temperature sensitivity for each element of this tri-trophic ecological network and the predictive temperature cues for their respective phenologies. I then test the impact of differing temperature responses on the degree of synchrony of one trophic level to another (Chapter 5).

Finally the results are discussed in light of the research aims, current theory and their significance in terms of further work (general discussion, Chapter 0). During the course of this doctoral research programme, the effect of territory quality and mate quality on the breeding strategy of sex ratio bias has been tested in this study system. This study is included in the thesis (Chapter 6).

**Thesis outline:**

**Chapter 2: A geospatial model of temperature that predicts phenology in wild populations of birds and trees** – construction of a model of temperature for the study site and comparison of microclimate temperatures in the prediction of the labile trait of blue tit first egg lay date and oak budburst.
Chapter 3: Does budburst predict Spring phenology of oak trees? – a comparison of temperature parameters in their prediction of oak leaf growth and defoliation and the association of caterpillar abundance with oak budburst.

Chapter 4: Incubation activity and female condition are predicted by microclimate temperature – test of incubation pattern against microclimate temperatures and the association of incubation pattern and microclimate temperature on female condition.

Chapter 5: The nesting success of a free-living bird is predicted by unequal Spring temperature change – comparison of temperature change across the different time-windows associated with phenology at different trophic levels of the simple foodchain and the impact of unequal temperature change across the different phases of Spring on the breeding productivity of the apex predator.

Chapter 6: Quality of breeding territory mediates the relationship between paternal quality and sex ratio bias in a free-living bird population – I show that variation in primary sex ratio is associated with paternal quality, but that the relationship hinges on the quality of the breeding territory.

Chapter 7: General discussion – conclusions drawn from research: efficacy of modelling temperature, space substituting for time in the study of phenological systems, different inferences to be drawn from different temperature parameters and that temperature change is not congruent across different phases of Spring.
2 A geospatial model of temperature that predicts phenology in wild populations of birds and trees

Climate change has led to earlier Springs in the Northern Hemisphere and shifts in recurring annual events such as budburst in plants and the first egg laying dates of birds. Most phenological studies document a trend for earlier population mean phenologies in warmer years. The variation among individuals within study populations, offers the opportunity to test for a response to temperature change at the individual level though. Here I present a novel method of temperature prediction across the landscape of a single study system, which can describe how minimum, mean and maximum temperature varies across the site and year to year. The range in temperature recorded across the site within years is equivalent to the greatest range between years. As predicted from studies of population means, I find that there is a microclimate effect on the phenology of both birds and trees, with eggs laid earlier and budburst occurring earlier in warmer areas. However, the bird and tree do not show the same associations with temperature, differing both in the time-window that best predicts changes in phenology and in the aspects of temperature that best predict phenology. By mapping temperature across a small study site I find that space may act for time in the study of species responses to temperature change, facilitating the study of individual responses to temperatures in the wild.

**Key words:** microclimate, ecological networks, climate change, *Cyanistes caeruleus, Quercus robur*
2.1 Introduction

A large body of empirical work has shown that climate change has led to shifts in the phenology and altitudinal and latitudinal ranges of a wide array of species (Beebee, 1995, Fitter and Fitter, 2002, Hickling et al., 2006, Lenoir et al., 2008, Lesica and McCune, 2004, Parmesan and Yohe, 2003, Perry et al., 2005, Root et al., 2003, Sparks and Carey, 1995, Sparks et al., 2005). This leads to the possibility that ecological networks may lose cohesion as species’ distribution and seasonal patterns of activity change with their perception of, and in reaction to, varying temperature cues, with a mismatch in prey availability and consumer demand (Edwards and Richardson, 2004, Liu et al., 2011, Memmott et al., 2007, Thackeray et al., 2010, Stenseth and Mysterud, 2002).

The relatively simple Spring food-chain of oak (*Quercus robur*), caterpillar (*Opretopthera brumata*) and passerine bird, has been studied intensely as a model system by which to observe the impacts of climate change on a network (Perrins, 1979, Visser and Holleman, 2001, Visser et al., 2003a). Oaks show large interannual variation in leaf emergence/budburst (VanDongen et al., 1997, Wint, 1983) and a high sensitivity to temperature in comparison to other deciduous tree species across altitudinal temperature gradients (Vitasse et al., 2009b). Translocation experiments across latitudes show such temperature dependent budburst to be a plastic response (Kramer, 1995, Vitasse et al., 2009a). The plant phenology of budburst determines the phenology of herbivorous invertebrates such as the oak wintermoth caterpillar, through the availability of palatable new leaves (Buse et al., 1998, Cleland et al., 2007). In such an immovable organism, individual leafing phenology relative to that of neighbouring conspecifics can however be an anti-herbivore defence and by shifting leafing phenology into an exploiter-free time, later leafing trees suffer less defoliation and herbivore damage (Hunter et al., 1997, Singer and Parmesan, 2010, Wesolowski and Rowinski, 2008).

For the Spring breeding passerine it is important to coincide the peak in food demand with the peak in caterpillar abundance, as chicks are more likely to fledge, be heavier (Tremblay et al., 2003) and have a better survival probability and likelihood of recruitment (Tinbergen and Boerlijst,
Verboven and Visser, 1998, Verhulst and Tinbergen, 1991, Both et al., 1999). Failing to match the peak in food demand of the nest to that of food availability can result in reduced nesting success for that year (Visser et al., 2006, Visser et al., 1998) and also impact on the future survival of the adult (Grosbois et al., 2006, Thomas et al., 2001b). Spring breeding in birds is triggered by increasing daylength and circannual rhythms (Silverin et al., 2008, Hau et al., 1998, Helm et al., 2013). While daylength is fixed from one year to the next, there is a variation in breeding dates between years which is associated with temperature (Sparks and Carey, 1995), with an aviary study demonstrating a causal link (Visser et al., 2009).

Numerous studies have tested the reaction norms of spring-breeding passerines against a temperature gradient using long term datasets of breeding activity over multiple years (Nussey et al., 2007, Gienapp et al., 2005). A survey of the literature by Dunn found 79% of papers reported earlier lay dates with an increase in temperatures (Dunn, 2004). Other studies have compared the rates of change within different populations across a latitudinal gradient finding comparable trends to those reported within populations over time (e.g. Both et al., 2004, approx. 3 day shift/degree increase). Another study by Visser (2003) conceded however, that even populations very close to one another (3km or 50km) showed different patterns of laying date which may be due to microclimate or habitat.

As with difference between populations, there is also variation in phenology among individuals within populations. This could be due to a heritable life history response of the individual (Husby et al., 2011, Nussey et al., 2005, Visser et al., 2011), but may be due to a variation in temperature at the small scale of the study site landscape. Just as temperature varies spatially across altitudes and latitudes it may vary substantially enough across a single habitat to account for the individual variation in phenology therein. An ability to respond to changing temperatures from one year to the next is adaptive (Nussey et al., 2005, Charmantier et al., 2008), and in a hole-nesting species such as the blue tit, where few chicks survive the first Winter and adults may not breed.
beyond a single Spring (Lambrechts et al., 2004, Perrins, 1979) this same sensitivity to temperature may be observable at the local landscape scale.

Locations may vary, not just by being warmer or colder on average, but in their minimum and maximum temperature and exposure to extremes of temperature (Bennie et al., 2008, Nelson and Martin, 1999, Saunders et al., 1999). Given that even within a day the coldest temperature is usually around sunrise and maximum temperature after midday, it is not to be expected that the three temperature characteristics of minimum, mean and maximum temperature will be collinear in their change. Temperatures vary across landscapes throughout the year due to topography and vegetation cover and these factors vary in turn with local or seasonal weather conditions (Bennie et al., 2008, Lennon and Turner, 1995, Pepin et al., 1999, von Arx et al., 2012). Such location specific temperature is referred to as a microclimate. Microclimates influence an organism’s physiological capacity and therefore its ecological performance (Chen et al., 1999, Wachob, 1996) to the extent that they have offered refugia from otherwise unfavourable climatic conditions (Thomas, 1993, Stewart and Lister, 2001).

Using a 12 year dataset of blue tit nesting activity and a seven year dataset of oak budburst dates, the aims of this study are three-fold. Primarily I set out to construct a robust predictive model of temperature across a single study site, based on geographical parameters and recorded weather trends. The trends of temperature variation are then used to predict temperatures in years and locations where temperatures were not recorded, to utilise the whole of the phenological dataset. Secondly, time windows are identified by which interannual variation in phenology for the oak and blue tit are most strongly correlated with interannual temperature variation. Finally, I seek to test if variation in microclimate temperature across a site within these time windows predicts variation in budburst and first egg dates in the oak-blue tit system.
2.2 Methods

2.2.1 Study area and data collection

The study was carried out at the 110 ha site of Silwood Park, approximately 40km west of London (51.25°N 0.4°W, ordnance survey grid reference SU 946 686), which ranges in elevation from 42 to 72m above sea level. The site is typical of lowland England, dominated by oak woodland with acid grasslands (NVC W10 community, Crawley, 2005) and weather typical of South East England, a region that experiences some of the highest U.K. average annual temperatures (10-11°C) and sunshine duration (1500-1600 hours) with frost days (40-60 days/year) in line with the national average (MetOffice, 2015).

The breeding activity of a study population of blue tits has been monitored since 2002 (Hadfield and Owens, 2006, Hadfield et al., 2006), specifically the breeding activity from 21st March - 20th June each year and the first egg lay date for each nest box. Care was taken in this study to only include nests known to be the first breeding attempt within that nest box or by that female in that year, excluding replacement clutches (Perrins, 1979). The sample size of nests for each year ranged from 112 in 2010 to 234 in 2011 (mean number of nests = 171.17 +/- 11.3). Nest boxes are of fixed locations across the site and have been mapped by a Geographical Positioning System (Bell et al., 2014, GPS, Magellan MobileMapper cx, Pocket Gis v2.4).

The phenology of 3215 Quercus robur oak trees were monitored across the site starting in 2007 with 347 trees, reaching a maximum between 2010 to 2013 with trees monitored in a biannual rotation (2010 = 1470, 2011 = 1819, 2012 = 1773, 2013 = 1848). A subset of 370 oaks have been monitored every year from 2010-2013 and the date of first leaf emergence, ‘budburst’ recorded. The location of each tree has been mapped by Geographical positioning system (Bell et al., 2014).

2.2.2 Temperature recording

A weather station has been recording hourly temperatures and sunlight on site since 1987. From 20th March 2012 until 28th May 2013, 99 dataloggers were set out across the site to record temperature
every 30 minutes. Loggers were placed across the site to capture as wide a range in geographical variables as possible. These were: aspect, slope, elevation and distance to forest edge (Figure 2.1). This was achieved by producing 1m by 1m rasters of aspect, slope and elevation from a digital elevation model (spatial resolution of 10m, available from Edina, 2012), and calculating the Euclidean distance to the forest edge, by mapping a polygon layer of canopy cover and buildings, from an aerial photo (resolution of 0.125m pixel size, captured on 8th October 2008 by UKAerialPhotos, Brightmaster Ltd © 2012).

To ensure that true differences in temperature were recorded across the site data loggers were consistently positioned on the north facing side of a tree or post, within white plastic pots, sheltered from rain or direct sunlight and extremes in temperature. Loggers were set out at two heights: c. 1.8m, (the average height of nest boxes within the site, n=64; Tinytag data loggers, Gemini Data Loggers UK ltd, resolution of <0.02°C) and canopy level (average height of 12.26 m (+/- 0.03, n=35, i-button, resolution of <0.0625°C). I-buttons were drawn up into place by catapulting lines into the canopy of oak trees to which a tinytag at 1.8m had been fixed, facilitating a comparison of temperatures at each of the two heights. Care was taken that the temperature sensitive elements of both the Tinytag and i-button loggers were approximately equal distances from the opening of their respective container (for logger set-up see Figure 8.1 and Figure 8.2 in the appendix). Average April temperatures recorded at 1.8m were highly predictive of temperatures recorded in the canopy for minimum, mean and maximum temperatures ($r^2 >= 0.79$, Figure 2.2). Analyses presented are therefore limited to temperatures recorded at 1.8 m height, at which a larger number of loggers were deployed.

Prior to deployment, loggers were placed in a constant temperature room set to 21°C, a mean temperature recorded for the population of loggers was calculated and the deviance of each logger from this mean was used to correct the daily temperatures collected in the field for each logger (Tinytag loggers (1.8m): -0.28 to +0.68; i-buttons (canopy): -0.51 to +0.55). Temperature outliers were identified as readings that were 1.5 times the interquartile range above the third
quartile or below the first quartile for mean temperature for the respective day (Figure 8.3; Crawley, 2013). To test whether there was any redundancy in recording minimum, mean and maximum temperatures the three temperature measures recorded by each logger were correlated against one another. Minimum, mean and maximum temperatures are not collinear (Table 8.2). Minimum and mean temperatures for April were highly correlated in 2012. In both 2012 and 2013 the average April minimum and maximum were inversely correlated (Table 8.2).

Figure 2.1: Maps of logger positions relative to geographical predictors used in the geospatial model of temperature prediction (map a: gradient or slope (°); map b: height above sea level (m); map c: predominant aspect (°); map d: density of oak trees – number of oak trees within a 50m radius).
Figure 2.2: Comparison of March, April and May 2013 temperatures recorded within the canopy and at nest heights (~1.8 m) of 32 trees (March: minimum: int. = -0.41, est. = 1, $r^2 = 0.90$; mean: int. = -0.01, est. = 0.93, $r^2 = 0.87$; maximum: int. = 0.48, est. = 0.92, $r^2 = 0.77$; range: int. = 0.30, est. = 0.99, $r^2 = 0.85$; $p<0.0001$, $n=835$. April: min: int. = -0.33, est. = 1.05, $r^2 = 0.95$; mean: int. = -0.15, est. = 1.01, $r^2 = 0.97$; max: int. = 0.98, est. = 0.90, $r^2 = 0.79$; range: int. = 0.99, est. = 0.90, $r^2 = 0.68$; $p<0.0001$, $n=691$. May: min: int. = -0.43, est. = 1.03, $r^2 = 0.92$; mean: int. = 0.01, est. = 1.02, $r^2 = 0.92$; max: int. = 2.90, est. = 0.88, $r^2 = 0.70$; range: int. = 1.35, est. = 0.97, $r^2 = 0.80$; $p<0.0001$, $n=456$).

### 2.2.3 Temperature prediction

To test if phenology such as budburst or first egg date varies with temperature in the wild one can record temperatures at each individual tree/box location, or by experimentally manipulating the temperature of the nest box (Nager and Vannoordwijk, 1992, Vedder, 2012). Recording temperature
in such a way, though ideal, is labour intensive, resulting in temperature data which is limited to the timespan of data collection (Bourgault et al., 2010, Schaper, 2012). Further to recording temperature across the site, I therefore set out to model the manner in which temperatures recorded by the loggers varied in association with landscape characteristics and the local weather and seasonal trends over the course of a year in order to predict temperatures where they had not otherwise been recorded. The geographical characteristics of a logger location do not vary and yet temperatures at these locations will vary from one day to the next and from season to season and year to year. The geographical, temporal and weather elements used to predict temperatures recorded by the loggers are outlined in Table 2.1.

A generalised additive model structure was used to predict temperature, enabling prediction based on non-linear forms of the predictors. Julian day in particular, with temperatures rising towards Summer and dropping again in Winter is expected to show a non-linear humped trend in changing temperatures. A maximal model of smoothed parameters was taken as the starting point in each case, with terms specified as a linear regressor if the effective degrees of freedom indicated that the effect of the smoother was negligible (i.e. close to 1; Wood, 2006). The two exceptions to this were the predictors ‘season’, as this is a factor and the daily weather station temperatures, as this is expected to be highly collinear with daily temperature measures across the site. The default thin plate regression spline smoother function (s) was used, meaning that far fewer coefficients than data points are used compared to other methods, to produce an optimised ‘smoothed’ trend. Comparison of model generalized cross validation (gcv) scores (Crawley, 2013), provides an assessment of the fitting process whereby a lower gcv score reflects the smoothing parameter fitting
Table 2.1: Topographic, geographic, seasonal and synoptic variables used to predict temperature variation across Silwood Park.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Site range</th>
<th>Logger range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Julian day</td>
<td>$1 = 1^{st}$ January, the number of hours daylight will affect the temperature, with days in Summer having longer for heat to accumulate and fewer hours across which the temperature can drop overnight.</td>
<td>1-366 (2012 = leap year)</td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>Describes the incidence of sunlight by which Northern hemisphere Summers have warmer temperatures than Northern hemisphere Winters.</td>
<td>Spring, Summer, Autumn, Winter</td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>There is natural variation in temperature from one year to the next due to solar radiation. In the UK interannual weather variation is associated with the North Atlantic Oscillation.</td>
<td>1987 - 2012-2013</td>
<td></td>
</tr>
<tr>
<td>Sunlight</td>
<td>Solar radiation determines temperature and the variation in its incidence will depend on land surface characteristics such as aspect and vegetation (Pincebourde et al., 2007).</td>
<td>$0 \text{ - } 14.4 \text{ MJ/m}^2$</td>
<td></td>
</tr>
<tr>
<td>Air pressure</td>
<td>Air pressure is incorporated as an indication of synoptic weather conditions (Lund, 1963, Mayes and Wheeler, 2002), recorded at Heathrow weather station. High pressure is typically associated with warmer temperatures and low pressure with cooler temperatures.</td>
<td>979.6 – 1037.4 HPa</td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>As the model is aimed to be predictive the temperatures recorded at the Silwood Park weather station are included as a reference from which to predict the spatial variation in temperature across the site.</td>
<td>-4.2-21°C</td>
<td>-4.2-22.8°C (range in mean)</td>
</tr>
<tr>
<td>Rainfall</td>
<td>May act to dampen temperature range across the site (Dai et al., 1999).</td>
<td>0 – 35.7 mm</td>
<td></td>
</tr>
<tr>
<td>Eastings and Northings</td>
<td>The location may capture spatial variations in temperature. When viewing the site at a larger landscape scale the topography of Silwood Park taken as a whole has a north-westerly facing tilt (Figure 2.1).</td>
<td>E: 168303-169468</td>
<td>N: 493635-494895</td>
</tr>
<tr>
<td>Aspect</td>
<td>Determines the exposure to sunlight of a surface, with Northerly aspects having the least sun-exposure in and Southerly aspects the highest incidence of sunlight in Northern latitudes (Merrill et al., 2008). Converted from radians to distance from 200°, the warmest aspect for the British Isles, producing a linear vector whereby 0° and 360° are both equivalent to true North (Lakhani and Davis, 1982, Suggitt et al., 2011).</td>
<td>0-358.8°</td>
<td>8-351.6°</td>
</tr>
<tr>
<td>Gradient</td>
<td>Determines a terrain’s aspect exacerbating differences in aspect, with the highest temperatures expected on the steepest south-facing slopes (Bennie et al., 2008).</td>
<td>0-22.6°</td>
<td>0-11.24°</td>
</tr>
<tr>
<td>Elevation</td>
<td>Temperatures typically decrease with increasing elevation (Daly et al., 2002), but at a low-lying site such as Silwood Park, changes in elevation are most likely to affect cold air drainage (Ashcroft and Gollan, 2012).</td>
<td>43.6-71m</td>
<td>44-69.9m</td>
</tr>
<tr>
<td>Vegetation</td>
<td>Can act to magnify or reduce prevailing climatic conditions, specifically incidence of sunlight (Saunders et al., 1999, von Arx et al., 2012, Prochazka et al., 2011). Measured as Euclidean distance from forest edge, calculated from a digitised polygon layer of contiguous forest cover.</td>
<td>-137.94-122.75 m</td>
<td>100.51 m</td>
</tr>
<tr>
<td>Buildings</td>
<td>Sources of heat (Kottmeier et al., 2007) or shade. Measured as Euclidean distance in metres from buildings.</td>
<td>0-373.2m</td>
<td>8.5-306.8m</td>
</tr>
</tbody>
</table>
the trend, but not overfitting the data and fitting the ‘noise’ (Wood, 2006). Tensor smooths (te) were used when fitting interactions of terms not on the same scale e.g. aspect (0-200°) and gradient (0-12.8°) (Wood, 2006). Final models were checked by plotting the residuals using the ‘gam.check’ function of the Mgcv package (Wood, 2006, Wood, 2013).

To verify the predictive models, the average minimum, mean and maximum temperature for April 2012 was predicted for each logger location with the data points to be predicted withheld from the model. This was repeated to predict April 2013 temperatures, again withholding April 2013 daily temperatures and using all others to entrain the model. Average minimum, mean and maximum temperatures for April 2012 and 2013 were compared to the observed logger readings by linear regression. ‘Null’ models of seasonal and weather variables, and Eastings and Northings only, excluding geographical variables and their interactions, were also plotted as a point of comparison. I therefore tested the efficacy of predicting two sets of April temperatures, from 14 months of temperature data collection. Finally the predictive geospatial models were used to predict temperature at each oak and nest box location, for each year (oaks = 2007 – 2013; nest boxes = 2002 – 2013) using the ‘predict’ function. All statistical tests were carried out using the statistical software package R (version 2.15.3 RDevelopmentCoreTeam, 2013).

2.2.4 ‘Time window’ analysis and annual trends

To predict phenology from location to location, it was necessary to identify a time-period for which temperatures would be used without incorporating confounding temporal effects, i.e. using temperatures for the month preceding first egg date. Rather than arbitrarily selecting a time period e.g. March temperatures, a ‘sliding-window’ approach was used to identify the best time-window for an association of each of the phenology measures (mean annual oak budburst = years 2007 – 2013; blue tit first egg date = years 2002 – 2013) with mean temperature (Phillimore et al., 2013). This is a straightforward approach that treats the relationship of the phenology with temperature as a
regression slope with an intercept and slope (Crick et al., 1997, Roy and Sparks, 2000, Sparks and Carey, 1995). The date of mean budburst (n=7 years) or first egg date (n=12 years) of each year was regressed against the daily mean temperatures of each corresponding year beginning from 1st January (Julian day 1) up to 1st June (Julian day 152, latest first egg = 141, latest budburst = 140), with each model increasing by a day in turn and starting from sequentially later start points (1 day increments, first egg date: 66,066 models; budburst: 10,153 models). The models are then compared by $r^2$ to select the start day and duration of the best time-window.

2.2.5 Testing for an association between phenology and microclimate

A mixed effects model structure was used to compare between year and within year associations of phenology with temperature by including the annual weather station temperature, and location specific deviance from the annual weather station temperature, as fixed effects (van de Pol and Wright, 2009). ‘Year’ was included as a random effect to avoid pseudoreplication in the prediction of phenology ~ annual temperature. All statistical tests were carried out using the statistical software package R (version 2.15.3 RDevelopmentCoreTeam, 2013).

2.3 Results

2.3.1 Temperature mapping

Recorded temperatures varied from -10.4°C (22nd January 2013) to 38.7°C (25th July 2012). Temperatures varied across the site by a maximum range of 15.59°C. The range in mean and maximum temperatures recorded across the suite of loggers each day was strongly correlated with the average daily temperature recorded at the weather station (minimum: estimate = -0.01, p = 0.25; mean: estimate = 0.02, F = 22.28, p < 0.0001; maximum: estimate = 0.23, F = 63.52, p<0.0001; 1 and 401 d.f.), with a greater range in temperatures recorded across the site on warmer days.
Variation in temperature across the site was predicted by geographical, seasonal and weather predictors. The Eastings and Northings of temperature logger locations and seasonal and weather parameters were able to predict temperatures across the site to between 0.35 and 0.78 $r^2$ (Table 2.2, ‘null’ model). The inclusion of location specific geographical characteristics, such as aspect, elevation and distance to the edge of forest cover, improved all models and by a doubling of the $r^2$ in some cases (Table 2.2; mean temperature in 2013). The predictions of the georeferenced model showed a high degree of collinearity with the observed average April temperatures ($r^2 \geq 0.7$; Table 2.2, Figure 2.3). The predictive models of minimum, mean and maximum temperature are outlined in Table 2.3. Their respective parametric terms are illustrated in Figure 8.4 and the response shapes of the smoothed terms in Figure 8.5, Figure 8.6 and Figure 8.7.

Table 2.2: Coefficients of the linear regressions of predicted and observed temperatures for April 2012 and April 2013 plotted in Figure 2.3. All regressions are highly significant (p<0.0001). 2012: 1 and 53 d.f.; 2013: 1 and 54 d.f.

<table>
<thead>
<tr>
<th>Model structure</th>
<th>Year</th>
<th>Temperature parameter</th>
<th>Intercept</th>
<th>Estimate</th>
<th>Standard error</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>georeferenced</td>
<td>2012</td>
<td>Minimum</td>
<td>-0.19</td>
<td>1.03</td>
<td>0.03</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>0.50</td>
<td>0.95</td>
<td>0.06</td>
<td>0.83</td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>Maximum</td>
<td>6.22</td>
<td>0.57</td>
<td>0.04</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Minimum</td>
<td>0.49</td>
<td>0.90</td>
<td>0.03</td>
<td>0.94</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>1.83</td>
<td>0.78</td>
<td>0.07</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Maximum</td>
<td>5.63</td>
<td>0.62</td>
<td>0.06</td>
<td>0.70</td>
</tr>
<tr>
<td>without geographical</td>
<td>2012</td>
<td>Minimum</td>
<td>0.39</td>
<td>0.86</td>
<td>0.06</td>
<td>0.78</td>
</tr>
<tr>
<td>predictors ('null’ model)</td>
<td></td>
<td>Mean</td>
<td>2.23</td>
<td>0.73</td>
<td>0.08</td>
<td>0.59</td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>Maximum</td>
<td>10.09</td>
<td>0.31</td>
<td>0.05</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Minimum</td>
<td>1.53</td>
<td>0.55</td>
<td>0.07</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>4.85</td>
<td>0.41</td>
<td>0.08</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Maximum</td>
<td>9.93</td>
<td>0.34</td>
<td>0.05</td>
<td>0.48</td>
</tr>
</tbody>
</table>
Figure 2.3: Linear regressions of predicted and recorded temperatures for the month of April in 2012 and 2013. Predictions are derived from the georeferenced models of temperature and plotted against data collected by loggers at those locations. Summary statistics of the regressions are given in Table 2.2.
Table 2.3: Predictive models of daily temperature. Parameters with a p<0.05 are highlighted by t-values given in bold.

<table>
<thead>
<tr>
<th></th>
<th>Maximum</th>
<th>Mean</th>
<th>Minimum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deviance explained (%)</td>
<td>96.4</td>
<td>99.4</td>
<td>98.1</td>
</tr>
<tr>
<td>GCV score</td>
<td>1.54</td>
<td>0.17</td>
<td>0.52</td>
</tr>
<tr>
<td><strong>Parametric coefficients</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1.71</td>
<td>0.83</td>
<td>-0.72</td>
</tr>
<tr>
<td>weather station equivalent</td>
<td>0.96</td>
<td>0.03</td>
<td>580.73</td>
</tr>
<tr>
<td>Spring</td>
<td>0.04</td>
<td>0.08</td>
<td>9.07</td>
</tr>
<tr>
<td>Summer</td>
<td>0.27</td>
<td>0.07</td>
<td>5.19</td>
</tr>
<tr>
<td>Winter</td>
<td>0.40</td>
<td>0.08</td>
<td>7.41</td>
</tr>
<tr>
<td>Aspect</td>
<td>-0.01</td>
<td>-0.53</td>
<td>2.00</td>
</tr>
<tr>
<td>Distance</td>
<td>0.02</td>
<td>0.68</td>
<td>2.09</td>
</tr>
<tr>
<td>Elevation</td>
<td>-0.02</td>
<td>-0.70</td>
<td>2.00</td>
</tr>
<tr>
<td>Nearest building</td>
<td>0.01</td>
<td>3.64</td>
<td>2.00</td>
</tr>
<tr>
<td><strong>Smoothed terms</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Julian</td>
<td>8.97</td>
<td>9.00</td>
<td>773.81</td>
</tr>
<tr>
<td>Air pressure</td>
<td>8.75</td>
<td>8.98</td>
<td>50.75</td>
</tr>
<tr>
<td>Sun</td>
<td>6.03</td>
<td>6.20</td>
<td>49.50</td>
</tr>
<tr>
<td>Rain</td>
<td>8.90</td>
<td>9.00</td>
<td>28.54</td>
</tr>
<tr>
<td>Eastings, Northings</td>
<td>13.62</td>
<td>13.76</td>
<td>7.74</td>
</tr>
<tr>
<td>Aspect, gradient</td>
<td>13.67</td>
<td>13.82</td>
<td>14.52</td>
</tr>
<tr>
<td>Aspect, distance</td>
<td>22.20</td>
<td>22.37</td>
<td>47.53</td>
</tr>
<tr>
<td>Aspect, sun</td>
<td>20.51</td>
<td>19.79</td>
<td>6.09</td>
</tr>
<tr>
<td>Distance, Sun</td>
<td>20.44</td>
<td>20.53</td>
<td>10.26</td>
</tr>
</tbody>
</table>
In all models the temperatures recorded across the site were strongly correlated with the temperature recorded at the weather station, with estimates for each of the 3 models greater than 0.87 (estimate for model of minimum temperature) and low standard errors (0.001 – 0.003, Table 2.3). Julian day showed the most significant trend with the hump of minimum temperatures rising between day 100-300 and peaking around day 250. Low air pressures had a significant association with low minimums, while very high pressures were associated with maximum temperatures. Rain effects were not straightforward: above a threshold of 15mm, rain was associated with a drop in temperatures, but the occasions of greatest rainfall occurred when temperatures were at their greatest (Figure 8.5). The three temperature parameters differ in their distribution across the site (Figure 8.7, Northing x Easting). Given such a complex model, the effect of each term is mediated by the other terms in the model and it is difficult to define their effect in isolation. Interactions are plotted in Figure 8.6 and Figure 8.7, with all other terms in the model held at their mean value.

The highest temperatures were expected to be on steep south-facing slopes and the coldest temperatures on steep North-facing slopes. This appears to be dependent on which temperature measure is the response variable. The range in temperatures for any measure was almost an order of magnitude greater at steep compared to shallow gradients. At low gradients, the lowest maxima were at North facing sites with low sun. Minimum temperatures increase with increasing levels of sun, but for a given sun level, there is a dip in temperature at around 120° from 200°, i.e. an aspect of East or North-west. The warmest temperatures were observed at steep South-facing slopes with high sun. At a steep gradient maximum temperatures showed a trend of decreasing as the aspect deviates from South-facing. At a steep gradient the lowest minima were at 60° from 200°, i.e. West or South-east, with the warmest minima on North-facing slopes.

The elevation varied by only 30 m across the site and had no significant role in temperature distribution, though as in other studies, showed a linear trend (Daly et al., 2003). Given varying air pressure, minimums were at high elevation and low pressure, with the warmest minimums at low
elevation and high pressure. Only mean temperatures showed the expected trend of low temperatures at low elevation and low pressure (Figure 8.7).

Maximum and minimum temperatures showed an inverse relationship with forest cover. The warmest temperatures are recorded at times of greater sunlight, but while vegetation dampens maximums with temperatures decreasing rapidly from the forest edge inwards, minimum temperatures increased with greater distance into vegetation cover, particularly at Northerly aspects (Figure 8.7).

2.3.2 ‘Time window’ analysis and annual trends

Across the 12 year study period, the average first egg lay date for this population was 19\textsuperscript{th} April (+/- 0.19 days) with the earliest first egg lay date being the 1\textsuperscript{st} April (one nest in 2011 and two nests 2012) and the latest first egg lay date recorded on 20\textsuperscript{th} May in 2013 and 19\textsuperscript{th} May in 2012. The average date of budburst for this population was 23\textsuperscript{rd} April (+/- 0.12).

The time-window for which the population mean lay date showed the strongest correlation with mean temperature is Julian day 48 – 102 (17\textsuperscript{th} February – 12\textsuperscript{th} April or 11\textsuperscript{th} April in a leap year: $r^2 = 0.83$, d.f. =1,10, p<0.0001, comparison across 10,153 models, Figure 2.4). First egg date occurred 3.4 days earlier with each degree increase in temperature over the 54-day period in this study system. The coldest mean temperature within this time-window was recorded for 2013 (2.60 +/- 0.32) with a corresponding first egg laid on 24\textsuperscript{th} April, the last clutch initiated on 20\textsuperscript{th} May and the mean first egg lay date occurring on 3\textsuperscript{rd} May (+/- 0.33). The warmest years were 2002 (8.02\degree C +/- 0.35), 2007 (8.20\degree C +/- 0.32) and 2009 (8.16\degree C +/- 0.29) the first egg of the population laid on 3\textsuperscript{rd}, 7\textsuperscript{th} and 5\textsuperscript{th} April respectively and the mean first egg lay date occurring on 12\textsuperscript{th}(+/- 0.40), 15\textsuperscript{th}(+/- 0.30) and 14\textsuperscript{th}(+/- 0.48) April respectively. The greatest inter-annual difference in mean temperature observed for this study system was 5.6\degree C. Annual maximum temperature for this period has a range of 6.64\degree C, while the range in annual minimum temperature was 4.73\degree C. The number of nests in each year was not correlated with mean temperature ($r^2 = -0.10$, n = 12, p=0.92).
Figure 2.4: Linear regression of (a) the mean first egg lay date of each year from 2002 to 2013 against mean temperature for Julian day 48 – 102 of the respective year ($R^2 = 0.83$, 1 and 10 d.f., $p<0.0001$) and (b) mean oak budburst of each year from 2007 to 2013 against the mean temperature of that year for Julian day 88 – 107 ($R^2 = 0.97$, 1 and 5 d.f., $p<0.0001$).

The time-window for which the population mean budburst showed the strongest correlation with mean temperature was Julian day 88 – 107 (29\textsuperscript{th} March – 17\textsuperscript{th} April: $r^2 = 0.97$, d.f. =1,5, $p<0.0001$, comparison across 66,066 models; Figure 2.4). Budburst occurred 4.2 days earlier with each degree increase in temperature over the 19-day period. The coldest mean temperature within this time-window was recorded for 2013 (5.79 +/- 0.45) with a corresponding mean budburst date of 4\textsuperscript{th} May (+/- 0.09). The warmest year was 2011 (11.03°C +/- 0.38), with a corresponding mean budburst date of 12\textsuperscript{th} April (+/- 0.10). The greatest inter-annual difference in temperature observed for this period of Spring was 5.24°C.
2.3.3 Association between phenology and microclimate

Across years there was a negative association between temperature and first egg date. First egg date was 2.5 – 3.5 days earlier with a degree increase in the minimum, mean and maximum 17\textsuperscript{th} February to 12\textsuperscript{th} April temperature from one year to the next. The trend of earlier first egg date with warmer mean and maximum temperatures was repeated across the later oak time window of 29\textsuperscript{th} March to 17\textsuperscript{th} April (Table 2.4).

Microclimate data show that first egg date also varied with temperature across the study site. Areas with warmer mean and maximum temperatures were associated with earlier first egg dates, with first egg date shifting by almost a day with each degree increase in temperature over this study site (Table 2.4). The trend of earlier first egg date with higher maximum temperatures was consistent across each year, and significantly so in 4 of the 12 years. In 2008 the shift in blue tit phenology across the site in association with maximum temperature was equivalent to that observed between years (2.55 days/1°C across site, 2.41 days/1°C across years).

Across years there was a negative association between temperature and oak budburst Table 2.5. A degree increase in mean or maximum temperatures, 29\textsuperscript{th} March - 17\textsuperscript{th} April, was associated with a shift in budburst of approximately 4 days. No association of interannually temperature variation and budburst was however observed for the earlier starting and longer blue tit time window of 17\textsuperscript{th} February to 12\textsuperscript{th} April. Oak budburst showed a similar shift toward earlier phenology in warmer areas within years, depending on the temperature measure tested. Warmer mean temperatures predicted earlier budburst by 1.36 days/1°C across site, but a higher average maximum temperature predicted later budburst by half a day per degree increase Table 2.5.
Table 2.4: Results of linear mixed effects models of first egg date predicted by year’s average temperature and location-specific temperature of the nest box for the blue tit and oak time-windows; n=1881, groups = 12 years. The intercept is given in Julian days.

<table>
<thead>
<tr>
<th>Time window</th>
<th>Predictor of first egg</th>
<th>Intercep</th>
<th>Slope</th>
<th>Standard Error</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue tit</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(17th February - 12th April)</td>
<td>year minimum</td>
<td>117.37</td>
<td>-3.59</td>
<td>0.85</td>
<td>-4.23</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>individual minimum</td>
<td>0.10</td>
<td>0.11</td>
<td>0.87</td>
<td>0.39</td>
<td></td>
</tr>
<tr>
<td></td>
<td>year mean</td>
<td>132.08</td>
<td>-3.40</td>
<td>0.53</td>
<td>-6.47</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>individual mean</td>
<td>-0.76</td>
<td>0.32</td>
<td>2.37</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>year maximum</td>
<td>137.78</td>
<td>-2.41</td>
<td>0.52</td>
<td>-4.63</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>individual maximum</td>
<td>-0.94</td>
<td>0.14</td>
<td>6.51</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td>Oak</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(29th March - 17th April)</td>
<td>year minimum</td>
<td>114.69</td>
<td>-1.55</td>
<td>1.11</td>
<td>-1.40</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>individual minimum</td>
<td>0.10</td>
<td>0.11</td>
<td>0.88</td>
<td>0.38</td>
<td></td>
</tr>
<tr>
<td></td>
<td>year mean</td>
<td>139.77</td>
<td>-3.39</td>
<td>0.81</td>
<td>-4.21</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>individual mean</td>
<td>-0.74</td>
<td>0.32</td>
<td>2.33</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>year maximum</td>
<td>142.49</td>
<td>-2.18</td>
<td>0.66</td>
<td>-3.34</td>
<td>0.008</td>
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<tr>
<td></td>
<td>individual maximum</td>
<td>-0.94</td>
<td>0.14</td>
<td>6.51</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>

Table 2.5: Results of linear mixed effects models of oak leaf budburst predicted by year’s average temperature and location-specific temperature of the oak tree for the blue tit and oak time-windows; n=1302, groups = 4 years. The intercept is given in Julian days.

<table>
<thead>
<tr>
<th>Time window</th>
<th>Predictor of budburst</th>
<th>Intercep</th>
<th>Slope</th>
<th>Standard Error</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oak</td>
<td>year minimum</td>
<td>122.12</td>
<td>-3.70</td>
<td>2.66</td>
<td>-1.39</td>
<td>0.30</td>
</tr>
<tr>
<td>(29th March - 17th April)</td>
<td>individual minimum</td>
<td>0.21</td>
<td>0.16</td>
<td>1.33</td>
<td>0.18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>year mean</td>
<td>149.36</td>
<td>-4.31</td>
<td>0.29</td>
<td>-14.68</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>individual mean</td>
<td>-1.36</td>
<td>0.44</td>
<td>-3.08</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td></td>
<td>year maximum</td>
<td>155.57</td>
<td>-3.47</td>
<td>0.28</td>
<td>-12.42</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>individual maximum</td>
<td>0.44</td>
<td>0.20</td>
<td>-2.22</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>Blue tit</td>
<td>year minimum</td>
<td>121.07</td>
<td>-6.38</td>
<td>3.17</td>
<td>-2.01</td>
<td>0.18</td>
</tr>
<tr>
<td>(17th February - 12th April)</td>
<td>individual minimum</td>
<td>0.21</td>
<td>0.16</td>
<td>1.31</td>
<td>0.19</td>
<td></td>
</tr>
<tr>
<td></td>
<td>year mean</td>
<td>133.26</td>
<td>-3.31</td>
<td>1.85</td>
<td>-1.79</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>individual mean</td>
<td>-1.39</td>
<td>0.47</td>
<td>-2.94</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td></td>
<td>year maximum</td>
<td>135.22</td>
<td>-2.25</td>
<td>1.48</td>
<td>-1.52</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>individual maximum</td>
<td>0.54</td>
<td>0.21</td>
<td>2.54</td>
<td>0.01</td>
<td></td>
</tr>
</tbody>
</table>
2.4 Discussion

This study focussed on establishing microclimates for a small study site and testing whether microclimate effects could be observed on phenology patterns therein, using the linear regression approach of time-window analyses, to compare temperature associations at two trophic levels. A temperature map was modelled of a 110 ha study site of oak and blue tit phenology, capturing the variation in the mean and extremes of daily temperature to a high degree of confidence ($r^2$>0.7) in relation to seasonal, topographical and geographical characteristics of the landscape. In agreement with the trends of other longitudinal datasets, the microclimate analyses showed that blue tit first egg date (3.4 days/1°C) and oak budburst (4.2 days/1°C) are earlier in years of warmer mean temperature (Both et al., 2004, Crick et al., 1997, Dunn and Winkler, 1999, Fitter et al., 1995, Sparks and Carey, 1995). Microclimate analyses also showed that an increase in mean temperatures predicted earlier first egg date by 0.8 days/1°C and oak budburst by 1.36 days/1°C. I found that in one year, the shift in first egg date per degree is equivalent to the interannual trend across the 12 year dataset (maximum temperature: 2.5 days/1°C). This suggests that space can act for time in the study of phenological responses to temperature variation in such a system, at even a within-population scale (Both et al., 2004, Kramer, 1995, Phillimore et al., 2013, Vitasse et al., 2009a).

Ideally temperatures would be recorded at each nest site or tree across the span of the dataset, but this is costly both in equipment and labour. The robust model of temperature distribution for Silwood Park models temperature regimes in the wild for locations and times where temperature had not been explicitly recorded and which would be ambitious to achieve in a controlled environment (Schaper et al., 2012). Mapping of temperatures and rainfall have been used extensively in climate studies and to predict microrefugia with climate change (Ashcroft and Gollan, 2012, Bennie et al., 2008, Dobrowski, 2010, Fridley, 2009, Jeffrey et al., 2001, Lenoir et al., 2008, Pincebourde et al., 2007, Scherrer and Körner, 2010). The advent of data logger technology means anywhere can easily become a weather station and fine-scale temperature data can be recorded (Bourgault et al., 2010, Pincebourde et al., 2007, Scherrer and Körner, 2010). To our knowledge we are the first to apply a
temperature mapping approach to an oak/caterpillar/bird system to explore the temperature variation and phenological associations there-in.

Effort was made to record temperatures across the whole microclimate of the blue tits and oak trees, at nest box height and within the canopy. I did not find a meaningful difference in minimum, mean or maximum temperatures between the canopy and nest box height recordings. Vegetation cover can buffer extremes in temperature (Abd Latif and Blackburn, 2010, Chen et al., 1999, Saunders et al., 1999), so it might be that a difference would be more pronounced in January or August, when the coldest and hottest temperatures are respectively recorded in the U.K. That is not however pertinent to this study of Spring phenology temperature associations.

By recording temperatures across the site I was able explore whether temperature parameters varied in the same way. While most studies use either mean (Visser et al., 1998), maximum (Mc Cleery and Perrins, 1998) or minimum (Brown et al., 1999) and likely have records of daily maximums and minimums used to produce a mean, I did not find that the temperature measures varied across the site in the same way as at a population-level or annual comparison. Maximum temperatures are greatest at steep south-facing aspects at high sun, decreasing as aspects become more northerly, while minimum temperatures show the opposite trend with aspect. The inverted trend of maximum and minimum temperatures is repeated in their association with distance to edge of cover, suggesting vegetation buffers locations from extremes in temperature (Chen et al., 1999, Saunders et al., 1999, von Arx et al., 2012). The greatest day's range of maximum temperatures was twice that of minimum temperatures (Table 8.2, 6.97 vs. 15.59°C).

The range in maximum temperatures for the site, but not minimum temperatures, increases with ambient temperature. This suggests that as temperatures increase with climate change, the disparity across a site in temperature and associated phenologies may increase, making population mean responses less representative. When testing the trends of phenology against mean temperatures, the oaks show a shift in budburst 0.9 days/1°C faster than that of first egg date between years, and 0.6 days/1°C across the site. This suggests that both between years and between
nesting territories within years, the acceleration in first egg date is not matching that of budburst to warming mean temperatures. My use of individual temperature profiles, that the microclimate approach allows, found that blue tit phenology is most strongly associated with increases in maximum temperatures at the microclimate level, and though there is still a delay of 0.4 days/1°C between the maximum temperature associated first egg date and mean temperature associated budburst, if the increase in maximum temperatures is greater than the increase in mean temperatures, this may be a moot point. Controlled aviary studies provide a mechanistic understanding by hypothesis-led experimental design (Schaper et al., 2012, Visser et al., 2009). A microclimate approach enables the comparison of a large range of individual temperature profiles, but also keeps the temperature trends within the context of the natural breeding environment of territory quality, food resource availability and social interactions. It becomes possible to test for nesting habitat selection based on abiotic as well as biotic characteristics (Nelson and Martin, 1999, Wachob, 1996, Wiebe, 2001).

Oaks show a high plasticity in phenology with temperature, demonstrated by altitudinal and latitudinal studies comparing temperature effects at a larger geographic scale (Kramer, 1995, Phillimore et al., 2013, Vitasse et al., 2009a), and by small-scale temperature variation documented in other studies (Aizen and Patterson, 1995, Buse and Good, 1996). I found that earlier budburst was associated with areas of warmer mean temperature, but unlike the study by Aizen et al. (1995), I found no association of oak budburst with minimum temperatures, either in the population mean response to annual temperatures or from one location to another within the site. Whereas Aizen et al (1995) had no variation in maximum temperatures, with their elevation gradient being more indicative of cold air drainage, I find that areas of higher maxima, but not years of higher maxima, are associated with later budburst, which would seem counter-intuitive. Forestry studies typically use a summed degrees measure of temperature, referred to as a ‘heatsum’, with phenology predicted by temperature increase above a certain threshold of temperature after a Winter ‘chill’ period (Buse and Good, 1996, Cannell and Smith, 1983a, Garcia-Mozo et al., 2002, Kramer, 1995, Bonhomme, 2000,
Kramer, 1994). It may be that areas of higher maxima are typically warmer throughout the year as well, resulting in fewer ‘chill days’. It has been demonstrated that the more chill days an oak experiences, the fewer warm days, or thermal time above a threshold is needed for budburst (Cannell and Smith, 1983a, Murray et al., 1989, Sparks and Carey, 1995).

First egg lay date was strongly correlated with maximum temperature variation which showed an inverse association with oak budburst at the landscape scale. In an aviary study, Schaper found temperature increase at the end of February and March ‘well in advance of laying’, predicted earlier first egg date (2012) and I found that areas that reach a greater extent in temperature across the mid-February - mid-April blue tit time-window, well in advance of both first egg dates and budburst in this study system also show earlier first egg date. In such dense oak woodland as this, budburst is earlier on average in warmer years and birds breeding earlier in areas of higher maximum temperature would be predicted to get ahead of the curve of prey availability within the woodland, and competition from conspecifics, with knock-on advantages for other life-history traits (Both et al., 1999, Forchhammer et al., 2001, Wilson et al., 2007, Both and Visser, 2005). A study of ‘green-up’ found that blue tit lay date was associated with trends before oak leafing, possibly green-up within the understorey reflecting temperature variation, and that green-up alone did not best predict blue tit nesting phenology, as temperature correlated traits such as altitude also play a role (Cole et al., 2015). The birds initiate the breeding attempt almost a month before the highly seasonal food resources on which it depends are needed, making it adaptive to anticipate the food resources to come using temperature as the proximate cue (Cresswell et al., 2003, Lack, 1968, Sheldon et al., 2003, Thomas et al., 2001b, Verhulst and Tinbergen, 1991, Brommer et al., 2005, Charmantier et al., 2008, Nussey et al., 2005, Visser et al., 2009). Despite warmer minimum temperatures being expected to alleviate metabolic costs to the bird (Nager and Vannoordwijk, 1992) and indicate a lifting of the metabolic constraint on the development of their invertebrate prey (Gilbert and Raworth, 1996, Partridge et al., 1994, Petavy et al., 2001), I found no correlation of blue tit first egg date with microclimate minimums, much as Schaper failed to in an aviary study (2012).
If organisms respond to temperature cues at different time-scales, than unequal temperature change across the Spring could lead to trophic mismatch (Visser and Holleman, 2001, Visser et al., 2006). The comparison of the oak and blue tit specific time windows finds that annual mean oak budburst is only predicted by temperatures within the 19-day oak time window, shortly before budburst, even though this time window sits within the much longer, earlier starting 54-day blue tit time window. Population mean first egg date is predicted by temperatures in either time-window. The 54-day window has been reported for this population in an analysis using 5-day increments (Thorley and Lord, 2015) and is of a similar duration to the phase of Spring temperature used by the Oxford Whytham wood study population (56 days; Charmantier et al., 2008), which has traditionally used a measure of summed maxima and is a geographically similar site in Southern England (McCleery and Perrins, 1998). A study of oak budburst across the U.K. found a much longer time-window (Phillimore et al., 2013) following Sparks and Carey’s February to April temperature trend (1995). The time-window reported here is similar to Nizinski and Saugier who found that it was the temperature sum in the 10 days before budburst that was most predictive (1988). The time window difference between the trophic levels may result from the differing sample size in years of available phenology data for each trophic level and was not found at the microclimate scale. The primary aim for deriving time-windows in this study was to identify a consistent time point across which to compare the association of temperatures with phenologies.

As researchers seek to quantify the resilience of populations to withstand climate driven changes to their habitat, via either plasticity or adaptation (Chevin et al., 2010), the focus has been on the longitudinal trends of population means. Mean responses may obfuscate individual trends within the population with the observed variance in phenology unexplained. To truly understand the ecology of a system we need to observe individual behaviours within the context of their realised habitat (Levin, 1992, Brommer et al., 2005). It has been argued that habitat structure and the resulting microclimate are important considerations in evaluating the impacts of climate change.
(Suggitt et al., 2011) in terms of maintaining suitable temperature regimes despite temperature increase (Thomas, 1993, Dobrowski, 2010, Scherrer and Körner, 2010).

In conclusion, I find that the range in maximum temperature across the Silwood Park study site is equivalent to that between years (6.17 vs. 6.64°C) and in one year, the shift in first egg date per degree is to the same order of magnitude as the interannual trend across the 12 year dataset (c. 2 days/1°C). In a study system where an ability to respond to changing temperatures from one year to the next is adaptive, much focus is given to the plasticity of breeding dates from one year to the next (Charmantier et al., 2008, Nussey et al., 2005). By mapping temperature across a single study site I found a responsiveness to local temperatures within one year, within a single study system, from one nest box or oak to another.
Does budburst predict Spring phenology of oak trees?

The springtime phenology of oak budburst underpins the temporal networks of Spring invertebrate and predator abundance. Earlier mean budburst with warmer annual temperatures presents a selection pressure for downstream organisms making it a model system for studies of climate change. Studies focus on the ‘yardstick’ of budburst, often of a small sample of oaks, without exploring variation in leaf growth and defoliation which may more accurately define the availability of edible leaves for organisms within the woodland. Here I test whether trees vary in their rate of leaf growth and defoliation in association with temperatures at the tree location and if early budburst is associated with accelerated leaf growth and a quicker rate or reduced magnitude of defoliation. Data is taken from a phenological study of over 3000 oaks within a 110 ha study site in Southern England, with temperature profiles and 4 years of consistent phenology and defoliation recorded for a subset of 370 trees. I find that oak leaf growth is significantly quicker in areas of higher maximum temperature, but that there is no significant association of the rate or magnitude of defoliation with microclimate temperatures. I find that earlier budburst is strongly associated with a longer period of leaf availability to chewing defoliants with higher peak defoliation scores recorded. This trend is not found between years, but only when comparing between trees within years. While trees show repeatable budburst phenology between years, they do not show the same repeatability in tanninisation. This heterogeneity has important implications for studies of oak Spring networks suggesting an early budburst tree means a longer period of caterpillar prey availability, counter to the expectation from between year trends.

Keywords: Quercus robur, Operopthera brumata, phenology, microclimate temperature
3.1 Introduction

An iconic feature of Spring in temperate regions is the ‘greening-up’ of habitats with the return of leaves to deciduous woodlands. The seasonality of Spring plant growth in temperate zones provides the base on which many organisms and networks reside (Cleland et al., 2007), particularly the boon in invertebrate abundance and concomitant Spring fecundity of secondary organisms (Crawley, 1983). As plants show a linear response to temperature in their growth rate (in the absence of any other limiting factor, Bonhomme, 2000), extensive interannual datasets of plant phenology have been applied to the study of climate, both as proxies of interannual temperature variation (Aono and Saito, 2010) and indicators of climate change (Menzel et al., 2006, Sparks and Carey, 1995). Recent trends for increasing temperatures associated with climate change have resulted in both earlier shifts in first flowering dates (Fitter and Fitter, 2002, Abu-Asab et al., 2001), but also in an increase in the growing season by 10-12 days due to the earlier start (Menzel, 2000, Linderholm, 2006).

Oak budburst has been known to be correlated with temperature change in the preceding three month period of January to March, following an initial Autumn ‘chill’ period (Sparks et al., 2005, Murray et al., 1989, Sparks and Carey, 1995, Kramer, 1994) and shows large interannual variation (VanDongen et al., 1997, Wint, 1983). Across altitudinal gradients, oak species show a high sensitivity to temperature in comparison to other deciduous tree species (Vitasse et al., 2009b) and translocation experiments across latitudes show such temperature dependent budburst to be a plastic response (Kramer, 1995, Vitasse et al., 2009a). Even within a single study site areas of warmer temperature are associated with earlier budburst (Chapter 2; Aizen and Patterson, 1995, Buse and Good, 1996).

Oak budburst is also a widely used measure of phenology (Dewar and Watt, 1992, Hunter and Lechowicz, 1992, VanDongen et al., 1997, Wesolowski and Rowinski, 2006) which in turn determines the phenology of herbivory through the availability of palatable new leaves (Buse et al., 1998, Cleland et al., 2007). As the final successional habitat typical of the north-west Atlantic region (Anderson et al., 1998) oak budburst underpins a spring network of invertebrates and secondary consumers: the
oak wintermoth caterpillar and Spring breeding passerines such as blue tits, great tits and the migrant pied flycatcher being the most studied (Both et al., 2010, Burger et al., 2012, Buse et al., 1999, Visser et al., 2003a, Visser and Both, 2005, Visser and Holleman, 2001). The date of budburst has therefore been used as a benchmark by which to measure adaptations to climate change at two dependent trophic levels (Visser and Both, 2005, Visser and Holleman, 2001, Buse and Good, 1996).

By hatching early relative to the oak, the oak wintermoth caterpillar risks starvation, a strong selection pressure for the caterpillar to synchronise hatching with the budburst of the oak, which results in tree-specific adaption (VanDongen et al., 1997, VanDongen et al., 1996, Wint, 1983, Hunter et al., 1997). Oak wintermoth egg hatch is not determined by the phenology of the host plant however, rather the adaptive close synchrony of plant and herbivore is considered to be maintained by the temperature experience common to both due to the shared location (Buse and Good, 1996, Visser and Holleman, 2001). Egg hatch is predicted by a constant temperature increase above a 4°C threshold (Embree, 1970, Kimberling and Miller, 1988) and oak wintermoth caterpillars have the ability to contract the growth period from fifty to twenty days (Buse et al., 1999).

Both budburst and the date of caterpillar peak abundance have been shown to be earlier with warmer temperatures in warmer years (Phillimore et al., 2013, Smith et al., 2011). Several studies have tested how the date of budburst determines the association of oak wintermoth egg-hatch (Buse and Good, 1996, Embree, 1970, VanDongen et al., 1997, Visser and Holleman, 2001) and the fall in caterpillar-digested material from the canopy (frass) or the date 50% of the larvae descend from trees to pupate in the soil (caterpillar half-fall date; Hinks et al., 2015, Smith et al., 2011, Visser et al., 2006, Zandt, 1994) can provide a curve of caterpillar volume from which a peak in caterpillar abundance is derived. The peak is earlier with warmer April-May temperatures and longer when the peak is later (Smith et al., 2011) and both the peak in frass fall and caterpillar half-fall date is positively correlated with the budburst of individual trees (Hinks et al., 2015). Some studies predict that increasing temperatures with climate change will benefit invertebrates (Bale et al., 2002, Roy et al., 2001, Thomas, 1993). We test whether an earlier budburst is associated with an equal
acceleration of leaf development, and what implications this has for defoliation within individual trees and the woodland from one year to the next. In a deciduous tree like the oak, leaves are edible until they have reached full-expansion at which point the concentrations of tannins increases and the leaves turn dark and waxy to reduce water-loss with increasing temperatures in Summer (Feeny, 1970). With most studies focusing on budburst and the date leaves become edible, the rate of leaf development is overlooked, but does vary among trees (Hinks et al., 2015). The rate of leaf growth and the amount of time leaves are edible may be due to temperature (Aizen and Patterson, 1995) and would influence both the timing and extent of the peak in caterpillars and prey availability to avian predators (Visser et al., 2006).

Given that both the oak leaf and the caterpillar are considered to show a high responsiveness to changing temperature regimes, this study tests whether the rate of leaf growth and leaf defoliation is predicted by microclimatic variation in temperatures within a single woodland site. I test for an association between variation among individual oak trees in leaf development and defoliation with microclimate temperatures, and secondly, for an association between individual variation in the timing of budburst and the rate and magnitude of defoliation.

3.2 Methods

3.2.1 Study site

The study site of Silwood Park lies approximately 40km west of London (51.25°N 0.4°W, ordnance survey grid reference SU 946 686) covering an area of 110 ha (Bell et al., 2014, Hadfield and Owens, 2006). The phenology of 3215 Quercus robur oak trees have been monitored across the site starting in 2007 with 347 trees, reaching a maximum between 2010 to 2013 with trees monitored in a biannual rotation (2010 = 1470, 2011 = 1819, 2012 = 1773, 2013 = 1848). The location of each tree has been mapped by Geographical positioning system and the diameter at breast height measured [dbm]. A subset of 370 oaks have been monitored every year from 2010-2013 (Figure 3.1). Oak trees
range in diameter at breast height from 6 to 156 cm, with the median size being 35 cm, dbm. The average approximate height of oak trees across the site is 12.26 m (+/- 0.03).

Figure 3.1: Map of oak trees (Quercus robur) across the Silwood park study site (n=3215) with the subset of oaks for which phenology is recorded in each year 2010-2013 shown in dark green (focal oaks, n=370) and oaks for which heights have been measured in red (n=32). Histograms of oak circumference (n=3176) and height (n=32) are also shown.

### 3.2.2 Oak phenology

Oak leaf development is recorded according to a 7-point scale, illustrated in Figure 3.2, from bud development through budburst to the final stage of leaf tanninisation, when the leaves turn dark green and waxy with a reduction in the nitrogen to carbon ratio (Tikkanen and Julkunen-Tiitto, 2003, Crawley and Akhteruzzaman, 1988). Only one bud need be observed at a certain stage of leaf development for the tree to be recorded as such. The date at which 50% of buds of a tree are at a stage is also recorded. Consequently a tree may be noted as being at the next stage before 50% of
the tree has entered the previous stage. Trees are monitored every other day from the Spring equinox, 21st March until 20th June, the Summer solstice. Only a handful of trees in each year are not recorded for tanninisation before the end of fieldwork and there is no difference in budburst date between trees scored for a stage 6 phenology and those that aren’t (2011: 6/1356 oaks, t=1.67, p=0.16; 2012: 28/1389, t=0.44, p=0.66; 2013=14/1447, t=1.78, p=0.10) with the exception of 2010 (103 oaks = mean budburst of 30.24 of April +/- 0.57, 1340 oaks = 27.12 April +/- 0.14, t=5.31, p<0.001).

I derived two measures of oak leaf growth from the phenology scoring. The rate of oak leaf growth was calculated as the number of days between the first sign of budburst of a tree (phenology score 3) and when more than 50% of that tree had undergone full leaf expansion (phenology score 4). The length of time a tree was edible to chewing defoliants was calculated as the number of days from the first sign of budburst to the date the leaves of a tree had become tanninised (phenology score 6).

Figure 3.2: Oak leafing phenology following a seven-point scale: 0 = dormant, woody buds; 1 = bud growth, starting to appear green; 2 = bud extension; 3 = budburst; 4 = full leaf extension; 5 = anthesis, pollen appears golden yellow; 6 = tanninisation: leaves dark green, thick and waxy. Adapted from Crawley and Akhteruzzaman (1988).

3.2.3 Herbivore phenology

Herbivore phenology was measured using an index based on the degree of leaf defoliation recorded for each tree once budburst was recorded, from 2010 onwards. This was restricted to the leaf area lost to chewing defoliants and scored according to a 7-point scale: 0, 3%, 7.5%, 20%, 49%, 99% and
finally complete defoliation at 100% (Crawley, 1985, Crawley and Akhteruzzaman, 1988). *Opteropthera brumata*, but also *Tortrix viridana* and *Erannis defoliaria* are the main species making up the guild of chewing lepidopterans and sawflies within this system (Crawley and Akhteruzzaman, 1988, Crawley, 1985), with *O. brumata* by far the most abundant in early Spring (Wesolowski and Rowinski, 2008; pers. obs.). An ideal measure of caterpillar abundance would be frass collection or direct counts (Wesolowski and Rowinski, 2008, Crawley, 1985), however these are highly labour intensive and would therefore be restricted to a small sample of trees (Zandt, 1994). The degree of defoliation here used as the indicator of herbivory and oak wintermoth caterpillar activity is available for each tree for which phenology has been scored.

Both the date of defoliation score and date of phenological progression are recorded in April days (days from 1st April: 1st April = 1). I used four measures of defoliation to quantify defoliant activity. Firstly the lag between budburst and defoliation, taken as the number of days between budburst and the first day a defoliation score was recorded. The second measure was a rate of defoliation, calculated as the number of days that elapsed between a defoliation score of 3% and 7.5%. A duration of defoliation activity was calculated as the number of days between the first day defoliation was recorded and the day the peak defoliation score was recorded. The final measure was the peak defoliation score.

### 3.2.4 Temperature data

A permanent weather station has been recording temperature and rainfall for the study site since 1987. Temperatures were used from 29th March – 17th April in 2010 - 2013. This 3 week period in early Spring is the period for which interannual variation in oak phenology is most significantly predicted by interannual variation in temperature (Chapter 2). Temperature profiles were predicted for each location of the 370 oaks that were monitored in each year from 2010-2013. This was achieved using a geospatial model of temperature outlined in Chapter 2, based on the Julian day and season, the temperature recorded at the permanent on-site weather station and measures of
synoptic weather conditions and the topographical and geographical variables of the oak location, within a generalised additive model structure.

The microclimate temperatures used here, though not as preferable as individual temperature traces recorded for each tree, do mean that the phenology and defoliation at 370 locations were compared, which would not have otherwise been possible given financial and labour constraints. The use of a robust temperature model (Chapter 2) enabled the hind-casting of temperature prediction to include years of data collection that preceded those of temperature data collection.

### 3.2.5 Data analysis

I tested for an association of leaf development and defoliation with temperature. Two measures of leaf development and four measures of defoliation were used as response variables: the rate of oak leaf growth and the length of time a tree was edible to chewing defoliants and defoliation, the lag between budburst and defoliation, the rate of defoliation, the date of a 7.5% defoliation score and the peak defoliation score.

The measures of leaf development and defoliation were tested against microclimate temperatures and annual average temperatures for the site using a mixed effects model structure to compare between year and within year associations of phenology with temperature by including the annual weather station temperature, and deviance of the tree location temperature from the annual weather station temperature, as fixed effects (van de Pol and Wright, 2009).

To assess the role of budburst timing on oak leaf growth and defoliation a mixed effects model structure was used to compare between year budburst trends and within year variation in budburst date by including the annual mean budburst, and deviance of the individual tree from the annual mean budburst, as fixed effects (van de Pol and Wright, 2009). In all mixed effects models ‘Year’ was included as a random effect to avoid pseudoreplication in the prediction of phenology ~ annual
temperature or mean budburst. All statistical tests were carried out using the statistical software package R (version 2.15.3 RDevelopmentCoreTeam, 2013).

3.3 Results

The average date of budburst for this population is 23\textsuperscript{rd} April (+/− 0.12), with defoliation starting on 17\textsuperscript{th} May (+/− 0.25). Date of tanninisation occurs on 26\textsuperscript{th} May (+/− 0.17). Mixed effects models to test for associations between temperature and oak leaf growth found that oak leaf development was significantly quicker in warmer areas, but not in warmer years (Table 3.1). Not only was growth of the leaf from budburst to full leaf expansion quicker in areas of higher maximum temperature, but also fewer days elapse between budburst and tanninisation of the leaf (Table 3.1). Areas of higher minimum temperature were associated with a greater number of days between budburst and tanninisation. Although the trend of a shorter period of edible leaf in years of higher minimum temperatures was almost significant across the 4 years where the same 370 trees were sampled in each year, it was not significant when testing the population mean for each of the 7 years (Intercept=38.72, estimate=−1.72, standard error = 1.66, t=−1.04, p=0.35, n=7250, groups=7 years).

Turning to the relationship between temperature and defoliation, I found that areas of higher maximum temperature were associated with fewer days between budburst and the first sign of leaf defoliation by chewing defoliants. This trend was not observed when comparing the maximum temperatures of different years – hotter years do not show a shorter lag between budburst and defoliation. The rate of defoliation is quicker in years of higher minimum temperature, with years of higher minimum temperatures also showing an earlier date of 7.5\% defoliation, though neither trend is repeated at the spatial scale between trees, I did however find that the date of 7.5\% defoliation score is earlier in areas where the mean temperature is higher. Finally, peak defoliation score was not predicted by temperature, either between years, or within a year between locations (}
Table 3.2). Peak defoliation from 2010 – 2013 is illustrated in Figure 3.3.

Figure 3.3: Barplot of the annual frequency of peak defoliation scores, given as the percentage of total leaf eaten below the bar, for the 370 trees monitored in each year 2010 – 2013 (2010 = 17.92 +/- 1.01, 367 trees; 2011 = 5.82 +/- 0.51, 367; 2012 = 11.08 +/- 0.36, 368; 2013 = 4.69 +/- 0.15, 366).

Table 3.1: Results of linear mixed effects models of leaf growth predicted by the year’s average temperature and the location-specific temperature of individual oak trees; groups=4 (2010-2013), n=1226. Significant results are shown in bold (p<0.05).

<table>
<thead>
<tr>
<th>Measure of phenology</th>
<th>Predictor of budburst</th>
<th>Intercept</th>
<th>Slope</th>
<th>Standard Error</th>
<th>t</th>
<th>p</th>
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Table 3.2: Results of linear mixed effects models of leaf defoliation predicted by the year’s average temperature and the location-specific temperature of individual oak trees with random effect structure of budburst date nested within year (2010-2013); budburst-first defoliation: n = 924, groups=97 budburst days across 4 years; defoliation rate: n = 455, groups = 4/82; 7.5% defoliation date: n= 746, groups = 4/107; peak defoliation score: n = 1302, groups = 4/121. Significant results are shown in bold (p<0.05).

<table>
<thead>
<tr>
<th>Measure of phenology</th>
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<th>Slope</th>
<th>Standard Error</th>
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When I tested for an association between budburst and tanninisation and herbivore activity, I found that the annual comparison shows tanninisation accelerating more quickly than budburst at approximately a twelve day advance in response to a ten day advance in budburst between years.
The slope at an individual tree level is much shallower, with a shift in budburst of ten days predicting a shift in tanninisation of only two and a half days (Table 3.3). Relative budburst is significantly repeatable between years (2010-2011: int.=-1.16, est.=1.01, s.e.=0.04, r²=0.6, 1and 341 d.f., p<0.0001) and though relative tanninisation date shows a significant positive trend between years, it could not be described as repeatable (2010-2011: int.=-1.29, est.=0.41, s.e.=0.06, r²=0.12, 1and 319 d.f., p<0.0001).

Aside from tanninisation date, in years of early oak budburst I did not find significantly quicker leaf growth, or fewer days of edible leaf availability from budburst to tanninisation. The range or variance in budburst date (variance: Int.= -72.93, est.= 1.01, s.e.=2.15, d.f.=1 and 5, F=0.22, p=0.66, years 2007 - 2013), or the number of days between budburst and tanninisation (variance: Int.= 23.39, est.= 0.18, s.e.=1.9, d.f.=1 and 5, F=0.01, p=0.93, years 2007 - 2013), did not vary with the mean date of budburst, i.e. early budburst years are not associated with a shorter period of budburst as a whole across the wood, or vice versa. I found that within a year, however, earlier budburst significantly predicts that a leaf was edible for longer (Figure 3.4), with a tree taking longer to reach full leaf expansion and tanninisation (Table 3.3).

When testing the effect of budburst date on the defoliation of the tree I found that in years of early budburst there are no significant associated trends of defoliation volume (Table 3.3). The proportion of trees that were defoliated varied between 0.83 and 0.9 between 2010 and 2013 and was not associated with the annual mean budburst date (int.=1.08, est.=-0.002, s.e.=0.002, d.f.=1 and 2, r²=-0.08, p=0.47). Comparing between trees however, I found that early budburst trees were significantly associated with a slower onset and rate of defoliation. Despite caterpillar activity beginning comparatively later, early budburst trees were defoliated for a significantly longer period of time and were significantly more defoliated with higher peak defoliation scores recorded (Table 3.3). It is important to note that there was a trend for bigger trees to go through budburst significantly earlier (Int.=114.75, est.=-0.03, s.e. = 0.001, t=-26.39, p<0.0001, n=7566, groups=7 years) and accordingly were edible to caterpillars for significantly longer (Int.=31.56, est.=0.01, s.e. = 0.001,
t=11.89, p<0.0001, n=7068, groups=7 years), but no significant reduction in the rate of leaf growth (Int.=12.30, est.=0.002, s.e. = 0.001, t=1.97, p<0.05, n=6643, groups=6 years). Bigger trees did not show a significantly higher percentage of leaf defoliation (Int.=22.38, est.=0.003, s.e. = 0.003, t=0.96, p=0.34, n=7103, groups=6 years).

Table 3.3: Results of linear mixed effects models of leaf growth and defoliation predicted by the year’s mean budburst date and the relative budburst of individual oak trees. The number of years (groups) and number of oaks sampled (n) are given. Significant results are shown in bold (p<0.05).

<table>
<thead>
<tr>
<th>Measure</th>
<th>Predictor</th>
<th>Intercept</th>
<th>Slope</th>
<th>Standard Error</th>
<th>t</th>
<th>p</th>
<th>groups/n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf growth</td>
<td>mean budburst</td>
<td>2.30</td>
<td>0.09</td>
<td>0.28</td>
<td>0.32</td>
<td>0.77</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>individual budburst</td>
<td>-0.28</td>
<td>0.008</td>
<td>-32.81</td>
<td>&lt;0.0001</td>
<td>6665</td>
<td></td>
</tr>
<tr>
<td>Budburst-tanninisation</td>
<td>mean budburst</td>
<td>6.17</td>
<td>0.24</td>
<td>0.41</td>
<td>0.59</td>
<td>0.58</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>individual budburst</td>
<td>-0.74</td>
<td>0.008</td>
<td>-93.77</td>
<td>&lt;0.0001</td>
<td>7084</td>
<td></td>
</tr>
<tr>
<td>Tanninisation</td>
<td>mean budburst</td>
<td>6.17</td>
<td>1.24</td>
<td>0.41</td>
<td>3.04</td>
<td>0.03</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>individual budburst</td>
<td>0.26</td>
<td>0.008</td>
<td>32.70</td>
<td>&lt;0.0001</td>
<td>7084</td>
<td></td>
</tr>
<tr>
<td>Budburst-defoliation</td>
<td>mean budburst</td>
<td>80.21</td>
<td>-0.51</td>
<td>0.23</td>
<td>-2.21</td>
<td>0.16</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>individual budburst</td>
<td>-0.38</td>
<td>0.02</td>
<td>-22.72</td>
<td>&lt;0.0001</td>
<td>4179</td>
<td></td>
</tr>
<tr>
<td>Defoliation rate</td>
<td>mean budburst</td>
<td>-50.81</td>
<td>0.55</td>
<td>0.33</td>
<td>1.66</td>
<td>0.24</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>individual budburst</td>
<td>-0.12</td>
<td>0.02</td>
<td>-4.94</td>
<td>&lt;0.0001</td>
<td>1846</td>
<td></td>
</tr>
<tr>
<td>Defoliation duration</td>
<td>mean budburst</td>
<td>-24.55</td>
<td>0.27</td>
<td>0.43</td>
<td>0.63</td>
<td>0.60</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>individual budburst</td>
<td>-0.35</td>
<td>0.02</td>
<td>-20.11</td>
<td>&lt;0.0001</td>
<td>5483</td>
<td></td>
</tr>
<tr>
<td>Peak score</td>
<td>mean budburst</td>
<td>113.33</td>
<td>-0.80</td>
<td>1.19</td>
<td>-0.67</td>
<td>0.54</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>individual budburst</td>
<td>-0.28</td>
<td>0.03</td>
<td>-8.12</td>
<td>&lt;0.0001</td>
<td>6546</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.4: The number of days between budburst and tanninisation predicted by individual tree budburst relative to the annual mean budburst (2010: int=33.61, est.=-0.71, s.e.=0.02, \( r^2 = 0.48 \), \( p<0.0001 \); 2011: int=24.13, est.=-0.51, s.e.=0.02, \( r^2 = 0.25 \), \( p<0.0001 \); 2012: int=45.70, est.=-0.80, s.e.=0.01, \( r^2 = 0.72 \), \( p<0.0001 \); 2013: int=33.31, est.=-0.58, s.e.=0.02, \( r^2 = 0.28 \), \( p<0.0001 \)) and an illustration of the duration of edible leaf predicted from the regressions, showing the mean budburst (black dotted lines) and mean tanninisation date (coloured dotted line) for the respective year.

3.4 Discussion

My individual-based models of tree and herbivore phenology showed that, within a year, early budburst trees are edible for longer than later budburst trees and that, for these early budburst trees with more time for defoliation, the peak defoliation score recorded is accordingly higher. Between years there is no association of mean budburst date with either the duration of edible leaf availability, or the magnitude of defoliation. Though between years, early budburst is matched by early tanninisation and trees become inedible to chewing defoliants earlier in the Spring (Feeny, 1970), I did not find this at the individual tree level; the shift toward an earlier tanninisation date is not equal to the shift in budburst date. This disparity between annual means and individual trends
may be important to distinguish when describing the woodland environment and the role of the oak and its herbivores in studies of Spring oak woodland networks.

Caterpillar abundance shows high interannual variation (Feeny, 1970, Varley and Gradwell, 1968), but I found no association of the interannual variation in defoliation with temperature or annual mean budburst over the four years of defoliation data. A previous study at the same study site also found no association of defoliation with phenological rank, though this was based on an average defoliation score of a smaller sample of trees for seven years of study (Crawley and Akhteruzzaman, 1988). Early budburst trees have long been connected with higher rates of defoliation (Varley and Gradwell, 1968), though based on a very small sample size, with later flushing trees showing reduced herbivore damage (Wesolowski and Rowinski, 2008, Hunter et al., 1997, Singer and Parmesan, 2010, Tikkanen and Julkunen-Titto, 2003). Feeny also found that higher caterpillar populations were associated with earlier budburst (Feeny, 1970). I found that earlier budburst trees were associated with a longer time to reach full leaf expansion and this may contribute to the greater defoliation, as leaves are more palatable at the early leaf stage (Buse et al., 1998, Feeny, 1970).

Studies of how the oak wintermoth caterpillar will respond to climate change and the associated earlier oak budburst have focussed on temperature changes. The result that earlier budburst trees show the greatest defoliation would seem to contradict the prediction that the oak and oak wintermoth differ enough in their responses to temperature that they will become uncoupled with climate change (Dewar and Watt, 1992, Primack et al., 2009). Testing leaf growth and defoliation against microclimate temperatures, I found that leaf growth is quicker and that the lag between budburst and defoliation is shorter in areas of higher maximum temperature. Budburst has been found to be earlier with warmer temperatures, in this study system, in agreement with other studies (Chapter 2; Aizen and Patterson, 1995, Fitter and Fitter, 2002, Sparks and Carey, 1995) and a trend of quicker leaf growth and defoliation with warmer temperatures has been found in a small-scale temperature gradient study (Aizen and Patterson, 1995). Comparing defoliation peaks across the U.K., Smith et al. found that the peak in frass fall was earlier in warmer sites as predicted (2011).
and between years I found that the rate of defoliation is quicker when minimum temperature is higher. Given that invertebrate growth rates depend on exceeding a minimum threshold (Embree, 1970, Partridge et al., 1994, Petavy et al., 2001), this is perhaps to be expected, and though I did not find an association of temperature and defoliation rate at the individual tree-location level, I did find that the date a defoliation score of 7.5% was recorded, occurred earlier in areas of higher mean temperature. A counter-intuitive trend of later budburst with higher maximum temperatures previously found for this study system (Chapter 2) means that the trend of quicker leaf development, onset of defoliation and tanninisation with higher maximum temperatures may be a reflection of the associations of late budburst, with earlier tanninisation and a shorter lag between budburst and defoliation.

In experiments of wintermoth development under simulated climate change temperature projections, with and without the oak tree, time to egg hatch accelerated in response to elevated temperatures, but was not affected by the oak phenology. In contrast, the feeding period and growth of the caterpillar was associated with leaf development rather than temperature, with temperature increases not affecting final pupal mass (Buse et al., 1998, Buse and Good, 1996). They found tannin build up in Quercus robur to be slow for the first 30-35 days, regardless of temperature regime, but beyond this period, leaves toughen and nitrogen content declines more quickly with elevated temperature (Buse et al., 1999, Buse et al., 1998). Caterpillars that are not in synchrony with their oak leaf food source will most likely die of starvation (Hunter et al., 1997, Leather, 1986, Tikkanen and Julkunen-Titto, 2003, Wint, 1983) making it difficult to test an actual degree of synchrony in the wild, but in their solardome study Buse et al. concluded that the oak and caterpillar were not decoupled by elevated temperatures and proposed that the projected increase in temperature with climate change was within the interannual variation of temperature for this Spring system (1999). Other studies suggest invertebrates may indeed benefit from increased temperatures with climate change, as earlier Springs would result in longer Spring/Summers, affording the invertebrates a longer growing period and resulting in greater fecundity (Bale et al., 2002, Feeny, 1970, Menzel and Fabian, 1999).
Due to the use of defoliation scores to quantify caterpillar abundance, we cannot distinguish if peak scores are due to a greater number of caterpillars or caterpillars getting bigger quicker and eating more. To avoid confounding a ‘rate’ with the variation in peak defoliation that is observed from tree to tree and year to year, I distinguished between the time taken between 3% and 7.5% defoliation and the peak score, rather than using time to a peak as used in other studies (Smith et al., 2011, Hinks et al., 2015). Despite this effort, years of higher caterpillar numbers may still be expected to score earlier phenologies and reach a threshold of 7.5% defoliation earlier, suggesting a faster rate, whereby rate is confounded by volume. A post-hoc test of average defoliation rate against average peak score found no such trend in this study (intercept=96.34, estimate=0.73, s.e.=0.86, F=0.73, p=0.48, years 2010-2013; Figure 8.9). Frass fall is a common measure of caterpillar availability, and gives an indication of caterpillar volume and caterpillar size, by the size of individual frass pellets (Fischbacher et al., 1998, Zandt, 1994). While highly valuable data, frass collection and sorting is highly labour intensive, limiting collection to a few trees per site (Smith et al., 2011) and is not without its errors, with weather impeding or impacting on the quality of collection (Zandt, 1994). The regular recording of a defoliation score, as used here, has been used before to monitor herbivore activity (Crawley and Akhteruzzaman, 1988, Crawley, 1985) and enables the comparison of oak phenology and defoliation for a greater sample size of trees. As trees are shown to have repeatable individual budburst ranks, but vary in their rate of leaf growth and peak defoliation score, we view the use of defoliation scores to assess a large sample size of trees as a worthwhile approach.

The results found here show the importance of scale (Levin, 1992, Miller-Rushing et al., 2008). There is variation at the level of the individual tree, in peak defoliation score and duration of edible leaf, which is not predicted at the population level. In the oak/caterpillar/tit study system the phenology of the oak and caterpillar are used as a ‘yardstick’ against which to compare the easily quantifiable labile traits of clutch size, fledging success and recruitment of young of avian predators (Visser and Both, 2005). Longitudinal studies show how missing the peak of caterpillar abundance predicts reduced fitness (Both et al., 2009, Both et al., 2010, Lambrechts et al., 2004, Perrins, 1991,
Visser et al., 2006, Visser et al., 1998). My results suggest the variation in the environment of food resource availability within a nesting territory may differ to that expected from annual means of budburst. While early budburst is associated with earlier peaks in half-fall date or frass (Hinks et al., 2015) and early tanninisation from year to year, I did not find an association of interannual budburst variation with peak defoliation.

Like other studies, I too found that individual oaks are repeatable in their budburst date, but I did not find relative tanninisation dates to be as repeatable as budburst dates between years (Crawley and Akhteruzzaman, 1988, Hinks et al., 2015, Linderholm, 2006, Menzel et al., 2001, Menzel and Fabian, 1999, VanDongen et al., 1997). Certainly between trees within a year the shift in budburst and tanninisation is far from 1:1. The point at which caterpillars pupate and drop from the canopy is predicted by tanninisation (Feeny, 1970). This suggests that counter to expectation an early tree in a nesting territory, may be an advantage, as in comparison to other trees it will provide a greater volume of defoliating caterpillars and for a longer portion of Spring. Further work should seek to address the association of tit fecundity and fitness with the availability of edible leaf within the nesting territory. If the duration of edible leaf is not associated with temperature to the same degree as budburst, than it cannot be assumed that the curves of food availability within oak woodlands simply shift to an earlier time point in Spring (Both et al., 2009); the shape of the curves themselves may change. In conclusion, the individual-based models of tree and herbivore phenology presented here, show that within a year, early budburst trees are edible for longer than later budburst trees suggesting a spatial heterogeneity in food resource availability that may be important in the study of how climate change affects a temperate woodland network.
4 Incubation activity and female condition are predicted by microclimate temperature

In species where only one parent incubates, there is a trade-off between maintaining optimal thermal conditions for the developing egg and time allocated to self-maintenance. Given that the development of the egg is highly dependent on the temperature within the nest and that this temperature is consistent across bird species it is unsurprising that incubation pattern and therefore the proportion of time spent incubating is strongly associated with ambient temperatures. To test if the incubation pattern of a study population of nest box breeding blue tits is associated with microclimate temperatures, temperatures specific to nest locations are predicted for the period of incubation. I find that warmer microclimates are associated with incubation bouts of shorter duration and a greater frequency of off-bouts. Warmer microclimates are also associated with a lesser decline in female condition across the breeding effort. This trend is predicted by a strategy of more off-bouts with typically shorter on-bouts. The breeding activity of a blue tit is highly constrained within a period of peak food availability, with research particularly focused on the impact of temperature variation on phenology. At the temperature dependent and energetically costly reproductive phase of incubation, I find that warmer temperatures have a favourable impact on the condition of the breeding individual.

Keywords: *Cyanistes caeruleus*, microclimate temperature, territory quality, incubation, condition, rainfall.

4.1 Introduction

All bird species, with the exception of the megapodes, incubate eggs (Bennett and Owens, 2005). Egg development depends on incubation temperatures within a narrow band common across most bird
species and climatic conditions, with 26°C marking the physiological zero-temperature for egg development, below which embryo development stalls (Webb, 1987, White and Kinney, 1974). Given global and interspecific variation in thermal experience it is expected that incubating birds must respond to ambient temperatures by adjusting their incubation strategy (Conway and Martin, 2000b). This involves a trade-off between maintaining an optimum temperature within the clutch of eggs and the requirements of the female in maintaining her own condition.

It is metabolically costly for a female to raise the temperature of a cooled egg (Biebach, 1986). The temperature of an egg drops rapidly when exposed, but the rate of temperature decrease then slows as the egg temperature approaches ambient temperature (Biebach, 1986). The rate of egg temperature loss will therefore be greater during exposure to lower ambient temperatures and greater cooling of the clutch during periods off the nest does mean a greater metabolic cost for the incubating bird when incubation is resumed (Haftorn and Reinertsen, 1990). Studies do indeed find incubation time decreases with increasing ambient temperatures (Haftorn, 1983, Haftorn and Ytreberg, 1988).

Time spent off the nest can take two forms: an increase frequency, or duration of off-bouts. It is expected that off-bouts should be of a shorter duration at lower temperatures, so as to minimise the drop in temperature within the clutch and re-heating costs (Conway and Martin, 2000a). The choice of strategy may depend more on food availability then the immediate temperature of the nest. A greater availability of food within a close proximity to the nest reduces the time needed for foraging and off-bout duration (Moreno, 1989, Tremblay et al., 2005), meaning that a female or a male-provisioning an incubating female can keep-up a high feeding rate and sustain a high incubation effort (Lifjeld and Slagsvold, 1986). The blue tit is a food-specialist during the Spring breeding season, with breeding success highly correlated with the abundance of oak wintermoth caterpillars, *Opteropthera brumata*, a major defoliator of oak trees, *Quercus robur*. The number of oak trees within a breeding habitat is a strong determinant of breeding onset and fledgling condition in an ecologically
similar species, the great tit (*Parus major*) (Wilkin et al., 2009, Wilkin et al., 2007) and to predict breeding strategy of blue tits in this population (Bell et al., 2014).

The thermal environment of a blue tit is a significant predictor of breeding strategy, not just the date at which breeding onset is initiated across years and spatially across a study site, but it has also been shown to be associated with shorter incubation periods (Matthysen et al., 2011). This thesis has focussed primarily on the role of temperature in determining phenology within the breeding ecology of a wild Spring-breeding bird. Whereas temperature may act as an adaptive cue for phenologies, it is expected to act directly on incubation behaviour (Conway and Martin, 2000a). The manner in which investment in incubation may vary with temperature may impact on the condition of the breeding female (Ardia and Clotfelter, 2007, Hanssen et al., 2005), with implications for future breeding success (Hanssen et al., 2005, Reid et al., 2000).

In this chapter I will first test for an association of incubation pattern, taken as the number of off-bouts and average duration of an on-bout, against microclimate, with the prediction that warmer temperatures are associated with more off-bouts and therefore on-bouts will be shorter on average. Incubation will also be tested against pre-incubation microclimate to assess if incubation pattern is associated with the temperature cue for blue tit phenology in this system. Interactive effects of territory quality and rainfall will also be tested. Foraging efficiency is not just determined by the structural habitat, but potentially by inclement weather impeding foraging (Cresswell et al., 2003, Pasinelli, 2001, Radford et al., 2001). High rainfall is predicted to be associated with fewer and longer off-bouts and on-bouts of longer average duration. A high number of within territory oaks is predicted to be associated with frequent short off-bouts and a greater frequency of shorter on-bouts (Stauss et al., 2005, Tremblay et al., 2005).

Further to this I will test if incubation pattern predicts a change in female condition between egg stage and chick stage. An interactive effect of incubation pattern with ambient temperature, microclimate, rain and territory quality will also be tested (Ardia and Clotfelter, 2007).
4.2 Methods

4.2.1 Study system

Silwood Park is a 110 hectare site with 275 woodcrete nest boxes distributed throughout. These nest boxes are readily used by blue tits and are easily accessible, enabling the easy capture of incubating females or adults when provisioning the chicks, and the counting of eggs laid within the nest cup. Blue tits typically lay an egg per day (Perrins, 1979). Nests were visited every other day from 1st April until the first egg was laid within a nest box. Nests were then revisited approximately ten days after the first egg is laid to record the number of eggs within the nest cup (clutch count). If 11 eggs are recorded on the second visit, the nest is revisited until the number of eggs in the clutch is less than the number of days since first egg lay date and the completed clutch has been counted. The hatch date is recorded by checking the nests ten days after clutch completion and on each subsequent day until the first egg has hatched. Fourteen days after hatching, all surviving chicks within a brood are counted, measured and given individual metal identity rings (Redfern and Clark, 2001). Adults are also captured and measured at day 15 of chick stage. The measurements of tarsus length and weight were used to calculate our index of parental quality based on body condition: the scaled mass index (Peig and Green, 2010, Peig and Green, 2009). The number of oaks within a 50 m radial distance of each nest box were counted using ArcGIS (version 9.3) and this count was used as the index of breeding habitat quality, hereafter referred to as territory quality [TQ].

4.2.2 Incubation data

Nest cup temperatures were recorded in 2012 and 2013 by placing a datalogger within the clutch of eggs from the fifth day after clutch completion. Temperatures within the nest cup were recorded every minute. Incubation pattern in this study is taken as the number of off-bouts, periods of decreasing temperature [offbouts] and the number of on-bouts, increasing and elevated temperature and total duration of both across a 4-hour recording period from 08:00 to 12:00. Only nests where
the temperature trace showed the female to have roosted in the nest box were used and data was then analysed for the 4 hour period of the following morning.

In 2012 Tinytag dataloggers were used and a thermistor cable was threaded through the base of the nest cup so that the thermistor tip sat level with the surface of the clutch of eggs. In 2013 ibuttons were used and placed in the centre of the nest cup under the clutch of eggs. As a result of differences in logger type and position within the nest cup, absolute measures of temperature are not used in this study.

4.2.3 Temperature and rain data

External temperature for each nest in each year was predicted using a geospatial model of temperature (See methods 2.2). This model was adjusted to predict hourly temperatures by using a dataset of hourly temperature recordings and including ‘hour’ as a parameter in the model (Table 8.3). An overall mean was calculated for each nest corresponding to the 4-hour incubation period for the respective day of recording. Average maximum temperatures across this time-window predict first egg lay date for this population (Chapter 2). The mean of the daily maxima for the time-window of Julian day 48-102, prior to incubation, were therefore calculated for each nest location in each year.

Rainfall is recorded on an hourly basis at a permanent on-site weather station (CS500H tipping rain gauge). Total rainfall for the morning of the incubation data recording, was summed across the 6 hour period from 6 a.m. to 12:00 a.m. The start point of 6 a.m. was chosen as roosting females are frequently still found on the nest at this time, with first feeds typically occurring after this time (pers. obs.).

4.2.4 Statistical analyses

To establish a trade-off in incubation behaviour, offbout and onbout duration were correlated against the number of offbouts. A difference in pattern between the two years was tested for by T-test.
The response variables of number of offbouts and the average duration of an onbout over the 4 hour period, were tested against the predicted temperature at the nest location for each year in turn. This temperature measure is specific to the timing of the breeding effort and any correlation may reflect a trend of incubation pattern as a result of first egg lay date and food availability at that point in the season. To account for this a linear mixed effects model structure was used with the Julian day of recording specified as a random effect, and models run with Julian day of recording nested within year. In 2013 this resulted in 14 groups of Julian days, of these only one nest was recorded on four of the Julian days. Analysis was restricted to those days for which a minimum of 3 recordings were taken. This resulted in 3 groups of Julian day in 2012 and 10 in 2013. In addition, pre-incubation temperatures of average daily maximum and the rate of increase in daily maximum temperatures for the period of Julian day 48 – 102 were also tested. The three temperature parameters were further tested in interaction with territory quality, rainfall and female condition recorded for females caught on the nest while incubating.

Finally, the effect of the number of offbouts and average duration of an onbout on the change in female condition from egg stage to day 15 chick stage was tested for. An interactive effect of incubation pattern with microclimate temperature, territory quality, rainfall and initial condition on the expected decline of female condition from egg stage to chick stage was also tested for.

Where the model for both years’ worth of data was insignificant, models were tested for each year separately. All statistical analyses were carried out within the R software package (RDevelopmentCoreTeam, 2013). Regressions were tested using linear models (Crawley, 2013). Linear mixed effects models were tested using the NLme package (Pinheiro et al., 2012).

4.3 Results

In total 38 incubation traces were successfully recorded in 2012 and 66 in 2013. The day of recording ranged from day 7 to day 13 in 2012 and day 5 of incubation to day 22 in 2013. The incubation period ranged from 11 to 33 days in 2012 with a mean of 18.58 +/- 0.52 and 9 -27 days in 2013 with a mean
of 13.74 +/- 0.29. There was a significant difference in incubation pattern depending on the day of incubation, calculated as the hatch day minus the day of first egg lay date plus the clutch size, in 2013 but not 2012 (2012: p>0.05; 2013: int.=6.90, est.=0.22, s.e.=0.06, t = 3.46, d.f.=1 and 59, p=0.001). Consequently all recordings from 2012, but only those recorded on days 5 - 7 in 2013 (no significant difference in the number of offbouts between day 5-7 in 2013, p>0.05) were used for subsequent analysis, resulting in a sample size of 38 nests from 2012 and 54 nests from 2013. Of the 38 nests recorded in 2012, 13 failed to hatch, but there is no significant difference in the number of offbouts between the abandoned and successfully hatching nests (p>0.05).

The pattern of incubation involves a trade-off between the total time spent incubating and the number of offbouts. The greater the frequency of offbouts the less time in total the female devotes to incubation over the 4-hour period (int. =190.34, est.=-1.93, s.e.=0.36, t=-5.43, n = 92, grps=2, p < 0.0001). A greater number of offbouts results in the female spending more time in total off the nest (int.=2.08, est.=0.13, r²=0.25, on 1 and 90 d.f., p<0.0001), though the average duration of an offbout is shorter (int.=10.94, est.=-0.34, r²=0.52, on 1 and 90 d.f., p<0.0001).

There is a significant difference in incubation pattern between the two years of recording. Fewer offbouts were recorded in 2013 (Figure 4.1, t = 8.04, d.f.=45.71, p<0.0001), and they were longer on average (2012 = 5.49 minutes +/- 0.32., 2013 = 8.22 minutes +/- 0.30, t = -6.52, d.f.=82.9, p<0.001), with nests showing a higher total incubation time over the 4 hours (2012 = 161.76 minutes +/- 3.86., 2013 = 173.67 minutes +/- 1.91, t = -2.81, d.f.=52.06, p=0.007). There was no difference in microclimate temperatures, territory quality, rainfall or female condition between the two years (p>0.05), but 2012 was a significantly warmer year with higher maximum temperatures for the Julian 48-102 time-window (2012=14.66 +/- 0.09, 2013=7.95 +/- 0.08, t=70.79, d.f.=580.34, p<0.0001) and first egg lay dates were over 2 weeks later in 2013 compared to 2012 (2012 = Julian day 107.17 +/- 0.70, 2013 = 123.99 +/- 0.46, t = -20.02, d.f.=299.82, p<0.0001).
Figure 4.1 Regressions of the number of offbouts recorded in 4 hours of incubation activity against the mean offbout length in minutes (2012: $r^2 = 0.34$, intercept = 23.53, estimate = -1.50, d.f. = 1 and 36, $p < 0.0001$; 2013: $r^2 = 0.34$, int. = 13.37, est. = -0.60, d.f. = 1 and 64, $p < 0.0001$) and the total time spent incubating (cumulative onbout duration, 2012: $r^2 = 0.14$, int. = 29.11, est. = -0.09, d.f. = 1 and 36, $p=0.01$; 2013: $r^2 = 0.23$, int. = 21.84, est. = -0.08, d.f. = 1 and 64, $p < 0.0001$). Data collected in 2012 is illustrated by the dashed blue regression line and filled blue circles. Data collected in 2013 is illustrated by the solid green regression line and green filled triangles.

The average onbout is shorter within a warmer microclimate (int.=29.39, est.= -1.05, s.e.=0.35, $t =-3.02$, n=59 groups = 2 and 13, $p=0.004$). There is a greater number of offbouts with warmer temperatures (int.=5.18, est. = 0.47, s.e.=0.21, $t =2.29$, n=59 groups = 2 and 13, $p=0.03$). There is no association of pre-laying microclimate on the number of offbouts in either year ($p>0.05$).

The condition of the female recorded during the egg stage does not predict the number of offbouts or average onbout duration and there is no interactive effect of female condition with
ambient temperature, rain or territory quality on the number of offbouts (p>0.05). There is no effect of female age on incubation pattern (p>0.05).

Table 4.1: Linear mixed effects models of incubation pattern, predicted by the interaction of ambient microclimate temperature and territory quality [TQ] and ambient microclimate temperature and summed rainfall and the change in female condition from egg stage to chick stage [FCC] as predicted by incubation pattern. Julian day of recording nested within year was specified as the random effect in each model. Models were tested on a single year’s worth of data and the year given in brackets, where the model of both 2012 and 2013 was insignificant.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>intercept estimate</th>
<th>Explanatory variable</th>
<th>S.e.</th>
<th>n</th>
<th>groups</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Offbout number</td>
<td>0.66</td>
<td>Temperature</td>
<td>0.87</td>
<td>0.24</td>
<td>59</td>
<td>3.66</td>
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<td></td>
<td></td>
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<td>0.04</td>
<td>2, 13</td>
<td>2.29</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Average onbout</td>
<td>41.22</td>
<td>Temperature</td>
<td>-2.05</td>
<td>0.44</td>
<td>59</td>
<td>-4.67 &lt;0.0001</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>TQ</td>
<td>-0.30</td>
<td>0.10</td>
<td>2, 13</td>
<td>-2.99 0.005</td>
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</tr>
<tr>
<td></td>
<td></td>
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<td>0.008</td>
<td>3.07 0.004</td>
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<tr>
<td>Offbout number</td>
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<td>Temperature</td>
<td>0.44</td>
<td>0.27</td>
<td>50</td>
<td>1.65 0.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rain</td>
<td>20.90</td>
<td>9.28</td>
<td>10 (2013)</td>
<td>2.25 0.05</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Temperature:rain</td>
<td>-2.20</td>
<td>0.90</td>
<td>-2.44 0.02</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FCC</td>
<td>-3.01</td>
<td>Offbout number</td>
<td>0.10</td>
<td>0.05</td>
<td>27</td>
<td>2.16 0.05</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-1.86</td>
<td>Average onbout</td>
<td>-0.03</td>
<td>0.01</td>
<td>30</td>
<td>-2.16 &lt;0.05</td>
<td></td>
</tr>
</tbody>
</table>

Offbout number – total number of offbouts within 4-hour recording period; Average onbout - mean onbout duration measured in minutes.

An interactive effect of territory quality and incubation pattern is observed. The greatest number of offbouts and the shortest onbouts are associated with territories where the temperatures are coldest, but there are lots of oaks within the territory (Figure 5.2; Table 4.1). In 2013, nests in the coldest territories where rainfall was high showed the greatest number of offbouts. There is no associated effect of rainfall on the average onbout duration, however (p>0.05; Table 4.1).

Female condition declined from egg stage to pre-fledging chick stage in all cases. The magnitude of this decline was predicted by the number of offbouts. The strategy of few offbouts with onbouts being of longer duration is costly to the female, with either incubation pattern predicting a
greater loss in condition from egg stage to chick stage (Figure 5.2; Table 4.1). Female condition declines less for those females for whom the microclimate at the nest location is warmer (int. = -4.21, est. = 0.16, s.e. = 0.07, t = 2.44, p < 0.03, n = 30, groups = 2, 13).

Figure 4.2: Trends for 2013 data. The association of offbout number (a) and onbout duration (b) with mean ambient microclimate temperature at different oak densities (observed range = 0-183; plot a: r²
= 0.29, d.f.=3 and 46, intercept = -0.97, estimate= -0.008, p <0.02; plot b: r² = 0.28, d.f.=3 and 46, intercept = 45.15, estimate= 0.03, p<0.002). Plots of the decline in female condition against the number of offbouts (c: r² = 0.55, d.f.=1 and 25, intercept =12.74, estimate=2.11, p <0.0001) and onbout duration (d: r² = 0.38, d.f.=1 and 25, intercept =11.74, estimate= -4.76, p <0.0006).

4.4 Discussion

Warmer microclimates are associated with a shorter average duration of an incubation onbout and a greater frequency of offbouts. This is in-line with prediction and the results of other studies, comparing across species and where experimentally manipulating temperatures within a single population (Haftorn and Reinertsen, 1990, Voss et al., 2006, Conway and Martin, 2000a, Conway and Martin, 2000b, Haftorn and Ytreberg, 1988). Territories with cold ambient temperatures and few oaks are associated with an incubation pattern of few offbouts and longer onbouts. This may reflect a greater investment in the current breeding effort, with a greater loss in female condition associated with such incubation behaviour. Female condition was shown to decline in other studies where incubation effort was increased (Dobbs et al., 2006, Hanssen et al., 2005, Reid et al., 2002). Shorter incubation periods are also observed when the female is in better condition (Nooker et al., 2005).

The increase in onbout duration with increasing territory quality suggests that by having lots of oaks nearby there is less of a trade-off to be made between self-maintenance and investment in reproduction (Eikenaar et al., 2003). Incubation is an energetically costly stage of the reproductive cycle (Bryan and Bryant, 1999). A higher density of oak trees near to a nest would mean greater foraging efficiency for the female or a provisioning male (Wilkin et al., 2009, Stauss et al., 2005, Tremblay et al., 2005). It is expected that greater food availability would alleviate the costs of increased incubation activity. This has not been explicitly tested here, but greater food availability during incubation is associated with a shorter total duration of incubation in the blue tit (Harrison et al., 2010). It would be interesting to combine incubation activity data with nest box camera...
observations of female foraging or male-provisioning for this study system, where fine-scale territory quality information is available.

Females breeding in cooler territories show a greater loss of condition between incubation and pre-fledging chick stage. A greater effort during incubation, predicted by cooler temperatures is associated with greater costs for the female. A direct association of temperature experience during incubation on female quality has also been found (Bryan and Bryant, 1999, Voss et al., 2006, Weathers et al., 2002). A study by Voss concluded that females were limited in their incubation pattern by the costs of incubation, as when nests were warmed the female invested more in self-maintenance taken as the total time spent off the nest, over egg development and time spent on the nest (2006). In female great tits (*Parus major*, an ecologically similar species to the blue tit), warmer ambient temperatures overnight, when over 80% of the time-period is spent actively incubating, are associated with a lower daily energy expenditure (Bryan and Bryant, 1999). Weathers et al did not find a difference within populations in the metabolic costs of incubation, but did find strong effects of temperature differences across populations differing in altitude and temperature regime. Females showed reduced energy expenditure where temperatures were warmer and had lower resting metabolic night time and daytime rates (2002).

I find that there are more offbouts with an increase in rainfall when temperatures are lower. A greater number of offbouts with an increase in rain is likely due to rainfall exacerbating the metabolic cost of cool temperatures (Gullett et al., 2014). A similar result was found by Cresswell et al: a greater frequency of offbouts with increasing rainfall (Cresswell et al., 2003). Predictions may vary however, depending on the degree of rainfall, for example short bursts versus long periods of inclement weather (Whitehouse et al., 2013). Females would be expected to sit out the rain if rain not only acted to dampen temperatures but also to impede foraging ability, as has been found in a study of nest box occupancy by females brooding young, which like eggs, chill quickly (Radford et al., 2001).
The degree of investment in incubation impacts on the condition of the breeding individual, with implications for breeding success within the current and future breeding attempts (Ardia et al., 2009, Hanssen et al., 2005, Pendlebury et al., 2004, Reid et al., 2000). Changes to the thermal environment have been found to affect the energetic costs of the current breeding effort independently of the impact of temperature change on food availability such as insect prey (Ardia et al., 2009, Hanssen et al., 2005, Pendlebury et al., 2004, Reid et al., 2000). I also observe an association of incubation pattern with temperature and by grouping analyses by Julian day and therefore time-point within the breeding season, this reflects an impact of temperature accounting for temporal trends in temperature within a species for which ‘timing’ is key (Norris, 1993, Sanz, 2002, Thomas et al., 2001b). An increase in temperatures may result in maladaptive changes in phenology in respect to valuable food resources at a costly stage of reproduction, that of the peak of chick food demand (Both, 2010, Visser and Both, 2005, Dijkstra et al., 1990). An increase in temperatures is however also associated with a reduced metabolic cost at another, previously overlooked phase of reproduction (Conway and Martin, 2000a, Conway and Martin, 2000b). This could result in a trade-off between the benefits of incubation coinciding with warmer temperatures and the selection pressure to match the peak in food demand of the brood with the peak in food availability (Visser et al., 2012).
5 The nesting success of a free-living bird is predicted by unequal Spring temperature change

If organisms within a network respond differently to changes in temperature, driven by climate change, trophic interactions may become uncoupled resulting in what is known as trophic mismatch. This may result when temperature is unequal in its change across the Spring season meaning that the thermal environment of the cue is disassociated from the temperature determining the environment of selection. Trophic mismatch has been well-studied in the oak/caterpillar/tit system, where the selection pressure of mistimed blue tit phenology in relation to the caterpillar peak of abundance can be easily quantified in the clutch size and number of chicks of the blue tit apex predator. In this study the thermal environment that predicts the phenology of the blue tit is compared to the thermal environment that predicts caterpillar abundance. The degree of discrepancy or asynchrony is then used to predict breeding success, the probability of pre-fledging chick survival. I find that the temperature experience is not equal across the two phenological phases. In years where the average maximum temperature is higher later in Spring there is reduced chick survival, this trend is also observed within a year when comparing between nest sites. This study highlights that it is the manner in which temperature change occurs that is important in determining species interactions and responses to climate change.

**Keywords:** *Cyanistes caeruleus, Operopthera brumata, Quercus robur*, time-windows, microclimate temperature, survival.

5.1 Introduction

A consequence of recent climate change has been ‘climate driven shifts’ in phenology, the timing of recurring life cycle events (Menzel et al., 2006, Parmesan and Yohe, 2003, Primack et al., 2009, Visser
and Both, 2005, Walther, 2010). If all organisms within an ecological network track the changing climate in concert, there will be no discernable impact other than the temporal change (or perhaps competition as the network overlaps with the previously antecedent phenologies of another network). If they do not show congruent changes, trophic interactions and network links may become uncoupled (Edwards and Richardson, 2004, Liu et al., 2011, Memmott et al., 2007, Thackeray et al., 2010). This is coined as the match/mismatch hypothesis (Stenseth and Mysterud, 2002).

Mismatch can occur if organisms respond differently to temperature, either due to differing temperature cues (Dewar and Watt, 1992) or a differing rate of response to the temperature cue (Both et al., 2009). A more direct dependence on temperature, or capacity for a rapid response to temperature change at one trophic level compared to another, would result in the phenology of the former shifting earlier relative to the phenology of the latter (Buse et al., 1999). Alternatively mismatch may occur if the temperature cues used differ between the trophic levels and are not collinear in their change. This may be due to trophic levels cueing off different temperature parameters or temperatures for distinct time periods.

The degree of mismatch can be quantified by a lower trophic level acting as a ‘yardstick’ and the difference in the phenological shift of a species compared to that of the food resource on which it depends (Visser and Both, 2005). The consequence of mismatch is then expected to be measurable by a decline in breeding performance at the higher trophic level (Lack, 1968, Arnold et al., 2010, Sanz et al., 2003, Thomas et al., 2001b).

The model tri-trophic system of oaks/caterpillars/tits, has been studied intensively as a model system of trophic mismatch as it is a simple food-chain which is highly temporally constrained (Perrins, 1979, Visser and Holleman, 2001, Visser et al., 2003a). The caterpillars are the major food source of the tit during the breeding season, providing a high nutritional content at a reduced handling time compared to other invertebrates (Banbura et al., 1999). The breeding success of the blue tit is strongly associated with the abundance of caterpillars (Tremblay et al., 2003). The caterpillars in turn feed on young oak leaves, only available for a short period in Spring before
increased temperatures with the approach of Summer render them unpalatable with an increase in tannins (Tikkanen and Julkunen-Titto, 2003).

The phenology of the blue tit and the caterpillar differ in their response to temperature. Caterpillars are capable of rapid temperature-mediated development (Buse et al., 1999). The blue tit by comparison uses temperature as a cue to initiate breeding (Chapter 2), with first egg lay date predicted by temperatures across a 54-day period starting over a month before the Spring solstice (Chapter 2). The peak in food demand of the blue tit brood is typically around day 10 of chick stage (Naef-Daenzer and Keller, 1999, Perrins, 1991), approximately a month after the first egg is laid given the breeding ecology of this species (Perrins, 1979). Within the respective time-window the blue tit phenology is predicted by maximum and mean temperatures, while the caterpillar responds to minimum and mean temperature (Chapters 2 and 3).

In this chapter I will compare the thermal environment that predicts the phenology of the blue tit to the thermal environment that predicts caterpillar abundance and test if differences in temperature regime between two different phases of Spring predicts bird breeding success. The prediction is that an unequal temperature change drives trophic mismatch with an observable impact on the nesting success of the avian predator.

5.2 Methods

5.2.1 Study system

The breeding activity of a study population of blue tits has been monitored since 2002 and the first egg lay date of each occupied nest box recorded. Nests are revisited approximately ten days after the first egg is laid to record the number of eggs within the nest cup (clutch count). Blue tits typically lay one egg per day (Perrins, 1979). If 11 eggs are recorded on the second visit, the nest is revisited until the number of eggs in the clutch is less than the number of days since first egg lay date and the completed clutch has been laid and counted. The hatch date is recorded by checking the nests ten days after clutch completion and on each subsequent day until the first egg has hatched. Fourteen
days after hatching, all surviving chicks within a brood are counted, measured and given individual metal identity rings (Redfern and Clark, 2001).

The phenology and defoliation of individual oak trees across the site is recorded every other day. Defoliation refers to the leaf area lost to chewing defoliants and is scored on a 7-point scale: 0, 3, 7.5, 20, 49, 99, 100%. The measure of 7.5% is taken as a robust measure of substantial herbivory (see methods section 3.2.3 and Figure 3.3).

Temperature is recorded for the study site by a permanent on-site weather station. Further to this a geospatial map of temperature has been modelled by which location specific temperature microclimates are predicted (Chapter 2). Individual temperature profiles are predicted for nest box or tree locations and the spatial variation in the timing of first egg lay date and the date at which trees are recorded for 7.5% defoliation has been compared to different temperature parameters (Chapters 2 and 3). Both first egg lay date and the date of 7.5% defoliation are earlier where temperatures are higher on average and in years when temperatures are warmer (Chapters 2 and 3).

5.2.2 Time-window temperature comparison

The time-windows in units of Julian days whereby interannual variation in phenology is predicted by the interannual variation in mean temperature, were identified using a sliding window approach (see 2.2.4). The approach involves the regression of the phenology measure against temperature (Crick et al., 1997, Roy and Sparks, 2000, Sparks and Carey, 1995). The date of mean budburst (n=7 years), 7.5% oak leaf defoliation date (n=4) or first egg date (n=12 years) of each year was regressed against the daily mean temperatures of each corresponding year beginning from 1st January (Julian day 1) up to 1st June for budburst and first egg date (Julian day 152, latest budburst = 140, latest first egg = 141) and up to 30th June for caterpillar defoliation (Julian day 181, latest 7.5% defoliation score date = 180). Models are run in turn, increasing by a day each time for sequentially later start dates (1 day increments, first egg date: 66,066 models for 12 years phenology data; budburst: 10,153 models, 7 years; defoliation: 15,931 models, 4 years). The models are then compared by $r^2$ to select the start
day and duration of the best time-window (budburst and first egg date: Figure 2.4, budburst and 7.5% defoliation: Figure 8.8).

A schematic of the three ‘best’ time-windows for the respective phenological datasets is illustrated in Figure 5.1, with Spring split into three distinct phases: an initial phase A (Julian days 48 to 88) where temperature only predicts the blue tit phenology of first egg lay date; a second phase B (Julian days 88 to 107) where temperature contributes to the prediction of all three trophic level phenologies; and a final phase C (Julian days 107 to 121) where temperature exclusively predicts the date of 7.5% defoliation of oaks by chewing defoliants.

Figure 5.1: Schematic illustrating the time-windows in Julian days across which mean temperature most significantly predicts phenology. The phenologies are blue tit first egg lay date (uppermost horizontal blue bar), 7.5% defoliation of oak trees by chewing defoliants (middle light green horizontal bar) and oak budburst (bottom dark green horizontal bar). The time-windows are split into 3 phases: A, B and C.

The temperature parameters of overall mean and average maximum temperature are predicted for phases A and C for each year using temperature data from the on-site weather station. Years (2002-2013) are ranked in descending order of magnitude for each temperature parameter for
both phase A and C, i.e. the year with the highest average maximum is ranked 1st, the year with the lowest average maximum temperature is ranked 12th.

To establish how temperatures differ within a year between the two phases, the degree of collinearity is assessed by regressing the rank of a year for phase A against its rank for phase C \([A \sim C]\), for two different combinations of temperature parameter: mean \(A \sim C\); average maximum \(A \sim \text{mean } C\); average maximum \(A \sim C\). The null expectation is that the annual ranks in temperature for phase A are equal to those of phase C \([A=C]\). This expectation and the implications of a deviance from this trend are illustrated in Figure 5.2. Years which fall above or below this line are predicted to show asynchrony between blue tit and caterpillar phenology. Such an asynchrony of the predictor of caterpillar phenology relative to the predictor of blue tit phenology or vice versa is measured by the residual deviance of the point (year) from the 1:1 line.

Figure 5.2: The null expectation is that the rank of temperature in phase A is equal to that of phase C, a 1:1 line. Years that fall above the line are where the rank of temperature in phase A is higher than the rank of temperature in phase C which would predict an earlier blue tit phenology relative to caterpillar phenology. Years that fall below the line are where the rank of temperature in phase C is
higher than the rank of temperature in phase A, predicting earlier caterpillar phenology relative to blue tit phenology.

To test if predicted asynchrony in the temperature trends of the two phases reflects true asynchrony in phenology, two measures of nesting success are modelled against the residuals from the A=C expectation. The two measures of nesting success used are: the proportion of occupied nests that survived to day 15 of chick stage and the proportion of eggs laid that hatched and survived to day 15. A vector of number of occupied nests and nests measured at day 15, or total number of eggs laid in that year and total number of chicks measured at day 15, with sample size implicit were used as the response variables in turn, within a global generalised linear model [glm] with binomial error structure (Crawley, 2007). Survival to day 15 is used as this is the latest day at which nests can be disturbed without risking force-fledging in this population. It is also after the peak in food demand has been reached (Perrins, 1991) so the impact of any food limitation on chick survival is expected to have already occurred. The number of chicks fledged would be the ideal measure, but this count is not as precise due to observer error in the counts of dead/decaying chicks found in nests or buried within the nesting material.

These analyses were repeated comparing across microclimates for the site within a given year. Two years were chosen; the years for which the hottest and the coldest mean Spring temperatures were recorded (taken here as Julian day 48-121): 2007 (9.47°C +/- 0.38) and 2013 (4.59 +/- 0.49; see Figure 1.3 and). In this instance, the response variable was limited to the proportion of the clutch that went on to survive to day 15 chick stage.

5.3 Results

Only in two years out of the 12 years tested did phases A and C show the same rank in temperature parameter. These are for the parameter of mean temperature in 2010, and maximum versus mean
temperature in 2005 and 2010. These two years account for the highest and lowest occupancy rates (2005 = 89%, 2010 = 41% of available nest boxes).

The ranks of temperatures in each year across the two phases are not correlated and the slopes of the regression do not show a 1:1 trend ($p>0.05$; Figure 5.3). There are more points below the 1:1 line in each plot (Figure 5.3), indicating that the rank in phase C is more often than not higher than the rank in phase A.

![Figure 5.3](image)

Figure 5.3: Regression of ranked annual temperatures for phase A (Julian day 48 -88) against phase C (Julian day 107 – 121) for the parameters of mean temperature (a), average maximum temperature in phase A compared to mean temperature in phase C (b) and average maximum temperature (c). The solid line illustrates the 1:1 slope. The dashed line illustrates the linear regression of phase A versus phase C ranks (a: intercept [int.] = 4.18, estimate [est.] = 0.36, $r^2$ = 0.13, $p$=0.26; b: int. = 4.09, est. = 0.37, $r^2$= 0.14, $p$=0.24; c: int. = 4.72, est. = 0.27, $r^2$ = 0.07, $p$=0.39.

A greater proportion of chicks survive to day 15 when the average maximum temperatures are of a higher rank in phase A compared to phase C (Table 5.1). In the comparison of mean temperature however, a greater proportion of chicks survive to day 15 when mean temperatures are of a higher rank in phase C relative to phase A and also when mean temperatures are of a higher rank
in phase C than the rank of maximum temperature for phase A (Table 5.1). There is no association of the proportion of nests that reach day 15 with the difference in any temperature parameter for phases A and C (p>0.05).

Table 5.1: Results of generalised linear models of chick survival probability tested against predicted temperature asynchrony for phases that predict blue tit phenology and caterpillar abundance, using a binomial error structure.

<table>
<thead>
<tr>
<th>Temperature parameter</th>
<th>Intercept</th>
<th>Estimate</th>
<th>Standard error</th>
<th>Z statistic</th>
<th>P value</th>
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</thead>
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<td>Mean</td>
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<td>0.003</td>
<td>2.05</td>
<td>0.04</td>
</tr>
<tr>
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<td>0.01</td>
<td>0.003</td>
<td>3.85</td>
<td>0.0001</td>
</tr>
<tr>
<td>Maximum</td>
<td>-0.71</td>
<td>-0.01</td>
<td>0.003</td>
<td>-4.15</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

The ranks of temperatures across the suite of microclimates for the site show high collinearity between phases A and C for the parameters of average mean and average maximum temperature in 2007 and 2013 (Table 5.2; Figure 5.4). Model checking of the regressions for plots c and d, produced a sigmoidal q-q plot, resulting from a high concentration of data points between ranks being either equal or inverted and not normally and uniformly distributed.

In the cold year of 2013, there is a greater probability of chicks surviving to day 15 when the rank of maximum temperature is greater for phase A than the rank of mean temperature for phase C (int. = -0.91, est. = -0.001, s.e. = 0.0006, z = -2.16, p=0.03), but this is not observed in the hot year of 2007 (p>0.05). There is no significant trend for differences between average maximum ranks or in the comparison of mean temperature ranks between phases A and C in the prediction of chick survival probability for either year (p>0.05).
Table 5.2: Linear regressions of ranked microclimate temperatures for phase A (Julian day 48 -88) against phase C (Julian day 107 – 121) in the years 2007 and 2013.

<table>
<thead>
<tr>
<th>Temperature parameter</th>
<th>Year</th>
<th>Figure plot</th>
<th>Intercept</th>
<th>Estimate</th>
<th>r²</th>
<th>p – value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>2007</td>
<td>a</td>
<td>0.39</td>
<td>1.00</td>
<td>0.99</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Mean</td>
<td>2013</td>
<td>b</td>
<td>1.09</td>
<td>0.99</td>
<td>0.99</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Max – Mean</td>
<td>2007</td>
<td>c</td>
<td>122.44</td>
<td>0.11</td>
<td>0.01</td>
<td>0.07</td>
</tr>
<tr>
<td>Max – Mean</td>
<td>2013</td>
<td>d</td>
<td>119.55</td>
<td>0.13</td>
<td>0.02</td>
<td>0.03</td>
</tr>
<tr>
<td>Maximum</td>
<td>2007</td>
<td>e</td>
<td>1.28</td>
<td>0.99</td>
<td>0.98</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Maximum</td>
<td>2013</td>
<td>f</td>
<td>3.83</td>
<td>0.97</td>
<td>0.95</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Figure 5.4: Regressions of ranked nest temperatures for phase A (Julian day 48 -88) against phase C (Julian day 107 – 121) for 2007 and 2013 for the parameters of average mean temperature (a, b), average maximum temperature (phase A) and mean temperature (phase C) (c, d), average maximum temperature (e, f). The solid red line illustrates the 1:1 slope. The dashed red line illustrates the linear regression and these are given in Table 5.2.
5.4 Discussion

The rank of temperature magnitude is not equal from one phase to the other. The warmest year for one phase is unlikely to be the warmest year for the other phase. This is not surprising given that long periods of constant weather trends during the British Spring time are very rare (Barry and Chorley, 1998). Across microclimates, unlike across years, a warm location for one phase is likely to be equally warm in another phase, i.e. a warm site will remain warmer relative to other sites, regardless of annual trends, be it a hot year or a cold year.

I find that a temporal asynchrony in temperature is a predictor of breeding success. The direction of this asynchrony is particularly important. A higher maximum temperature in phase A, the time-window which exclusively predicts the phenology of the blue tit apex predator, compared to increasing temperature across the caterpillar phase C, is associated with a greater proportion of chicks surviving to day 15, both for that year and for that location in a cold year. Blue tits are highly constrained in their ability to respond to temperature change, limited only to changes in the timing of first egg lay date and the number of eggs laid in a clutch and duration of incubation (Matthysen et al., 2011, Cresswell and McCleery, 2003). Across microclimates in 2013, there is a greater probability of chicks surviving to day 15 when the rank of maximum temperature is greater for phase A than the rank of mean temperature for phase C. Higher temperatures earlier in Spring as opposed to late in Spring would give the blue tit an adaptive head-start relative to its caterpillar prey (Cresswell and McCleery, 2003).

It is curious however that there is a greater probability of surviving to day 15 in a given year when mean temperature is of a higher rank in phase C relative to phase A or when mean temperatures in phase C are greater relative to maximum temperatures in phase A. This may reflect a cost of producing eggs too early in the season (Visser et al., 2012, Stevenson and Bryant, 2000). Mean temperature predicts the incubation pattern and further to this the degree of decline in female condition (Chapter 4). The average first egg lay date for this population is 19\textsuperscript{th} April, 3 weeks after the close of phase A and within phase C. Warmer average temperatures reflect an increase in minimum
temperatures and such an increase is associated with a reduced energy expenditure during the costly reproductive stage of incubation (Bryan and Bryant, 1999, Weathers et al., 2002).

Temporal asynchrony in temperature magnitude or change is predicted to be a driver of trophic mismatch (Stevenson and Bryant, 2000). The trophic interactions of a network will become uncoupled, with potentially catastrophic consequences if the temperature cue at one level is no longer predictive of the environment of selection (Visser, 2008). Two long term study systems, that of Oxford in the UK and the Hogue Veluwe of the Netherlands, both show warming Spring temperatures and correlated changes in the bird phenology, but with differing consequences (Both, 2010). The Oxford tit population has experienced an increase in temperatures across the Spring season and continues to thrive (Stevenson and Bryant, 2000). The Hogue Veluwe has experienced temperature increase later in the season (Visser et al., 2012) and the earlier shift in caterpillar peak abundance three-times that of the mean lay date of the bird has had concomitant impacts on breeding success (Visser et al., 1998). It is proposed that such different scenarios are due to temporal differences in the temperature change (Visser et al., 2003b, Visser et al., 2012, Stevenson and Bryant, 2000). Indeed the Dutch population uses temperature recorded across a shorter period (16th March – 20th April) compared to the Oxford population (1st March – 25th April).

This study explicitly tests the impact of non-synchronous changes in temperature across the Spring period on nesting success. Though the method used is simple and a ranks approach may lose temperature information, regressing models of ranked data is not without precedent (Crawley and Akhteruzzaman, 1988). Indeed where previously in this thesis temperatures were compared by their degree of deviance from the weather station temperature and this would be possible for the microclimate temperature comparisons in 2007 and 2013, this would not be possible in the comparison of temperature differences across the different phases between years. The use of a temperature rank in the comparison of annual temperatures focusses the comparison on the degree of temperature change across Spring, which was the focus of this study, rather than absolute
temperature comparisons, for example maximum temperatures may be expected to be consistently higher toward the end of Spring than at the beginning.

Temperatures are expected to increase by approximately 2°C over the next 80 years (IPCC, 2013) and though there will still be interannual variation in Spring temperatures, they will on average be warmer. The blue tit breeding success will depend on when, within a timeframe of 73 days, this warming occurs. In contrast to cross-population comparisons (Visser et al., 2003a), I confirm that unequal temperature change predicts nesting success in this system. This study highlights the need to use relevant temperature measures in the study of trophic mismatch to better understand the impact of climate change on a network.
6 Quality of breeding territory mediates the relationship between paternal quality and sex ratio bias in a free-living bird population.

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The version of record [Quality of breeding territory mediates the influence of paternal quality on sex ratio bias in a free-living bird population, Sophie C. Bell; Ian P.F. Owens; Alexa M. Lord, Behavioral Ecology 2013; doi: 10.1093/beheco/art112] is available online at:

7 General discussion

The thermal experience determines the energy budget of an organism (Brown et al., 2004). The activity of poikilotherms, such as insects and trees, slows down with cold temperatures and speeds up with warm temperatures provided there are no other limiting factors (Bonhomme, 2000, Gilbert and Raworth, 1996). An endothermic organism, such as a bird, buffers its internal environment against external temperatures, but this in itself is costly (Ardia and Clotfelter, 2007, Ardia et al., 2009). Temperature distribution therefore governs the physiological capacity of any organism with adaptations including habitat preference or diurnal or seasonal patterns of activity (Brown et al., 2004).

The focus of this thesis is a seasonal trend in activity with temperature, a well-known Spring phenology: the timing of oak budburst and herbivory and the concomitant seasonal fecundity of a small passerine, the blue tit. Spring in the high latitudes is a period of transition as the earth tilts towards the sun and days lengthen, leading to an increase in heat and available energy (Graf et al., 1982, Wilson and Baldocchi, 2000). This results in congruent growth and fecundity across trophic levels and networks (Pocock et al., 2012). The tri-trophic network of tree-caterpillar-bird is a simple example of this.

Spring temperatures in the UK are highly variable from year to year with March historically showing the greatest range in temperature of any month (MetOffice, 2011, Webb and Meaden, 2000). The extent of maximum temperatures is determined by the incidence of sunlight, while cold ocean temperatures lead to overnight drops in temperature. Typically winds blow from the Southwest, but interannual variation in Spring temperatures result from changes in the North Atlantic Oscillation [NAO], with a negative NAO bringing about Easterly winds and cold weather, for example the recent Spring of 2013 (Figure 1.2; Slingo, 2013). Despite high interannual variation in Spring temperatures, an overall trend for warmer Springs with climate change (Houghton et al., 1996, IPCC(WGI&II), 2001) has been matched by earlier budburst from dormant winter buds (Abu-Asab et

Studies show that phenologies vary with temperature across space in a comparable manner to trends observed across time and responses to temperature are often largely plastic (Kramer, 1995, Phillimore et al., 2013). Most studies, whether comparing against temporal or spatial trends in temperature, use population level comparisons, but within a population there is variation which is largely ignored. Temperature varies across space as the incidence of sunlight varies with latitude, topography and landuse (Bennie et al., 2008, Lennon and Turner, 1995, Pepin et al., 1999, Dai et al., 1999, Kottmeier et al., 2007, Suggitt et al., 2011). Habitats can vary in terms of temperature conditions even at the micro-scale of a leaf-mine (Pincebourde et al., 2007), with implications for organism function and fitness (Lindo and Winchester, 2013, Serio-Silva and Rico-Gray, 2002, Doody et al., 2006, Nelson and Martin, 1999, Xu et al., 1997). It is predicted that microclimate may exacerbate temperature differences within a population in a way comparable to latitudinal differences at a macro-scale (Rorison et al., 1986).

The aim of this thesis was to determine to what extent temperature varies across a single study system and whether this variation predicted the variation in phenology observed at each level of the network. Further to this, I set out to explore how the different trophic levels may differ in their response to microclimate temperatures and how this impacts on network cohesion. In addition, a study of primary sex ratio variation in this population, carried out during the tenure of this PhD, has also been included.

Modelling temperature

Temperatures were recorded at 64 locations across the study site, incorporating as much of the known environmental variation as possible. This environmental variation in combination with known weather conditions recorded at the on-site weather station was then used to inform general additive
models in a linear regression approach to predict temperature (Lennon and Turner, 1995, Jeffrey et al., 2001). Chapter 2 presented a robust temperature map for the study site enabling the prediction of temperature at any given point in time or space for the period of data-collection at the permanent on-site weather station. This model was then adapted to predict daily temperature extremes and rates (Chapter 2), hourly temperatures (Chapter 4) and even temperatures within the forest canopy (Chapter 2). The timeframes across which temperature was predicted were adjusted with ease according to the time-windows of interest.

The benefits of such an approach are manifold. Firstly, the constraints of a restricted data-collection period are lifted, with the scope of temperature data no longer limited to when loggers are placed out in the field. Secondly, data is not limited to the site or position of the logger. It is possible to interpolate between a network of data-loggers (either through interpolated distance-weighting or ordinary krigging approaches; Hengl et al., 2007, Jeffrey et al., 2001), but this does not necessarily incorporate known landscape variation between the data-points. A third benefit is therefore that known variation in topography can be used to inform predicted temperature variation at otherwise novel locations as observed temperatures vary according to their ‘known’ location.

Further benefits are the reduction in labour and setup costs. Temperature traces can be predicted with ease using the statistical modelling approach and given the known environmental, seasonal and synoptic weather trends for the location and time of interest. This massively limits the necessary effort and cost of placing loggers in the field, time spent recording data and time involved in preparing temperature traces for analysis, not to mention unforeseen complications which may lead to missing data (woodpecker attack of thermistor cables, gale-force winds dislodging loggers or even entire trees, ibuttons falling from the sky to stay forever hidden under leaf litter, battery life failure and accidental resetting of loggers before downloading data or failing to reset at all at the end of a long wet day in the woods; pers.obs).

The production of individual-specific temperature microclimates has also facilitated an assessment of incubation pattern in relation to temperature experience. The reproductive effort of
the blue tit consists of three stages: egg production, incubation and chick provisioning. While temperature may act as a cue for the blue tit in predicting when conditions will be most suitable for chick provisioning and therefore determine the timing of first egg lay date, microclimate is shown to act directly on the temperature dependent stage of incubation. By using modelled temperatures, loggers were not split between outside and inside nest boxes, freeing up the number of loggers available to record incubation patterns across the site.

The construction of a temperature map means that temperature profiles are produced that are relevant to the micro-habitat of the individual, as opposed to individual variation solely informing the mean response of a population, tested in turn against a single local temperature measure. While the latter is sufficient for establishing temperature-related trends, there is information in individual variation that is important for quantitative predictions of organism responses (Pincebourde et al., 2007, Schaper et al., 2012) and the work presented here in this thesis is just the tip of the iceberg of potential work to investigate the role of the thermal environment and variation in temperature regimes on network synchrony, social interaction or nest site fidelity and recruitment.

Variation in temperature across space equivalent to variation in temperature across time

Temperature change as a consequence of climate change is occurring at a rapid rate, with the greatest increases observed year on year in just the last ten years (MetOffice, 2014). There are longitudinal datasets that exist from pre-1970 to now, covering the span of observed temperature change with climate change (McCleery and Perrins, 1998, Roy et al., 2001, Sparks and Carey, 1995, Visser and Holleman, 2001, Johnson et al., 2011, Kauserud et al., 2010). Testing mean population trends against annual variation in temperature is however inherently retrospective and time-consuming and requires a change to have manifested before a prediction can be made.

Birds and trees track temperature across time (Crick et al., 1997, Sparks and Carey, 1995) but also across space, over latitudinal and altitudinal gradients (Both et al., 2004, Bourgault et al., 2010, Smith et al., 2011, Vitasse et al., 2009a). An aim of this study was to explore if such temperature
correlated variation was observed across space over the limited area of a single study system (Rorison et al., 1986). I find that spatial variation matches interannual variation in temperature even within a 30m altitudinal range and 1km² area. I have demonstrated that similar patterns of phenology are observed across the microclimates of this study system as are observed for the same study system over time: the slopes and intercepts of spatial models are comparable to those of temporal models.

The benefit of testing across spatial gradients is that it does not require an annual or even decadal long time-investment in data collection. Most advantageous is that, in terms of individual responses, one can compare amongst individuals as opposed to within individuals. The latter is limited by generation times (Charmantier et al., 2008) and by the very nature of reproduction as the response of interest, in the case of the bird, is confounded by other temporal variables such as current versus future reproductive investment strategies (Svensson and Nilsson, 1997) and cohort effects, such as population densities or sex-ratios (Both et al., 1999, Hjernquist et al., 2009).

**One temperature parameter is not equal to another**

The manner in which phenological trends are associated with different temperature parameters can lead to different inferences as to the role of temperature (Schaper et al., 2012). It is only in comparing different temperature regimes that this is possible. The impact of different temperature regimes on behaviour or activity can be achieved under laboratory or aviary conditions, but the combination of temperature parameters e.g. high min, high max, high mean; or high min, low max, medium mean; or low min, high max medium mean, are numerous and the ability to carry out such experimental regimes under suitable sample sizes, even before considering individual behaviours due to phenotype require a large financial and labour investment (for a rare example of where this has been achieved see Schaper et al., 2012, Visser et al., 2011).

The beauty of mapping temperature microclimates means that the many permutations of temperature distribution can be tested as they occur naturally across space or across time. By
predicting and mapping temperature across the site it is possible to compare how temperature parameters vary in relation to one another. By mapping temperature, one can see that areas differ in their temperature extent, with the potential to evaluate if different areas of woodland are associated with different rates of change and adaptation. This is admittedly a correlative study and correlation does not mean causation, but a study such as this provides support for experimental studies that seek to establish causation (Schaper et al., 2012) and provides an interesting focus for future work. The temperature model presented here, while robust and highly parameterised is still a simple description of the thermal environment. Other elements may also play a role in the microclimate and associated phenologies, for example differences in budburst phenology across a single oak crown, which can be many metres in radius, or the orientation of a nest box on a tree.

**Unequal temperature change**

A conclusion of this study is that the temperature regime that characterises one time window does not necessarily predict the thermal environment of another. The temperature cue environment of one organism is not the same as that of another organism. Critically, temperature change can be unequal even across one season or a comparatively small area.

I find that it is the timing of temperature change that is important. To have warmer temperatures at the start of the season relative to later in the season promotes greater blue tit productivity. Higher relative temperatures during the time-window that cues for the bird, promotes activity at the trophic level slowest to respond to temperature and this finding fits with other studies (Marcel et al., 2003, Stevenson and Bryant, 2000).

Comparisons across populations are important for understanding how temperature change with anthropogenic climate change will impact on network cohesion. Populations may differ in their forest cover, their vegetation type and their seasonal rate of temperature increase, with trends in phenologies and the degree of network cohesion being population specific. This study finds that
phenological trends with temperature can be observed across microclimates within a single study system.
8 Appendix

8.1 Temperature recording

Figure 8.1: Tinytag data logger field setup. Exposure to ambient air flow is indicated by the blue arrow.
Figure 8.2: i-button data logger field set up. Exposure to ambient air flow is indicated by the blue arrow.
Figure 8.3: Plots of logger recordings of mean temperature per day of data series (21st March, Julian day 82, of 2012 until 26th May, Julian day 148, of 2013). Plots a and c illustrate all recorded data (n = 27524). Plots b and d are of the data set with outliers removed (n=23866).
Table 8.1: Correlation matrix of Pearson’s pairwise correlation coefficients of temperature parameters derived from hourly temperatures recorded by loggers (n=56) from March 2012 – May 2013. Collinear terms, with a correlation coefficient $[r^2] >0.70$ are given in bold.

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Mean</td>
<td></td>
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<td></td>
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<td></td>
<td></td>
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<td>2. Maximum mean</td>
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<td></td>
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<tr>
<td>3. Minimum mean</td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>4. Average maximum</td>
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<td>0.32</td>
<td>0.46</td>
<td></td>
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<tr>
<td>5. Greatest maximum</td>
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<td>0.44</td>
<td>-0.12</td>
<td><strong>0.70</strong></td>
<td></td>
<td></td>
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<tr>
<td>6. Lowest maximum</td>
<td><strong>0.86</strong></td>
<td>0.11</td>
<td><strong>0.96</strong></td>
<td>0.58</td>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>7. Average minimum</td>
<td><strong>0.84</strong></td>
<td>0.33</td>
<td><strong>0.77</strong></td>
<td>0.20</td>
<td>-0.23</td>
<td>0.62</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>8. Highest minimum</td>
<td>0.34</td>
<td>0.52</td>
<td>0.21</td>
<td>-0.19</td>
<td>-0.19</td>
<td>0.02</td>
<td><strong>0.71</strong></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>9. Lowest minimum</td>
<td><strong>0.70</strong></td>
<td>0.25</td>
<td><strong>0.75</strong></td>
<td>0.08</td>
<td>-0.30</td>
<td>0.59</td>
<td><strong>0.91</strong></td>
<td>0.68</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>10. Summed daily range</td>
<td>-0.25</td>
<td>0.06</td>
<td>-0.54</td>
<td>0.43</td>
<td>0.68</td>
<td>-0.43</td>
<td>-0.51</td>
<td>-0.36</td>
<td>-0.66</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11. Maximum daily range</td>
<td>0.01</td>
<td>0.17</td>
<td>-0.16</td>
<td>0.64</td>
<td><strong>0.72</strong></td>
<td>-0.06</td>
<td>-0.27</td>
<td>-0.26</td>
<td>-0.41</td>
<td><strong>0.76</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12. Number of frost nights</td>
<td><strong>-0.71</strong></td>
<td>-0.24</td>
<td><strong>-0.77</strong></td>
<td>-0.09</td>
<td>0.26</td>
<td>-0.59</td>
<td><strong>-0.93</strong></td>
<td><strong>-0.72</strong></td>
<td><strong>-0.93</strong></td>
<td>0.62</td>
<td>0.31</td>
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<tr>
<td>13. Summed degree days (daily minima &gt;5°C)</td>
<td>0.33</td>
<td>0.32</td>
<td>0.03</td>
<td>-0.12</td>
<td>-0.18</td>
<td>-0.13</td>
<td>0.62</td>
<td><strong>0.72</strong></td>
<td>0.45</td>
<td>0.00</td>
<td>-0.16</td>
<td>-0.45</td>
</tr>
</tbody>
</table>
Table 8.2: Descriptive statistics of temperature parameters recorded at nest box height across the site. The correlation coefficients of estimate and $r^2$ for April averages of minimum, mean and maximum temperature and the ranges in temperature recorded across the site, with day of recording, are presented. Asterisks denote statistical significance (*=p<0.05, **=p<0.01, ***=p<0.001).

<table>
<thead>
<tr>
<th>year</th>
<th>minimum</th>
<th>mean</th>
<th>smallest day’s range (°C)</th>
<th>greatest day’s range (°C)</th>
<th>mean daily range (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>minimum</td>
<td>1.59°C, 28th April 2012</td>
<td>6.97°C, 13th April 2012</td>
<td>3.17</td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean</td>
<td>2012</td>
<td>1.58, 0.51***</td>
<td>0.74°C, 3.84°C,</td>
<td>1.54</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>1.19, 0.28***</td>
<td>8th April 2012, 25th July 2012</td>
<td></td>
<td></td>
</tr>
<tr>
<td>maximum</td>
<td>2012</td>
<td>-0.15, 0.08*</td>
<td>0.07, 0.09*</td>
<td>1.22°C, 15.59°C,</td>
<td>6.17</td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>-0.19, 0.15**</td>
<td>0.07, 0.12*</td>
<td>26th Feb. 2013, 28th May 2012</td>
<td></td>
</tr>
</tbody>
</table>

8.2 Temperature prediction

Figure 8.4: Plots of significant parametric terms in the georeferenced models of minimum, mean and maximum temperature; A=Autumn, S=Spring, Su=Summer, W=Winter.
Figure 8.5: Response shapes of smoothed terms in the georeferenced models of minimum, mean and maximum temperature. The trend is shown by the smooth curve, dashed curves indicate standard error bounds and dashed lines inside of the x axis show the distribution of data points.

Figure 8.6: Illustration of temperatures predicted by the interaction of aspect (degrees from 200°) and sunlight (MJ/m²) given a near flat (1°) and steep (12°) gradient.
Figure 8.7: Illustrations of interactions from the generalised additive models of temperature prediction. All other terms in the models are held at their mean value.
Table 8.3: Predictive generalised additive model of hourly mean temperature at a height of 1.8 m, for Silwood Park from 21st March 2012 until 26th May 2013. Deviance explained = 97.7%, n = 619728, scale estimate = 0.82.

<table>
<thead>
<tr>
<th>Parametric coefficients</th>
<th>Estimate</th>
<th>Standard error</th>
<th>t value</th>
<th>p value</th>
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<tr>
<td>Intercept</td>
<td>1.07</td>
<td>1.13</td>
<td>0.95</td>
<td>0.34</td>
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<tr>
<td>Weather station temperature</td>
<td>0.88</td>
<td>0.0003</td>
<td>2522.65</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Season: Spring</td>
<td>-0.09</td>
<td>0.02</td>
<td>-5.87</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Season: Summer</td>
<td>0.10</td>
<td>0.01</td>
<td>7.04</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Season: Winter</td>
<td>0.15</td>
<td>0.001</td>
<td>10.38</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Aspect</td>
<td>-0.01</td>
<td>0.009</td>
<td>-1.49</td>
<td>0.14</td>
</tr>
<tr>
<td>Building</td>
<td>-0.001</td>
<td>0.001</td>
<td>-1.13</td>
<td>0.26</td>
</tr>
<tr>
<td>Distance</td>
<td>-0.008</td>
<td>0.01</td>
<td>-0.64</td>
<td>0.52</td>
</tr>
<tr>
<td>Elevation</td>
<td>0.04</td>
<td>0.007</td>
<td>5.17</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Smoothed terms</th>
<th>E.d.f.</th>
<th>Ref. d.f.</th>
<th>F value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>s(Hour)</td>
<td>8.68</td>
<td>8.70</td>
<td>775.74</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>s(Julian day)</td>
<td>8.99</td>
<td>9.00</td>
<td>892.68</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>te(Julian with hour)</td>
<td>19.40</td>
<td>19.51</td>
<td>3331.41</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>s(Air pressure)</td>
<td>8.96</td>
<td>9.00</td>
<td>2288.70</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>s(Sun)</td>
<td>7.64</td>
<td>7.92</td>
<td>20.16</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>s(Rain)</td>
<td>7.29</td>
<td>8.13</td>
<td>43.66</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>te(Eastings with Northing)</td>
<td>18.93</td>
<td>18.96</td>
<td>124.61</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>te(Aspect with gradient)</td>
<td>17.33</td>
<td>17.37</td>
<td>76.00</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>te(Distance with sun)</td>
<td>18.02</td>
<td>18.18</td>
<td>479.44</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>s(Aspect with distance)</td>
<td>21.45</td>
<td>21.49</td>
<td>192.76</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>te(Aspect with sun)</td>
<td>14.50</td>
<td>16.00</td>
<td>71.52</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
8.3 Phenological trends

Table 8.4: Slopes of linear models of first egg lay date predicted by location-specific temperatures of nest boxes in each year (2002-2013). The sample size of nests in each year is given (n). Asterisks denote statistical significance (.=p<0.1, *=p<0.05, **=p<0.01, ***=p<0.001). The slope of the regression in each year, for either of the 3 temperature parameters was not predicted by the sample size of nests (p>0.69).

<table>
<thead>
<tr>
<th>Year</th>
<th>n</th>
<th>Maximum intercept estimate</th>
<th>Mean int. est.</th>
<th>Minimum int. est.</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>103</td>
<td>104.70 -1.04.</td>
<td>102.53 -0.24</td>
<td>102.41 -0.10</td>
</tr>
<tr>
<td>2003</td>
<td>156</td>
<td>114.53 -0.55.</td>
<td>113.50 -0.62</td>
<td>112.85 <em>0.62</em></td>
</tr>
<tr>
<td>2004</td>
<td>140</td>
<td>114.30 -0.10.</td>
<td>113.56 0.95</td>
<td>114.02 0.38</td>
</tr>
<tr>
<td>2005</td>
<td>185</td>
<td>113.29 -1.62***</td>
<td>109.60 -0.002</td>
<td>109.59 0.17</td>
</tr>
<tr>
<td>2006</td>
<td>160</td>
<td>116.99 -0.61.</td>
<td>116.12 -0.91</td>
<td>115.62 -0.03</td>
</tr>
<tr>
<td>2007</td>
<td>175</td>
<td>105.50 -0.19.</td>
<td>105.31 -0.53</td>
<td>105.07 0.44</td>
</tr>
<tr>
<td>2008</td>
<td>152</td>
<td>118.69 -2.55***</td>
<td>109.37 -1.68</td>
<td>108.56 -1.10*</td>
</tr>
<tr>
<td>2009</td>
<td>121</td>
<td>107.97 -1.54*</td>
<td>106.06 -3.07*</td>
<td>104.45 -0.13</td>
</tr>
<tr>
<td>2010</td>
<td>99</td>
<td>111.92 -1.03</td>
<td>109.29 0.57</td>
<td>109.28 1.17*</td>
</tr>
<tr>
<td>2011</td>
<td>208</td>
<td>105.65 -0.81.</td>
<td>103.64 0.19</td>
<td>103.66 0.23</td>
</tr>
<tr>
<td>2012</td>
<td>198</td>
<td>109.96 -1.25*</td>
<td>107.83 -2.69*</td>
<td>107.02 -0.18</td>
</tr>
<tr>
<td>2013</td>
<td>160</td>
<td>122.83 -0.04.</td>
<td>123.32 -0.75</td>
<td>122.80 -0.15</td>
</tr>
</tbody>
</table>

Table 8.5: Slopes of linear models of oak bud burst predicted by location-specific temperatures of each tree in each year (2002-2013 n=370). Asterisks denote statistical significance (.=p<0.1, *=p<0.05, **=p<0.01, ***=p<0.001).

<table>
<thead>
<tr>
<th>Year</th>
<th>n</th>
<th>Maximum intercept estimate</th>
<th>Mean int. est.</th>
<th>Minimum int. est.</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010</td>
<td>330</td>
<td>116.19 0.22</td>
<td>115.84 -1.16.</td>
<td>116.07 0.27</td>
</tr>
<tr>
<td>2011</td>
<td>328</td>
<td>101.59 0.44.</td>
<td>102.23 -0.72</td>
<td>102.67 0.04</td>
</tr>
<tr>
<td>2012</td>
<td>320</td>
<td>111.45 0.96</td>
<td>111.28 -2.99.</td>
<td>113.23 0.50</td>
</tr>
<tr>
<td>2013</td>
<td>316</td>
<td>123.32 0.24</td>
<td>124.18 -0.73</td>
<td>123.98 0.02</td>
</tr>
</tbody>
</table>
Figure 8.8: The correlation of mean temperature with mean oak budburst date (plot a: Julian days 88 – 107, Intercept= 33.90, estimate= -0.22, s.e. = 0.03, d.f. = 1 and 5, r²=0.92, p<0.0005) and 7.5% defoliation (plot b: Julian days 96 – 121, Intercept= 47.07, estimate= -0.26, s.e. = 0.0006, d.f. = 1 and 2, r²=0.1, p<0.0001).

Figure 8.9: Plot of annual mean defoliation rate, derived as the number of days between 3 and 7.5% defoliation, and the annual mean peak defoliation score (percentage of canopy eaten) for 2010-2013
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