Diet flexibility of a declining long-distance migrant allows it to escape the consequences of phenological mismatch

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1   **Diet flexibility of a declining long-distance migrant allows it to escape the**

2   **consequences of phenological mismatch.**

3

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1 **Summary**

2 Recently, concerns have been raised that climate-driven shifts in prey phenology have lead to

3 asynchrony with the timing of peak resource requirements of their predators, leading to a

4 reduction in productivity and population declines. Migrant species that cannot adjust their arrival

5 times may be particularly at risk, especially those that breed in seasonal environments and rely

6 on a temporarily super-abundant prey source; such as insectivorous passerine birds that depend

7 on the seasonal flush of caterpillars to feed their young. We test whether the declines of one such

8 species, the Wood Warbler, a trans-Saharan migrant that has shown little advance in arrival times

9 on the breeding grounds, are likely to have been caused by phenological mismatch. We measured

10 seasonal invertebrate biomass and various fitness parameters, including the timing of breeding

11 and breeding success, in two time periods: 1982-84, prior to the species' decline in the UK, and

12 2009-11, as the reduction in numbers has continued. Although birds bred on average a week

13 earlier in 2009-11 than 1982-4, this was not adequate to track the more rapid advancement of

14 peak caterpillar biomass, which advanced by 12 days and was closely correlated with spring

15 temperatures. However, although caterpillars were the dominant prey fed to nestlings, and there

16 was some evidence that productivity was positively related to caterpillar biomass in the

17 environment, nests more synchronous with the food peak did not produce heavier nestlings or

18 more fledglings. We conclude that the lack of a negative effect of observed mismatch is due to

19 Wood Warblers' capacity to switch to other prey types with no adverse consequences. Although

20 other studies have demonstrated that climate driven asynchrony of predator and prey populations

21 can have impacts on avian demography, this study highlights the importance of investigating the

22 generality of those findings.

23

1   **Introduction**

2   The timing of breeding has far-reaching consequences for an individual bird's fitness, with

3   strong selection against those that do not breed at the optimal time (Nilsson 1999). Such timing

4   will depend on interactions with other species at both lower (food) and higher (predators) trophic

5   levels (Daan 1989; Both *et al*. 2009). Many species have responded to recent climate change by

6   advancing their phenology (Crick *et al*. 2004), however, such responses to warming may disrupt

7   interspecific interactions (Bretagnolle & Gillis 2010). Phenological responses to warming have

8   tended to be slower at higher trophic levels (Thackeray *et al*. 2010), thus advancement of

9   breeding has not been sufficient to adequately track the shifting phenology of prey populations,

10   often invertebrates at lower trophic levels, leading to a temporal mismatch and resulting in

11   lowered reproductive success and population declines (Visser *et al* 1998; Both *et al*. 2006).

12

13   Such mismatch is most likely to occur in seasonal environments (Both *et al*. 2010) where species

14   are dependent upon a food source that is abundant for only a short period (relative to the length

15   of the breeding season); such as single-brooded insectivorous passerine birds and their caterpillar

16   prey in deciduous forest (Both 2010). Migratory species are thought to be at particular risk from

17   the effects of phenological mismatch (Möller *et al*. 2008; Both *et al*. 2010), as they may not be

18   able to respond to changing conditions on their breeding grounds as their arrival may be

19   constrained by both endogenous factors (Gwinner 1996) and conditions on their wintering

20   grounds and along their migration routes (Tøttrup *et al*. 2008).

21

22   Much of the evidence for the negative impacts of phenological mismatch has come from studies

23   of the insectivorous bird communities of temperate deciduous forests, where population trends of

1   one migratory species (Pied Flycatcher *Ficedula hypoleuca*) have been linked to the failure to

2   adequately respond to climate-driven shifts in prey phenology (Both *et al*. 2006). However, such

3   impacts have not been uniform, even between populations of a single species (Both *et al*. 2004),

4   with variation in responses attributed to variable levels of spring warming, habitat type and diet

5   (Burger *et al* 2012). There is, consequently, a need for studies on other species to examine how

6   widespread are the putative negative impacts of phenological shifts.

7

8   The Wood Warbler *Phylloscopus sibilatrix* is a species that is potentially very sensitive to the

9   effects of phenological mismatch. It is a long-distance migrant wintering in sub-Saharan Africa

10   (Urban *et al*. 1997), which has not significantly advanced its arrival on the breeding grounds

11   (Moller *et al*. 2008; Ockendon *et al*. 2012). In the UK, they are most abundant in oak woodland

12   (Bibby 1989), a habitat with pronounced seasonality in invertebrate abundance (Smith *et al*.

13   2011). Although across their range a diverse diet has been recorded (Pavelka & Korytář 1992;

14   Lippek 1996; Temrin *et al*. 1997; Maziarz & Wesołowski 2010), caterpillars are the dominant

15   prey type in upland oak woodlands (Stowe 1987). Previous studies in the primeval forests of

16   Poland (Wesołowski & Maziarz 2009; Maziarz & Wesołowski 2010) have shown little temporal

17   trend in breeding phenology and no negative effects of mismatch with their caterpillar prey.

18   However, these studies did not measure changes in caterpillar phenology over the entire period

19   of recent climate warming. Unlike in central and eastern Europe, Wood Warbler populations

20   have declined in the north and west of their range (Birdlife International 2004), and as the effects

21   of phenological shifts have been shown to vary between populations of the same species (Visser

22   *et al*. 2003; Both *et al*. 2004; Burger *et al*. 2012), it is important to investigate possible effects of

23   phenological mismatch across their entire range.

4

1

2 In the UK, Wood Warblers have declined by 65% since 1995 (Eaton *et al*. 2012), and have been

3 lost from much of their range in south and south-east England (Balmer *et al*. 2013), and are now

4 mainly confined to the upland oak woods of western Britain. Our aim here is to assess whether

5 this decline has been driven by an insufficient response to shifts in their prey's phenology. We

6 use data on caterpillar abundance and breeding success from two periods: 1982-84, before the

7 onset of the nationwide population decline, and 2009-11, as the decline continued. Firstly, we

8 ask whether caterpillar and Wood Warbler phenology has advanced since the 1980s due to

9 warming spring temperatures. Secondly, has the mismatch between predator and prey phenology

10 increased with increasing spring temperatures, and between the two time periods? Finally, we

11 assess whether increasing phenological mismatch, reducing caterpillar food availability, has led

12 to reduced breeding success, both within seasons and between time periods, and whether this is

13 related to nestling diet.

14

15 **Methods**

16 STUDY AREA

17 The study was conducted in 6 upland oakwoods in 1982-84 (Stowe 1987), and extended in 2009-

18 11 to a further 15 sites; all forests were located in Carmarthenshire (formerly Dyfed) and Powys,

19 mid Wales, UK (Fig 1), at a mean (± SE, range) altitude of 240m (±8.8, 140-300m). The median

20 area of the woods was 16.3 ha (range, 4.9-29.7 ha). Wood Warblers declined in Powys by 19%

21 between the 1980s and 2000s (Mallord *et al*. in press). The canopy of the study forests was

22 dominated by Sessile Oak *Quercus petraea*, with lesser amounts of Silver Birch *Betula pendula*,

23 with a poorly developed understorey, mainly comprised of Rowan *Sorbus aucuparia* and Hazel

5

1   *Corylus avellana*, with occasional Hawthorn *Crataegus monogyna* and Holly *Ilex aquifolium*

2   bushes. Typical of such upland woods was a sparse ground cover of mosses, grasses, Bracken

3   *Pteridium aquilinum*, Bramble *Rubus fruticosus*, Bilberry *Vaccinium myrtillus* and Heather

4   *Calluna vulgaris*. Woodlands were situated within a matrix of permanent pasture and, at higher

5   altitudes, moorland and coniferous plantations.

6

7   TEMPERATURE DATA

8   Temperature data from the period 1980-2011 collected at the Cwmystwyth weather station in

9   Powys, mid Wales (long/lat: 52.3582, -3.8019, altitude, 301m), were supplied by the British

10   Atmospheric Data Centre / Meteorological Office, UK. The mean (± SE, range) distance from

11   the weather station to our study sites was 32km (± 2.9, 19-53km). To assess changes over time

12   and the response of caterpillar phenology, we used mean temperatures for the period April 1st to

13   May 31st, and for Wood Warbler phenological responses we used mean temperature over the

14   period April 16th to May 15th, encompassing the time of peak arrival and egg laying.

15

16   INVERTEBRATE ABUNDANCE

17   Invertebrates were collected in water traps, which consisted of commercially available grey cat

18   litter trays (length x width x depth, cm: 33.5 x 23.5 x 6.5; Wilkinsons Ltd). Five trays were

19   placed randomly within each study wood from mid April to early July and the same locations

20   were used in each year. Trays were filled with water to 3-5cm depth with a drop of detergent to

21   break the surface tension and covered by a 1.5cm-mesh plastic horticultural netting, which was

22   pegged down to prevent contamination with falling leaves and other debris, and to limit

23   disturbance from sheep (Ausden 1996). The contents of each tray were emptied on a weekly

6

1   basis, being sieved through muslin (Dijon Muslin Voile Fabric, John Lewis Partnership, UK)

2   then stored in a 70% alcohol solution so that they could be sorted at a later date. Water and

3   detergent were replaced on each visit. Invertebrates were collected from six sites in 1982-1984

4   and 20 in 2009-11, including four from the earlier period; although invertebrates were not

5   collected at every site in all years, as some sites were replaced each year to increase the number

6   of Wood Warblers in our study population (data from one year only, N = 2 sites, two years, N

7   =4, three years, N = 10, six years, N = 4).

8

9   Although many different invertebrate groups were caught, water traps are not ideal for sampling

10   canopy-dwelling species, except for caterpillars which fall under their own volition to pupate.

11   Caterpillars, not identified to species, were individually measured to the nearest millimetre. Dry

12   mass was calculated by taking a known number of each length and heating them in an oven until

13   no further loss of weight was recorded (usually at least two hours). The total mass was then

14   divided by the numbers in the sample to determine the average dry mass of each individual

15   which, when plotted produced the formula: mass = $0.0273 \times \text{length}^{1.8731}$ ($R^2 = 0.9743$), which

16   was then used to calculate the mass of all caterpillars. The seasonal variation in caterpillar

17   biomass was described in three ways (Visser *et al*. 2006): peak height, the highest weekly

18   biomass recorded; peak date, the day (assigned to the midpoint between this and the previous

19   visit) on which highest biomass was recorded; and peak width, arbitrarily defined as the number

20   of weeks on which biomass exceeded mean weekly biomass (± SE; 250 ± 27.3) from all six

21   years of the study.

22

7

1   To confirm the validity of using water traps to measure caterpillar biomass, in 2009-11 we

2   deployed 2-3 frass traps at 2-8 sites, at the same location as water traps. Frass traps consisted of a

3   plastic seed tray (24cm x 37cm) lined with horticultural fleece, and covered with netting trays

4   (Smith *et al*. 2011). Horticultural fleece allowed drainage of water through holes in the trays.

5   Caterpillar biomass from water traps (mg/m2) was positively correlated with weekly frass fall

6   (mg/tray, both natural log transformed; $R^2 = 0.49$, $F_{1,75} = 73.2$, $P < 0.0001$). The peak dates

7   assigned by each method were also strongly, positively correlated ($R^2 = 0.88$, $F_{1,11} = 82.0$, $P <$

8   0.0001).

9

10   WOOD WARBLER BREEDING SUCCESS

11   We collected data on the initiation of breeding, clutch size, nestling weights and fledging

12   success. Territories were identified by the presence of singing males on weekly visits to each

13   wood, conducted from the time of arrival of birds in mid-late April until the end of the breeding

14   season (mid July). Arrival date, the date on which a male was first seen, was recorded only for

15   2009-11. Within territories, females were located usually by their vocalisations and watched for

16   30-60 minutes to confirm whether there was an active nest (females will readily return to the

17   nest, at all stages, even if a person is standing nearby). First egg dates (FED) were either

18   recorded directly at nests found during egg-laying, or were back-calculated after chicks had

19   hatched, assuming an incubation period of 13 days and the laying of one egg per day with

20   incubation starting after the last egg has been laid (Fourage 1968). When hatching date was not

21   known, the age of nestlings was estimated by comparing the degree of feather development with

22   nestlings of known age. Of 243 nests monitored across both time periods, 102 (41.9) were found

23   during building or egg-laying, 89 (36.6%) during incubation and 52 (21.4%) during the chick

1   stage. Ten nests were either abandoned before egg-laying or deserted before the onset of

2   incubation and were not included in analyses. At approximately seven days old (7.3 ± 0.9, 4-9

3   days, N = 134), nestlings were weighed with an electronic balance (to nearest 0.1g), and wing

4   and tarsus measurements taken (maximum cord and tarsus; Redfern & Clark 2001; weight only

5   in 1984). Nests were visited every 3-4 days to confirm fledging; nests were assumed to have

6   failed if eggs, or chicks younger than 10 days old, disappeared from the nest, and there were no

7   signs from nearby adults to suggest that chicks had fledged.

8

9   NESTLING DIET

10   In 2009-11, faecal samples were collected from nestlings at the same time as biometrics taken,

11   nestlings often producing sacs upon handling. Out of 114 broods handled, samples were

12   collected from 81. After collection, faecal samples were stored in 70% ethanol. Contents of each

13   pot were poured into a petri dish, and each sac broken up using water and fine forceps, and

14   examined under a binocular microscope at 40 x magnification. A reference collection of common

15   invertebrate fragments was made by crushing identified individuals (collected in our water traps)

16   and photographing parts through a microscope. This reference collection was used along with the

17   plates in Moreby (1987) and Ralph *et al.* (1985) to identify all arthropod parts to order or class.

18   The minimum number of individuals of each invertebrate type was recorded e.g. two caterpillar

19   mandibles equal one individual, six legs equals one individual fly.

20

21   Faecal analysis can bias estimates of the importance of certain prey groups within avian diets,

22   mainly due to differential digestibility, (Jenni *et al*. 1990; Robinson & Stebbins 1993), leading to

23   the under-representation of soft-bodied taxa in faecal samples. As well as being safer than other

9

1 methods of sample collection (Moreby & Stoate 2000; Carlisle & Holberton 2006), faecal

2 analysis can provide estimates similar to other methods (Poulsen & Aebischer 1995), possibly

3 due to rapid passage through the gut. Given adequate sample sizes, the most important prey

4 items are likely to be identified (Cummins & O'Halloran 2002), and although our assessment of

5 the seasonal importance of caterpillars could be biased if birds systematically shifted to prey that

6 was absent from our samples, the relationship between the composition of caterpillars in the diet

7 and their biomass in the environment suggests that our conclusions concerning the importance of

8 this group are valid.

9

10 A minimum of 188 faecal sacs were collected from 81 broods in 2009-2011, containing a

11 minimum of 1304 individual prey items. Over half of the prey items were the larvae of

12 Lepidoptera (Table 2), and 84% of all items were comprised of caterpillars, Dipteran flies and

13 spiders (Araneae). Over 97% of broods were fed caterpillars and flies, and nearly 78% were fed

14 spiders. Prey items that could not be identified accounted for less than 1% of all items collected

15 (Table 2).

16

17 In addition to the three main prey types (caterpillars, flies and spiders), all other prey items were

18 grouped as 'others'. Since the proportions of all prey types have a sum of 1, they are difficult to

19 analyse as they are not independent, the so-called 'unit sum constraint' (Aitchison 1986). To

20 overcome this, we calculated the composition of caterpillars, flies and spiders within the diet as

21 the natural log of the ratio between the proportion of each prey type and the proportion of

22 'others' (+ 0.0001 to allow for zero proportions). These values are independent of the group that

23 was used as the denominator in the transformations (Aebischer *et al*. 1993).

10

1

2   STATISTICAL ANALYSIS

3   Unless otherwise stated, all analyses were carried out in a generalised linear modelling (GLM)

4   framework, with normal or Poisson errors where appropriate, in SAS v.9.2 (SAS Institute Inc.

5   2002–08).

6

7   *Advances in phenology*

8   The timing of peak caterpillar biomass was related to site, year (or period for comparison

9   between 1982-84 and 2009-11) and the value of peak biomass, and to average spring

10   temperatures in a simple regression. Arrival dates and the initiation of breeding were compared

11   between years or periods.

12

13   *Increasing mismatch*

14   We modelled to what extent the advance in nesting activity has kept pace with advancing

15   caterpillar phenology by relating FED to the date of peak caterpillar biomass, and assessed what

16   this means for the degree to which peak resource abundance and requirements are mismatched

17   by relating relative hatch date to the peak caterpillar date. Relative hatch date was defined as the

18   difference, in days, between hatch date (+10 as peak resource requirements of Wood Warblers is

19   when nestlings are 10 days old [Temrin *et al*. 1997]) and the site and year-specific peak

20   caterpillar date.

21

22   *Impacts on productivity*

11

1   Seasonal trends in productivity were modelled by relating fledging success and chick weights to

2   relative hatch date and the timing and value of peak caterpillar biomass, as well as to site and

3   annual variation. Fledging success was controlled for brood size, and chick weights for wing

4   length (a surrogate for the age of the chicks). The contribution of each prey type to the diet was

5   related to site, year, brood size, nestling age, relative hatch date and all two-way interactions. As

6   a varying number of faecal sacs were collected from each brood, log ratios were weighted by the

7   natural log of the total number of invertebrates collected from each brood. To investigate the

8   effects of diet on productivity, we substituted measures of caterpillar biomass and timing, and

9   nesting phenology, with the log ratios of the proportions of the main prey types as derived from

10 faecal analysis.

11 Except when first nests were abandoned without eggs being laid, all second nests within a

12 territory (unless synchronous with the first – males can be polygynous; Temrin *et al*. 1984) had

13 FED in June. This was confirmed by three colour-ringed females who paired with new males in

14 different territories for their second nesting attempts. Therefore, unless otherwise stated,

15 probable re-nesting attempts (i.e. FED after 31st May) were excluded from analyses.

16

17 **Results**

18 HAVE CATERPILLAR AND WOOD WARBLER PHENOLOGY ADVANCED AS A REULT

19 OF INCREASING SPRING TEMPERATURES?

20 Mean April-May temperature increased between 1980 and 2011 by an average of 0.07 °C per

21 year (temperature $= -122.3 + 0.066$ x year; $R^2 = 0.45$, $F_{1,30} = 24.5$, $P < 0.0001$; Fig 2). Our two

22 study periods (1982-84 and 2009-11) included one particularly cool and one particularly warm

23 spring (mean April-May temperatures, 1983: 6.5°C, 2011: 10.6°C).

12

1

2   The timing of peak caterpillar biomass varied annually ($F_{5,58} = 46.0$, $P < 0.0001$) and was earlier

3   when peak biomass was higher ($F_{1,58} = 13.4$, $P = 0.0005$), and   was negatively related to average

4   April-May temperatures ($F_{1,4} = 77.9$, $P = 0.0009$, $r^2 = 0.95$, Fig 3). Variation in peak dates

5   ranged from 20th June in 1983 to 18th May in 2011, a difference of 33 days. The greatest

6   advancement between two consecutive years (2010-2011) was 19 days (Fig 3). Timing of the

7   caterpillar peak was earlier in 2009-11 than in 1982-84 ($F_{1,22} = 7.8$, $P = 0.01$; Table 1). Peak

8   height varied between years in 2009-11 ($F_{5,45} = 8.7$, $P < 0.0001$; 2009 v 2010, $t_{43} = 2.6$, $P = 0.01$;

9   2009 v 2011, $t_{44} = 3.3$, $P = 0.002$; 2010 v 2011, $t_{42} = 0.8$, $P = 0.4$), but not in 1982-84, (all

10   pairwise comparisons, $t < 1.02$, $P > 0.31$). Comparing only those four sites sampled in both

11   1982-84 and 2009-2011, there was a significant reduction in caterpillar biomass between the two

12   periods ($F_{1,16} = 52.4$, $P < 0.0001$). This varied between sites ($F_{3,16} = 80.3$, $P < 0.0001$), and was

13   driven by a substantial reduction in caterpillars on two of the four sites (site x period, $F_{3,16} =$

14   72.1, $P < 0.0001$; Table 2). The mean ($\pm$ se, range) width of the peak was 1.95 weeks ($\pm$ 0.21, 0-

15   6), and varied between years ($F_{3,54} = 3.2$, $P = 0.03$), was narrower when the peak was later in the

16   season ($F_{1,54} = 6.8$, $P = 0.01$) and was wider when peak biomass was high ($F_{1,54} = 88.1$, $P <$

17   0.0001).

18

19   Arrival time of males on territories was about a week earlier in 2011 than in either 2009 or 2010

20   ($F_{2,182} = 12.7$, $p < 0.0001$; mean dates, 2009, 3rd May; 2010, 4th May; 2011, 27th April; 2009 v

21   2010, $z = 0.6$, $P = 0.53$; 2009 v 2011, $z = 3.9$, $P < 0.0001$; 2010 v 2011, $z = 4.6$, $P < 0.0001$).

22   Both arrival times and laying dates were negatively related to spring temperatures (Fig 4). On

13

1   average, birds started nesting earlier in 2009/11 than in 1983/84 ($F_{1,158} = 36.8$, $P < 0.0001$; Table

2   1). Variation in FED ranged from 24th May in 1983 to 11th May in 2011, a difference of 13 days.

3

4   HAS THERE BEEN INCREASING MISMATCH BETWEEN PEAK RESOURCE

5   ABUNDANCE AND REQUIREMENTS?

6   Excluding probable re-nesting attempts, birds' laying dates tended to be earlier when the peak in

7   caterpillar abundance was earlier ($F_{1,158} = 86.6$, $P < 0.0001$); however, egg-laying advanced less

8   than did the food peak, 0.37 days for every day's advancement by caterpillars (laying date = 22.5

9   + 0.37 x peak caterpillar date). This slower advancement of breeding meant that birds could only

10   partially track changes in caterpillar phenology, with relative hatch date at its greatest (i.e. least

11   synchronous) when caterpillar peak date is at its earliest ($F_{1,147} = 58.0$, $P < 0.0001$; Fig 5) after

12   controlling for the effects of peak height ($F_{1,147} = 18.7$, $P < 0.0001$) and a peak date x height

13   interaction ($F_{1,147} = 18.2$, $P < 0.0001$). Between 1982-84 and 2009-11, relative hatch date

14   increased, i.e. nesting became less synchronous with the food peak ($F_{1,149} = 13.9$, $P = 0.0003$;

15   Table 2). The average timing of peak resource requirements for nestlings in 1982-4 was seven

16   days after the food peak, compared to 14 days in 2009-11.

17

18   HAS INCREASING MISMATCH RESULTED IN REDUCED PRODUCTIVITY?

19   *Seasonal variation*

20   After controlling for brood size ($F_{1,94} = 473.3$, $P < 0.0001$), the number of chicks fledged was not

21   related to relative hatch date ($F_{1,93} = 1.5$, $P = 0.23$), peak caterpillar date ($F_{1,93} = 0.1$, $P = 0.77$),

22   height ($F_{1,93} = 0.1$, $P = 0.8$) or width ($F_{1,93} = 0.1$, $P = 0.82$). Including probable re-nesting

14

1   attempts, and accounting for smaller brood sizes, fledging success was lower in later nests ($F_{1,101}$

2   = 9.3, P = 0.003).

3

4   Modelling nests from 2009-11 only, controlling for wing length ($F_{1,85}$ = 202.3, P < 0.0001), and

5   variation between sites ($F_{11,85}$ = 1.9, P = 0.056), the mean weight of chicks per brood was

6   positively related to peak caterpillar biomass ($F_{1,85}$ = 4.6, P = 0.04) and relative hatch date ($F_{1,85}$

7   = 4.0, P = 0.05). However, the predicted effect of relative hatch date was positive, suggesting

8   that birds that were later than the food peak had heavier chicks. There was also a negative peak

9   height x relative hatch date interaction ($F_{1,85}$ = 4.0, P = 0.05), suggesting that synchrony with the

10   food peak was more important when peak height was large.

11

12   Neither clutch size ($F_{1,117}$ = 0.8, p = 0.36) nor the number of chicks fledged from successful nests

13   ($F_{1,100}$ = 0.3, P = 0.56) varied between the two time periods, although mean chick weights per

14   brood were greater in 2009/11 than in 1984 ($F_{1,110}$ = 5.6, P = 0.02; Table 2).

15

16   *Productivity in relation to diet*

17   The proportion of caterpillars in the diet varied between sites ($F_{11,56}$ = 3.7, P = 0.0006) and years

18   ($F_{2,56}$ = 15.2 P < 0.0001), but not with nestling age ($F_{1,56}$ = 2.2, P = 0.14) and was lower in later

19   (less synchronous) nests ($F_{1,56}$ = 4.0, P = 0.05; Fig 6. The proportion of flies ($F_{2,78}$ = 3.5, P =

20   0.03) and spiders ($F_{2,74}$ = 4.2, P = 0.02) varied annually, the latter also increasing with age ($F_{1,74}$

21   = 3.1, P = 0.08), but only in 2011 (age x year interaction, $F_{1,74}$ = 3.8, P = 0.03). To test whether

22   caterpillar composition in the diet was related to their abundance in the environment, we related

23   site estimates from the model of nestling diet (with the effects of year, age and date controlled

15

1   for) to mean weekly biomass. Biomass values were taken from the exact sites, years and weeks

2   in which the faecal samples were collected, and were log transformed. Caterpillar composition in

3   the diet was non-linearly related to caterpillar biomass, initially increasing, then levelling off (log

4   biomass, $\chi^2_1 = 5.8$, $P = 0.02$, log biomass^2, $\chi^2_1 = 3.9$, $P = 0.05$, Fig 7).

5

6   In addition to significant annual variation ($F_{2,58} = 3.6$, $P = 0.03$), and the positive effect of brood

7   size ($F_{1,58} = 196.1$, $P < 0.0001$), fledging success was positively related to the caterpillar

8   composition of the diet ($F_{1,58} = 3.8$, $P = 0.05$), but only in 2011 (an outbreak year for defoliating

9   caterpillars; year x diet interaction, $F_{2,58} = 4.2$, $P = 0.04$). The proportion of flies ($F_{1,62} = 0.03$, P

10 $= 0.86$) in the diet was not related to fledging success, while there was no relationship with the

11 proportion of spiders ($F_{1,61} = 3.5$, $P = 0.07$). Chick weight was not related to the caterpillar

12 composition of the diet (wing length, $F_{1,72} = 175.7$, $P < 0.0001$; caterpillars in diet, $F_{1,72} = 1.8$, P

13 $= 0.18$). Chick weight was not related to the proportion of flies in the diet ($F_{1,72} = 0.3$, $P = 0.59$);

14 and positively to the proportion of spiders ($F_{1,69} = 4.2$, $P = 0.04$), although the near-significant

15 negative brood size x spider interaction ($F_{1,69} = 3.6$, $P = 0.064$) suggested the effect was reduced

16 in larger broods.

17

18 **Discussion**

19 We show that Wood Warblers' favoured prey in upland oak woods is caterpillars which had a

20 short period of often super-abundance, the timing of which varied predictably with spring

21 temperatures, advancing in warmer years. The birds' breeding season also advanced, but at a

22 slower pace, resulting in a mismatch between peak resource availability and requirements.

23 However, despite many of the assumptions of the phenological mismatch hypothesis being met,

16

1   there is no apparent advantage in synchronising nesting activity with the food peak, with those

2   pairs better matched not producing heavier nestlings or more fledglings. We conclude that birds'

3   ability to switch to other prey sources when caterpillars are not available frees Wood Warblers

4   from the negative consequences of phenological mismatch.

5

6   There are certain conditions under which it would not be expected for the phenological mismatch

7   hypothesis to be supported. Firstly, spring temperatures may not have increased (Visser *et al*.

8   2003; Burger *et al*. 2012), leading to a lack of advancement in prey phenology, and hence no

9   requirement for earlier breeding. This is not the case in our study: April-May temperatures

10   increased by an average of 0.07°C annually from 1980-2011, and the timing of peak caterpillar

11   abundance varied by up to 33 days. Secondly, certain habitats exhibit less seasonality in the

12   abundance of their invertebrate populations, even within a single group such as caterpillars

13   (Burger *et al*. 2012); however, this was not so in the current study, which was carried out in

14   upland oak forests, where caterpillar abundance was strongly seasonal, with a high proportion of

15   annual biomass being recorded in a single week (Smith *et al*. 2011). Thirdly, even when there

16   has been an advance in prey phenology, some bird species have been able to maintain synchrony

17   by advancing egg laying (Crick *et al*. 1997), and/or by increasing the length of the incubation

18   period (Cresswell & McCleery 2003). However, although Wood Warblers commenced nesting

19   earlier in warmer springs, varying by up to 13 days between 1982-84 and 2009-11, this was

20   insufficient to maintain synchrony with the food peak, which advanced at a faster pace (33 days

21   over the same period).

22

17

1   If species are not dependent upon a single prey source, then food may be plentiful throughout the

2   season (Halupka *et al.* 2008), and consequently there is no selection pressure on synchronising

3   breeding with peak abundance of that prey (Dunn *et al.* 2011). Although caterpillars comprise

4   the majority of the diet in our study, across the species' range, a wide variety of prey is taken

5   (Stowe 1987; Pavelka & Korytář 1992; Lippek 1996; Temrin *et al.* 1997; Maziarz &

6   Wesołowski 2010), and our results suggest that, even when caterpillars are plentiful, a greater

7   variety is favoured (Fig 7), perhaps to provide key nutrients (Ramsay & Houston 2003).

8   However, although synchrony with the food peak was not important, in common with other

9   species (Great Tits *Parus major*, Eeva *et al.* 1997; Pied Flycatchers, Burger *et al.* 2012), there

10   was some evidence that the biomass of caterpillars in the environment and their contribution to

11   the diet had a positive effect on the number of chicks fledged. However, nests that were active

12   after the caterpillar peak were no less successful. Although spiders may be present at only a low

13   biomass in upland oak forests (Arnold *et al.* 2010), flies probably constituted an ample food

14   source throughout the season (RSPB, unpublished data), especially after the disappearance of

15   caterpillars (Maziarz & Wesołowski 2010).

16

17   Even in the 1980s, the timing of peak resource requirements for nestling Wood Warblers

18   occurred after the food peak, a similar pattern to that found in primeval conditions in Poland

19   (Maziarz & Wesołowski 2010). However, given that caterpillar peaks can last up to three weeks

20   (Visser *et al.* 2006; Smith *et al.* 2011), caterpillars are likely to have still been an abundant

21   source of food. The mean width of the peak in this study was about two weeks, suggesting that

22   by 2009-11 when the timing of peak resource requirements was 14 days after the food peak,

23   caterpillars may not have been a viable food source for many nesting birds. The discrepancy

18

1   between this study in terms of the width of the food peak (c.2 weeks) and the studies cited above

2   (c.3 weeks) may be in our method of measuring caterpillar biomass. Our water traps are reliant

3   on caterpillars falling to the ground to pupate, including species such as *Erannis defoliaria* and

4   *Operophtera brumata*; however, there are numerous other species that pupate amongst leaves in

5   the canopy which would not have been recorded in our traps but would have contributed to the

6   frass collected in other studies (e.g. *Tortrix viridana*), one of which (Smith *et al*. 2011) included

7   some of the same study sites.

8

9   Such prey-switching, i.e. greater reliance on other food sources with increasing mismatch,

10   suggests that Wood Warblers may benefit from physiological adaptations that enable them to

11   thrive on what, in other species, may be considered a poorer quality diet (Brzęk *et al*. 2009,

12   2010). Being able to shift nestling diet to other prey types also ensures a more regular provision

13   of food than if parents spent longer searching for an ever-decreasing supply of caterpillars (Naef-

14   Daenzer & Keller 1999), with benefits for nestling growth and survival. Parent birds could also

15   compensate for lower food quality by increasing provisioning rates (Naef-Daenzer *et al*. 2000)

16   which, however, could increase predation risk (Weidinger 2002), through increased begging by

17   hungry nestlings or increased activity around the nest (Haskell 1994; Leech & Leonard 1997;

18   Martin *et al*. 2000). Interestingly, nest predation rates were highest in 2011 (Mallord *et al* 2012),

19   the year in which most pairs were mismatched with peak abundance of caterpillars.

20

21   Although insufficient to maintain synchrony with peak caterpillar abundance, and although

22   earlier successful nests were not more productive, Wood Warblers did advance nesting in

23   warmer springs, suggesting that earlier nesting could still be beneficial. Much of the evidence for

19

1   the effects of phenological mismatch has come from studies of hole-nesting species, which tend

2   to suffer relatively low rates of predation (Martin 1993; Wesołowski & Tomiałojć 2005). In

3   contrast, the greatest cause of nest failure in Wood Warblers is predation (Wesołowski &

4   Maziarz 2009; Mallord *et al*. 2012), and nest mortality rates increased significantly as the season

5   progressed (Mallord *et al*. 2012), suggesting that advancement of breeding could still give early

6   nesting birds a selective advantage. The dominant predators in our study are Jays *Garrullus*

7   *glandarius* and Buzzards *Buteo buteo* (Mallord *et al*. 2012), and early nesting may serve to

8   decouple the synchrony between warblers and their predators (Both *et al*. 2009). Further

9   advancement of laying dates may be beneficial, but could be constrained by arrival times (Both

10 & Visser 2001), which is possible given the relatively short period between arrival (of males)

11 and breeding (15-17 days, Fig 4; Goodenough *et al*. 2011). Alternatively, food shortages in the

12 pre-laying period may have prevented females from achieving adequate condition to initiate

13 earlier egg-laying, as suggested by supplementary feeding experiments (Robb *et al*. 2008; Smith

14 & Smith 2013).

15

16 There is evidence of widespread Lepidopteran declines (Thomas *et al*. 2004; Conrad *et al*. 2006),

17 and this was supported on two of the four sites surveyed in both periods. However, given Wood

18 Warblers' more varied diet, it is perhaps not surprising that such a decline has not resulted in

19 reduced productivity. In fact, the only difference between the two time periods was that nestling

20 weights were higher in 2009-11. Also, in line with the general increase in spring temperatures,

21 caterpillar phenology has advanced, on average by 11 days since the 1980s, and although this has

22 been partially matched by advancement in Wood Warbler breeding activity, synchrony is

23 reduced in particularly warm springs. However, the birds' diet flexibility again ensured that

1   productivity was not negatively affected by such temporal mismatch. Although much of the

2   evidence for the negative effects of phenological mismatch has come from studies of

3   insectivorous birds in seasonal woodland habitats, and that it has been implicated in the declines

4   of at least one migrant species (Both *et al*. 2006), our study highlights the importance of

5   extending our knowledge to other species to elucidate under what conditions it is likely to be

6   important, and ultimately whether it has played a role in the widespread declines of migrant

7   species.

8

9   **Acknowledgements**

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1   **Table 1** Comparison of fitness parameters and phenology measures between 1982-4 and 2009-
2   11. Relative hatch date (days) = hatch date – peak caterpillar date; fledged refers to the number
3   of chicks fledged from successful nests only. In the first period, data from 1983-4 only (FED,
4   relative hatch date), 1982-4 (clutch, brood, fledged and peak caterpillar date), 1984 only
5   (weight).
6

Parameter	1982-84			2009-11		
	N	Mean	SE	N	Mean	SE
FED	66	26 May	1.04	168	19 May	0.95
Clutch size	43	5.95	0.09	140	5.97	0.07
Brood size	51	5.45	0.16	142	5.39	0.1
Fledged	40	5.35	0.2	96	5.29	0.13
Chick weight	20	9.0	0.36	114	9.72	0.1
Peak caterpillar date	50	11 June	0.69	170	30 May	0.84
Relative hatch date	28	7.14	0.9	123	13.83	0.83

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1 **Table 2** Comparison of model estimates of peak caterpillar biomass (g/m^2) between four oak
2 woods sampled in 1982-84 and 2009-2011, with results of post-hoc comparison of log-
3 transformed values.
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Site	1982-84	se	2009-11	se	z	P
ap	3.47	0.99	0.11	0.04	8.1	< 0.0001
arg	2.64	0.89	0.10	0.04	7.6	< 0.0001
dinE	2.91	0.69	4.13	1.48	0.7	0.5
dinW	3.51	0.95	4.80	2.86	0.5	0.61

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1 **Table 3** Main invertebrate groups in diet of nestling Wood Warblers derived from analysis of
2 faecal samples, expressed as the proportion (mean ± SD) of individuals from each order based on
3 a) the total number sampled and b) the number sampled per brood; and c) the percentage of
4 broods in which each group occurred. All invertebrates refer to adults of each group unless
5 specified as larvae (l).
6

Group	overall (n = 1304)	per brood (± sd) (n = 81)	% occurrence
Lepidoptera (l)	0.54	0.49 (0.22)	97.5
Diptera	0.20	0.21 (0.16)	97.5
Araneae	0.10	0.11 (0.11)	77.8
Coleoptera	0.06	0.07 (0.08)	58.0
Hymenoptera	0.04	0.04 (0.06)	40.7
Opilones	0.02	0.03 (0.05)	29.6
Symphyta	0.01	0.01 (0.03)	16.0
Hemiptera	0.008	0.01 (0.05)	12.3
Acarina	0.008	0.005 (0.02)	8.6
Neuroptera	0.006	0.006 (0.02)	9.9
Unidentified	0.005	0.006 (0.03)	6.2
Coleoptera (l)	0.003	0.003 (0.02)	3.7
Collembola	0.002	0.002 (0.02)	3.7
Neuroptera (l)	0.002	0.001 (0.007)	2.5
Lepidoptera	0.0008	0.002 (0.02)	1.2
Plecoptera	0.0008	0.001 (0.01)	1.2
Isopoda	0.0008	0.0008 (0.007)	1.2

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1 **Figure 1** Map showing the location of our study sites. Data were collected in both 1982-84 and

2 2009-11 from Dinas (divided into East and West), ARG, AP, Bylc (bird data only) and TRG

3 (bird data only).

4

5 **Figure 2** The trend in mean April-May temperatures, 1980-2011. Filled diamonds denote years

6 in which study was undertaken

7

8 **Figure 3** The trend in the timing of peak caterpillar biomass in relation to mean April-May

9 temperature

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11 **Figure 4** The trend in a) arrival times and b) laying dates in relation to mean April 16th-May 15th

12 temperatures

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14 **Figure 5** Variation in the level of synchrony with the food peak (difference in hatching date and

15 peak caterpillar date) in relation to the date of peak caterpillar abundance. Slope fitted after

16 accounting for the parameter estimates of other significant variables, assuming the median value

17 of each.

18

19 **Figure 6** The trend in the proportion of caterpillars in the diet in relation to relative hatch date.

20 Slope fitted after accounting for the parameter estimates of other significant variables, assuming

21 the median value of each.

22

23 **Figure 7** Variation in the proportion of caterpillars in the diet in relation to the level of

24 caterpillar biomass as measured by water traps, specific to the site, year and week in which

25 faecal samples were collected. Site estimates taken from model explaining variation in caterpillar

26 composition of the diet, accounting for variation according to year, age and date.
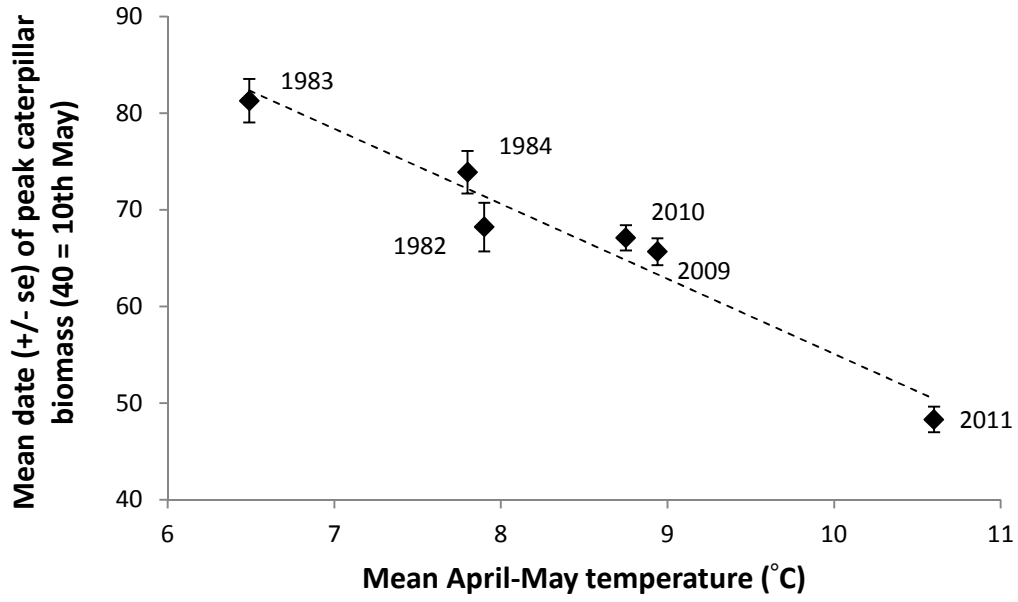
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1   **Figure 2**
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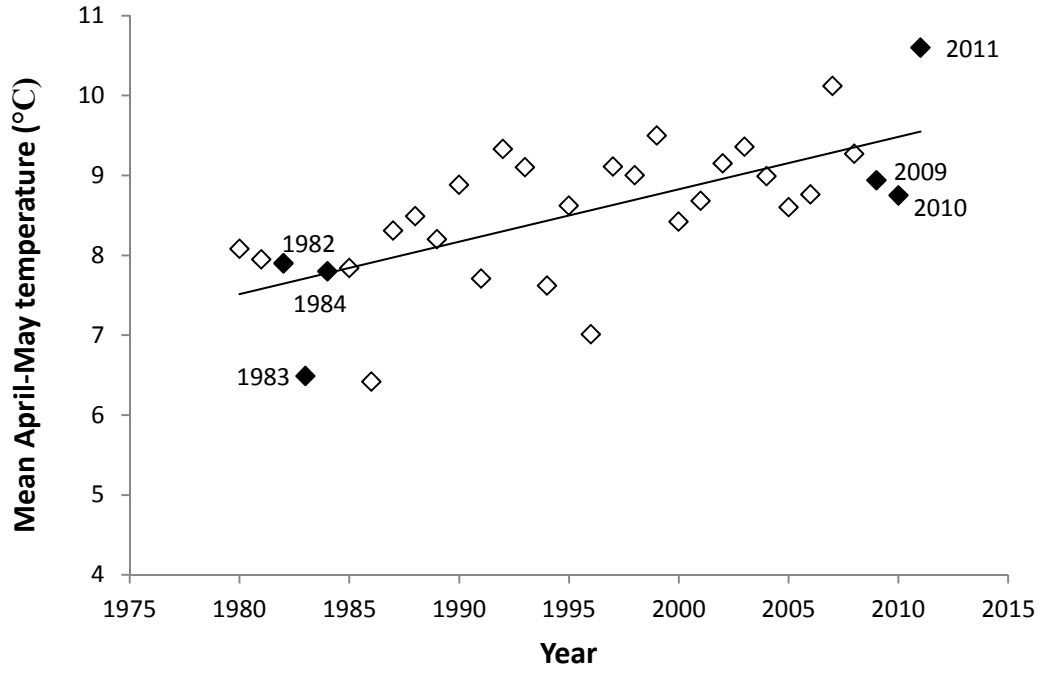
1 **Figure 3**
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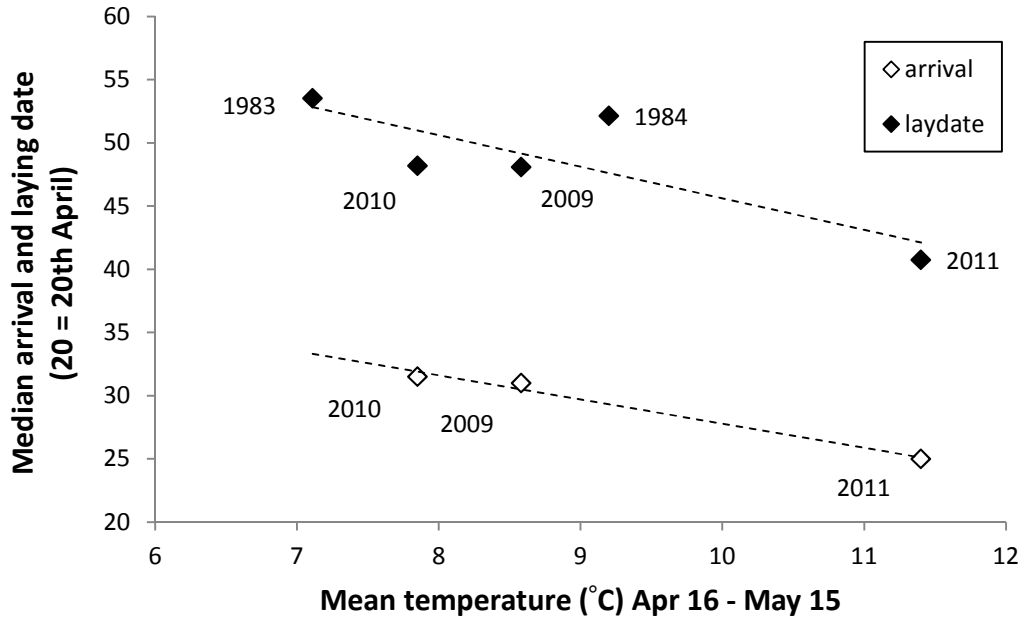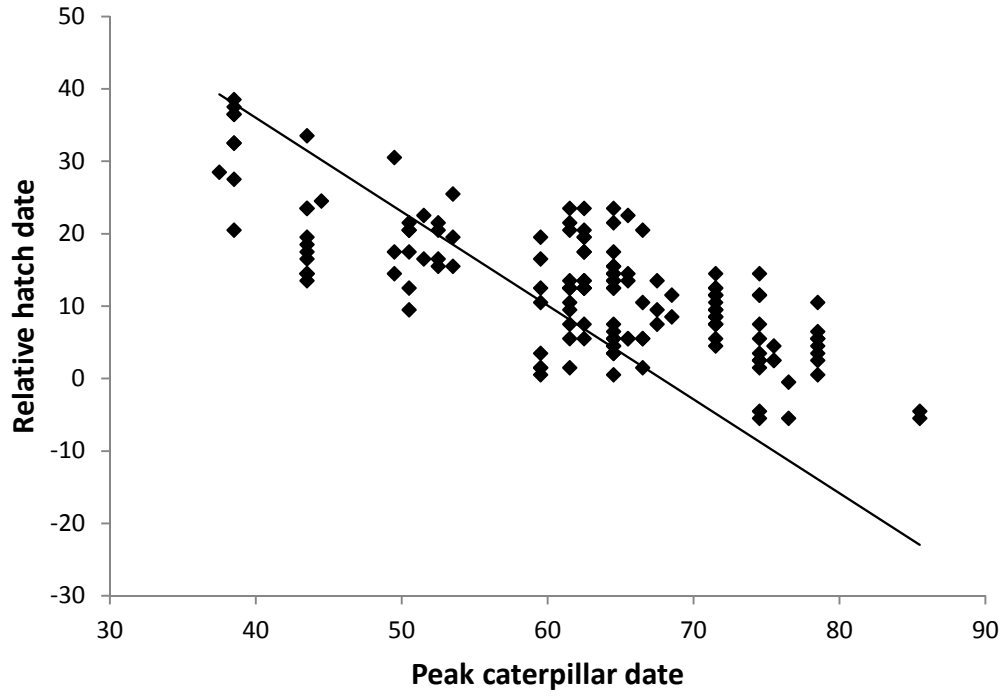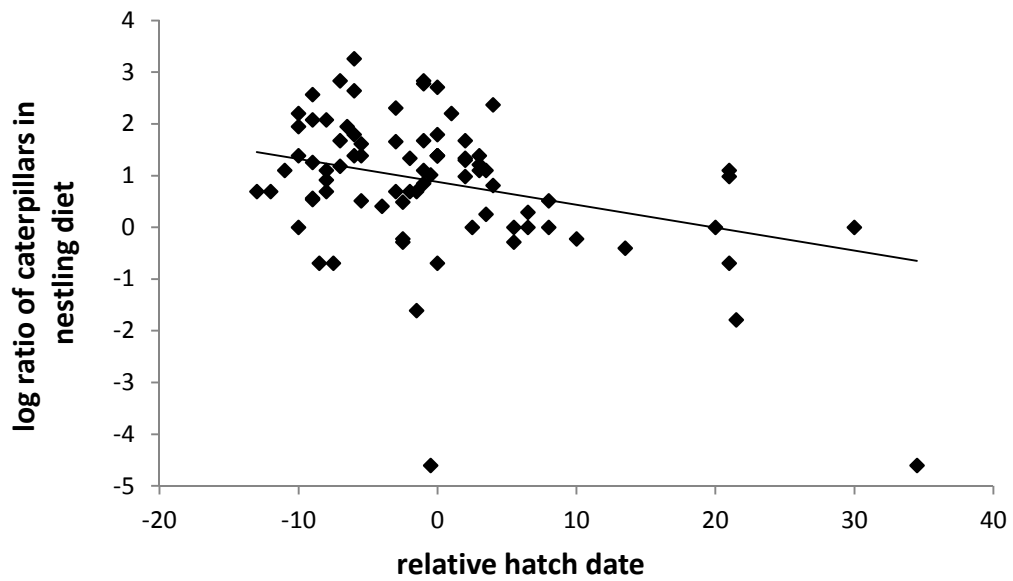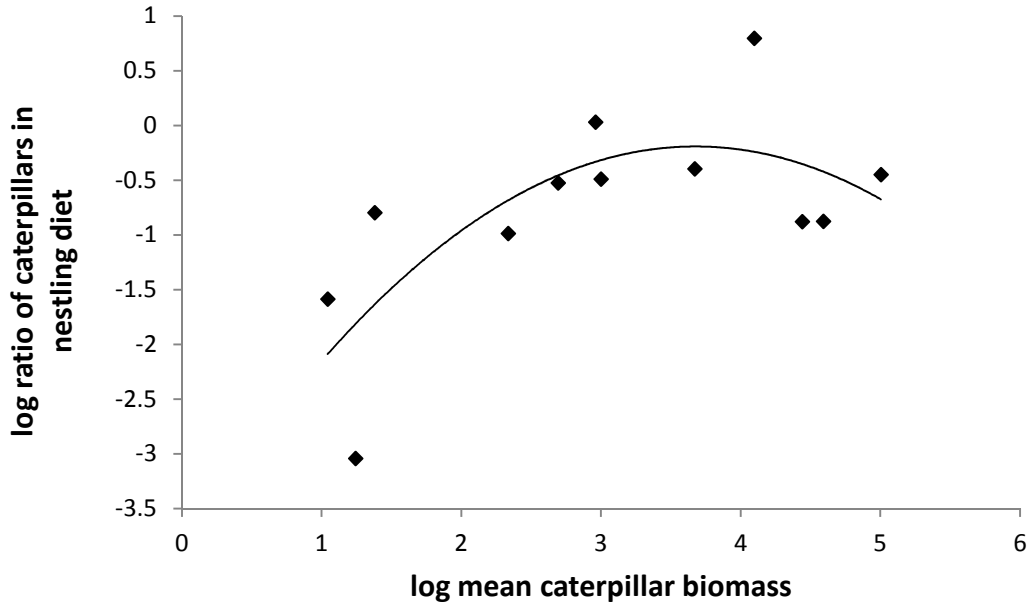

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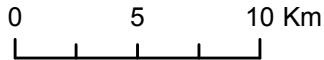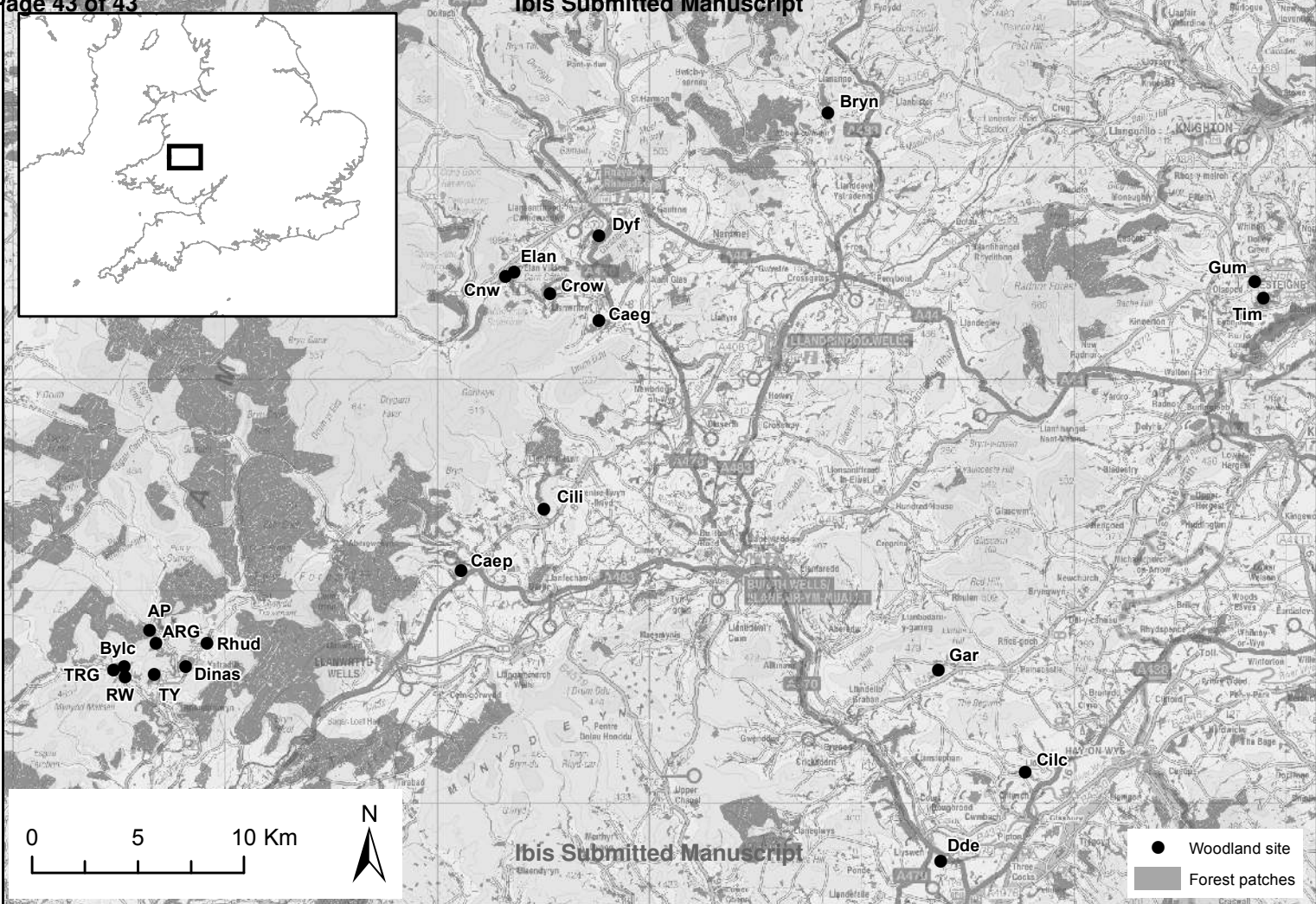17
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1   **Figure 4**
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1   **Figure 5**
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1   **Figure 6**
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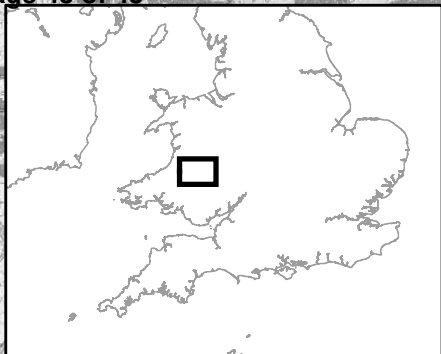11
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1 **Figure 7**
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Woodland site
Forest patches