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# 1 **Tritrophic phenological match-mismatch in space and** 2 **time**

3

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29

30 **Increasing temperatures associated with climate change may generate**  
31 **phenological mismatches that disrupt previously synchronous trophic**  
32 **interactions. Most work on mismatch has focused on temporal trends, whereas**  
33 **spatial variation in the degree of trophic synchrony has largely been neglected,**  
34 **even though the degree to which mismatch varies in space has implications for**  
35 **meso-scale population dynamics and evolution. Here we quantify latitudinal**  
36 **trends in phenological mismatch, using phenological data on an oak-caterpillar-**  
37 **bird system from across Britain. Increasing latitude delays phenology of all**  
38 **species, but more so for oak, resulting in a shorter interval between leaf**  
39 **emergence and peak caterpillar biomass at northern locations. Asynchrony found**  
40 **between peak caterpillar biomass and peak nestling demand of blue tits, great tits**  
41 **and pied flycatchers increases in earlier (warm) springs. There was no evidence**  
42 **of spatial variation in the timing of peak nestling demand relative to peak**  
43 **caterpillar biomass for any species. Phenological mismatch alone is thus unlikely**  
44 **to explain spatial variation in population trends. Given projections of continued**  
45 **spring warming, we predict that temperate forest birds will become increasingly**  
46 **mismatched with peak caterpillar timing. Latitudinal invariance in the direction**  
47 **of mismatch may act as a double-edged sword that presents no opportunities for**  
48 **spatial buffering from the effects of mismatch on population size, but generates**  
49 **spatially consistent directional selection on timing, which could facilitate rapid**  
50 **evolutionary change.**

51

52 Temperature changes are impacting phenology<sup>1</sup>, prompting concern that previously  
53 synchronous trophic interactions may be disrupted and lead to negative impacts on  
54 consumer fitness and demography<sup>2-4</sup>. Trophic asynchrony or mismatch appears to be  
55 most prevalent in the food webs of seasonal habitats, such as deciduous forests and

56 aquatic systems<sup>5</sup>, where resource peaks are ephemeral. Most studies of natural variation  
57 in mismatch and its impacts on the fitness and population trends of terrestrial  
58 consumers are on temporal data. However, it is also possible for mismatch to vary in  
59 space, if species respond differently via plasticity or local adaptation to geographic  
60 variation in cues. The scarcity of studies addressing the spatial dimension of variation in  
61 mismatch<sup>6</sup> means that we have little evidence as to whether the insights into mismatch  
62 estimated at one site can be extrapolated to others.

63

64 The degree to which mismatch varies in space has the potential to impact on both  
65 population trends and evolution of consumer species on a meso-scale (Supplementary  
66 Table 1). Consider the following latitudinal trends in the phenology of a consumer and a  
67 resource, assuming that latitudinal variation in consumer phenology has a plastic basis<sup>7</sup>.  
68 If all consumer populations, regardless of their latitude, experience the same magnitude  
69 and direction of mismatch (Supplementary Table 1b), which impacts negatively on vital  
70 rates, all consumer populations may decline in the short term. If populations of the  
71 consumer possess additive variance for phenology, over longer time periods spatially  
72 consistent directional selection arising from directional mismatch may facilitate  
73 adaptation to reduce mismatch<sup>8</sup>, although the rate of evolutionary change will also  
74 depend on the effect of mismatch on population size and the standing genetic variation.  
75 In a second example (Supplementary Table 1c), if the consumer phenology varies less  
76 over space than the resource phenology<sup>9</sup>, and this generates spatial variation in the  
77 direction of mismatch, then in the short term there may be spatial buffering that limits  
78 population declines. In this case the consequences of mismatch on one population may  
79 be buffered by dispersal from a matched population elsewhere<sup>6</sup>. With gene flow, spatial  
80 variation in the direction of selection may oppose the adaptation of mismatched  
81 populations to their local optima<sup>8</sup>.

82 Here, we use the well-studied tri-trophic deciduous tree–caterpillar–passerine bird food  
83 chain, a highly seasonal system, to identify the extent to which consumer phenology  
84 tracks resource phenology over time and space. The phenology of these three trophic  
85 levels advance with warmer spring temperatures, though birds typically advance by less  
86 than trees or caterpillars<sup>10,11</sup>, causing bird-caterpillar mismatch to be most pronounced  
87 in warm springs and associated with strong directional selection for earlier laying<sup>12</sup>.

88

89 We estimate the spatial (latitudinal) and temporal (among year) trends in relative  
90 phenology of consumer (caterpillar) and primary resource (oak) species, and the  
91 synchrony of secondary consumer (bird) peak nestling demand and peak caterpillar  
92 resource availability. Fig. 1 shows the distribution of sampling across Britain and among  
93 years. We used 10073 observations of pedunculate oak (*Quercus robur*) first leafing for  
94 the period 1998-2016. The timing of peak arboreal caterpillar community biomass was  
95 inferred from frass captured in traps set beneath oak trees at sites across Britain for the  
96 period 2008-2016<sup>13</sup> (trap:years = 696). Bird phenology was calculated using first egg  
97 dates (FED) from across Britain for the period 1960-2016, comprising 36839 blue tit  
98 (*Cyanistes caeruleus*), 24427 great tit (*Parus major*) and 23813 pied flycatcher (*Ficedula*  
99 *hypoleuca*) nests. The phenology of oak<sup>14</sup> and all three bird species<sup>7</sup> have been shown to  
100 respond negatively to mean spring temperatures over time and space, in a manner that  
101 suggests plasticity is responsible for the majority of the spatiotemporal variation and  
102 that temperature may be the proximate or ultimate phenological cue. Here we show that  
103 frass timing exhibits similar trends, correlating negatively with temperature over time  
104 and space, albeit more shallowly and non-significantly over space (supplementary  
105 materials).

106

107 Our focus is on the relationship between the phenology of interacting species<sup>15</sup>. Where  
108 timing changes more in one species than the other, this is indicative of spatial or  
109 temporal variation in the magnitude, and potentially direction, of mismatch. In Britain

110 latitude provides a major temperature cline along which phenology varies at large  
111 scales<sup>16</sup>, therefore, the spatial component of our study addresses latitudinal trends in  
112 relative phenology of species pairs. We also consider the relationship between the  
113 timing of the consumer and resource as the major axis (MA) slopes estimated over time  
114 (years) and space (i.e. among 50km grid cells after de-trending for the latitudinal  
115 gradient in the phenology of each species). For the bird – caterpillar interaction we can  
116 derive predictions in the timing of peak consumer demand and peak resource  
117 availability which enables us to estimate the absolute departure from synchrony  
118 (demand earlier or later than supply).

119

## 120 **Results and discussion**

121

122 Starting at the base of this food chain, for the average latitude (52.63°N) and year (in  
123 terms of phenology) in our dataset, there is a 27.6 day interval between oak first leaf  
124 and the peak caterpillar biomass. With increasing latitude the delay in oak leafing is  
125 significantly steeper than that of the caterpillar peak (Fig. 2a, Supplementary Table 3a).  
126 This results in a reduction of the predicted interval to 22 days at 56°N. After de-trending  
127 for latitudinal effects, the spatial relationship between the phenology of these species is  
128 poorly estimated (Table 1) and caterpillar phenology varies more over time than space  
129 (Supplementary Table 3). Among years, the timing of oaks and caterpillars is strongly  
130 positively correlated (Table 1a) and the MA slope does not depart significantly from 1  
131 (Fig. 2b, Table 1b). This result is consistent with the caterpillar consumer perfectly  
132 tracking the timing of the resource over time. This is consistent with earlier work  
133 showing that oaks and one of their main caterpillar consumers – the winter moth – are  
134 similarly sensitive to temperature<sup>17</sup>. The shortening of the time between first leaf and  
135 peak caterpillar availability as latitude increases may result from the action of a third  
136 variable, such as photoperiod acting on one or both species. Alternatively, it may

137 represent an adaptation of the life cycle of Lepidoptera species to the shorter spring and  
138 summer period in the north<sup>6</sup>.

139

140 In the average year and at the average latitude, FEDs of blue tits (posterior mean ordinal  
141 day 118.30 [95% credible interval = 116.83 –119.85], Supplementary Table 3b) and  
142 great tits (day 118.95, [117.20 –120.61], Supplementary Table 3c) are approximately  
143 one month earlier than peak caterpillar availability (~day 148). However, peak demand  
144 is when nestlings are around 10 days old<sup>18,19</sup>, and once we allow for average clutch sizes  
145 and incubation durations (see methods), we find that peak demand occurs soon after  
146 peak resource availability, with mean peak demand–mean peak resource = 3.39 [-6.63 –  
147 8.86] days in blue tits and 2.01 [-3.99 – 7.71] days in great tits. Pied flycatchers also lay  
148 earlier (day 135.04 [133.55–136.53, Supplementary Table 3d) than the peak caterpillar  
149 biomass, but predicted peak nestling demand occurs 12.87 [6.69 – 19.40] days later  
150 than peak caterpillar availability, suggesting substantial trophic mismatch in the  
151 average UK environment.

152

153 With increasing latitude the phenology of caterpillars is delayed by ~ 1.3 days °N<sup>-1</sup> and  
154 the point estimates for the equivalent latitudinal trend in birds are from 1.67 – 1.93 days  
155 °N<sup>-1</sup> (Supplementary Tables 3b-d). While the slope for birds is marginally steeper than  
156 for caterpillars, such that birds in the north are slightly more mismatched, we have no  
157 evidence for a significant latitudinal trend in mismatch (Fig. 3a-c). Moreover, the effect  
158 size of any latitudinal trend in mismatch is small, as the point estimate of the magnitude  
159 of change in the relative phenology of consumer – resource over the latitudinal range of  
160 our data (50 – 57°N) is < 5 days in each case.

161

162 Across years, the timing of the caterpillar peak date and bird FED is strongly and  
163 significantly positively correlated for all three bird species (Table 1a). The MA slope is  
164 significantly <1 for all three bird species. This means that among years FED varies by

165 less than the timing of the caterpillar resource peak (Table 1b, Fig. 3d-f), which gives  
166 rise to year-to-year variation in the degree of mismatch. For every 10-day advance in  
167 the caterpillar peak, the corresponding bird advance is estimated to be 5.0, 5.3 and 3.4  
168 days in blue tit, great tit and pied flycatcher respectively. In late springs (i.e. under  
169 colder conditions) peak demand from blue tit and great tit nestlings is expected to  
170 coincide with the peak resource availability, and pied flycatcher peak demand occurs  
171 soon after the resource peak (Fig. 3d-f). When caterpillar phenology is earlier (i.e.  
172 warmer springs), the peak demand of nestlings is predicted to be substantially later  
173 than peak resource availability, rendering the nestlings of all three species mismatched,  
174 and pied flycatchers most mismatched. For example, in the earliest year for which we  
175 have caterpillar data (2011), at the average latitude the peak demand of the nestling  
176 birds is predicted to occur 17.78, 11.74 and 27.03 days after the peak availability of  
177 caterpillars. The patterns of temporal variation in mismatch we identify for these  
178 species are very similar to those reported for great tits in the UK<sup>20</sup> and all three species  
179 in the Netherlands<sup>15</sup> and are likely to result from the caterpillars being more  
180 phenologically plastic in response to spring temperatures (supplementary materials).  
181 Warmer conditions also produce shorter duration food peaks<sup>13</sup>, which may strengthen  
182 the selection against mismatched individuals. It is also possible that bird populations  
183 may advance timings in response to temperature cues experienced after first lay date by  
184 varying clutch size, laying interruptions or the initiation and duration of incubation<sup>21-24</sup>.  
185  
186 One of our key findings is that in the average year there is little latitudinal variation in  
187 the magnitude of caterpillar-bird mismatch. Therefore, meso-scale geographic variation  
188 in mismatch in the average year is unlikely to buffer metapopulations from the negative  
189 consequences of mismatch, or explain spatial variation in population trends. Thus, more  
190 negative declines in population trends of insectivorous birds in southern Britain, driven  
191 by low productivity<sup>25</sup>, do not appear to be caused by greater mismatch in the south than  
192 the north. Directional adaptive evolution is expected to be more rapid for connected



193 populations when selection pressures are spatially consistent compared to being  
194 spatially variable<sup>8</sup>. This result also has the practical implication that insights into the  
195 degree of mismatch in one location can be generalized to trends at different latitudes. In  
196 the average spring, the timing of blue tit and great tit nestling demand is quite  
197 synchronous with the peak resource, which is consistent with birds being able to track  
198 spatial variation in optimal timing. Spatial variation in mismatch will still occur if there  
199 is substantial year by site variation in spring temperatures, as would arise if the rate of  
200 warming varies spatially.

201

202 Of the three bird species, migratory pied flycatchers showed the greatest mismatch with  
203 caterpillar availability, the predicted peak nestling period being consistently later than  
204 peak caterpillar timing. If pied flycatcher migration times are mediated by African  
205 conditions<sup>26-28</sup> or constraints en-route<sup>29</sup>, this may limit their ability to advance their  
206 arrival times, even if once they have arrived they are able to respond to spring  
207 temperatures on breeding grounds<sup>30</sup>. However, pied flycatchers provision nestlings  
208 with fewer caterpillars and more winged invertebrates compared to blue tit and great  
209 tit<sup>31</sup>, so may be less dependent on seasonal caterpillar peaks.

210

211 Our study focuses on mismatch judged from population means within a year and site (or  
212 in the case of oak leafing the first date in a population – see methods). There is of course  
213 potential for some individuals within a population to be matched even when population  
214 means are mismatched, and this could serve to reduce effects of mismatch on local  
215 populations<sup>32</sup>. The residual variance for caterpillars and birds, which corresponds to  
216 variance within a year and site, is >30 (Supplementary Table 3), which corresponds to  
217 95% of individuals within a 5km grid cell and year being in the range  $\pm 10.74$  days of the  
218 population mean. All three of our focal bird species are able to inhabit woodland types  
219 other than oak and such habitats may differ in the timing or ephemerality of the

220 caterpillar resource<sup>33</sup>, which may have further impacts on spatial variation in  
221 demography and selection.

222

223 While phenological mismatch is frequently raised as a potential impact of climate  
224 change, there is an urgent need to compile evidence on the consequences of mismatch  
225 for population trends across realistic spatial or ecological (e.g., habitat generalist)  
226 settings. A Dutch study on pied flycatchers found that population declines were greater  
227 in areas where the caterpillar peak (assumed to be a proxy for mismatch) was earlier<sup>34</sup>,  
228 but the spatial relationship between mismatch and population trends remains largely  
229 unstudied<sup>35</sup>. Our study presents the first assessment of whether latitudinal variation in  
230 mismatch exists, as is sometimes proposed as a mechanism whereby the adverse  
231 impacts of climate change might be buffered, for example, more northern populations  
232 being less adversely affected by spring warming compared to southern populations<sup>36</sup>.  
233 The lack of evidence we find for latitudinal variation in mismatch between birds and  
234 their caterpillar resource suggests mismatch is unlikely to be a driver of spatially  
235 varying population trends found in avian secondary consumers<sup>37</sup>.

236

## 237 **Methods**

238

239 **Phenology data.** We obtained pedunculate oak first leafing dates from the UK  
240 Phenology Network (<https://naturescalendar.woodlandtrust.org.uk/>). As a quality  
241 control step we excluded outliers (ordinal day  $60 \leq$  leafing date  $\geq 155$ ) and retained only  
242 observations from individuals who submitted records in multiple years. Our data for oak  
243 leafing differ from the other trophic levels in that they are of first dates within local  
244 populations. First dates will be earlier than mean dates, but would only be biased if  
245 there is a trend (latitudinal or correlating with year earliness) in sampling effort,  
246 population abundance or variance. We suggest that the first two are unlikely to pose a  
247 problem<sup>14,38</sup>, but we do not have the data to rule out the third source of bias.

248

249 Arboreal caterpillar biomass was monitored by collecting frass fall from traps set  
250 beneath oak trees at 47 sites across Britain<sup>13</sup>. Frass was collected, sorted and the dry  
251 weight obtained approximately every 5 days (mean = 4.63) during spring up until day  
252 180 at the latest, from which we calculated a frass fall rate in  $\text{g square m}^{-1} \text{ day}^{-1}$ . For  
253 traps where frass had been collected on at least five occasions during a spring we  
254 identified the sampling period over which the rate of frass fall was highest and then  
255 identified the start and end of this interval. Where the highest rate was found over two  
256 or more separate periods then we allowed the peak frass interval to span the combined  
257 period. At one site, Wytham Woods, the timing of peak frass was estimated  
258 statistically<sup>32</sup>. For these estimates we assumed that the interval was the peak date  $\pm 3$   
259 days.

260

261 First egg dates (FED) for blue tit, great tit and pied flycatcher were obtained from nests  
262 monitored across Britain for the BTO Nest Record Scheme<sup>7,39</sup>. Few nests were visited  
263 daily, and so a minimum FED was calculated by combining information collected over  
264 repeated visits before and after laying, including the date of previous visits with no eggs  
265 present, clutch size, laying rate and incubation period. A maximum FED was calculated  
266 as the date on which eggs were first observed minus the product of the number of eggs  
267 and the maximum laying rate, i.e. one egg per day. We excluded observations where the  
268 interval between minimum and maximum FED exceeded 10 days.

269

270 We imposed a 'population' structure on all observations by dividing Britain into 50km x  
271 50km grid cells. To spatially match observations at a finer scale within these  
272 'populations' and to address some of the spatial pseudoreplication of observations we  
273 generated a smaller grid structure corresponding to 5km x 5km.

274

275 **Analysis.** All analyses were conducted in R<sup>40</sup>. We assessed the degree to which  
276 consumer species were able to track the phenology of resource/primary producer  
277 species across space and time using a generalized linear mixed model<sup>41</sup> with the  
278 phenology of the two interacting species included as a bivariate Gaussian response<sup>6,42</sup>.  
279 With the exception of oak, the response was interval censored, meaning that an event  
280 was considered to be equally likely to occur at any time within the given interval<sup>43</sup>. The  
281 model included the intercept and latitude as the only fixed effects for each of the  
282 response variables, and 50km grid cell, 5km grid cell, year and residual as random  
283 effects. For each random term we estimated the (co)variance components, with the  
284 exception of the residual term for which we estimated variances but not covariance. For  
285 caterpillars we also included trap as a random effect. Our ability to estimate covariances  
286 between trophic levels depends principally on the replication of grid cells or years for  
287 which we have data for both trophic levels. However, locations where we have data for  
288 one trophic level inform our estimates of latitudinal trends, among grid cell variance and  
289 year means for that level. Similarly, years for which we have data for only a single  
290 trophic level inform our estimates of among year variance and grid cell means or that  
291 level. Precise estimates of these means and variances inform our estimates of  
292 relationships between the phenology of trophic level pairs.  
293  
294 We used parameter expanded priors for (co)variances across years and grid cells and  
295 inverse-Wishart priors for the residual term. Models were run for 440,000 iterations,  
296 with 40,000 iterations removed as burnin and sampling every 100. We assessed model  
297 convergence via visual inspection of the posterior distribution trace plots and by  
298 running a second chain and ensuring that the multivariate potential scale reduction  
299 factor for fixed effects on the two chains was  $< 1.1$ <sup>44</sup>. The effective sample sizes for all  
300 focal parameters exceeded 1000.  
301

302 The model intercepts estimate the mean phenology of each species at the average  
303 latitude in the average year. We used the (co)variance components estimated for grid  
304 cells and years to obtain correlation estimates between the two species over space  
305 (50km grid cells only) and years, respectively. We estimated the major axis rather than  
306 type I regression slope<sup>45</sup>, because we were interested in the degree of phenological  
307 tracking, rather than the degree to which the phenology of one species predicts the  
308 phenology of another.

309

310 We considered the following bivariate models: (i) peak caterpillar date versus oak first  
311 leafing date, (ii) each of the three bird species FED versus peak caterpillar date, and (iii)  
312 each bird FED with oak first leafing date. For the bird versus caterpillar we compared  
313 the predicted peak resource availability to the predicted peak consumer demand, which  
314 we calculated as the predicted FED across latitudes or years plus mean clutch size which  
315 varies little at the scale of our study<sup>46</sup>, and incubation duration (both from BTO nest  
316 record scheme <http://app.bto.org/birdfacts/results/>) and the 10 day duration between  
317 hatching and peak nestling food demand<sup>47,48</sup>. While the tree versus bird comparisons are  
318 not trophic interactions, we consider them here because we anticipate that oak leafing  
319 may be a proxy for peak caterpillar date, with the spatiotemporal replication of first  
320 leafing observations greatly exceeding those of peak caterpillar.

321

#### 322 **Data availability**

323

324 Supplementary materials are available in the online version of the paper. The data that  
325 support the findings of this study are available at the following datashare repository:

326 <http://dx.doi.org/10.7488/ds/2215>. Correspondence and requests for materials and

327 data should be addressed to M.D.B.

328

#### 329 **Code availability**

330

331 Example R code is available at the following repository:

332 [https://github.com/allyphillimore/birds\\_frass\\_oak](https://github.com/allyphillimore/birds_frass_oak).

333

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335

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343

### 344 **Author contributions**

345

346 M.D.B., A.B.P. and K.W.S. conceived the study. M.D.B led and coordinated the study, A.B.P.  
347 analyzed the data and M.D.B and A.B.P wrote the manuscript with K.L.E. making  
348 significant contributions. M.D.B., K.W.S., C.J.B., K.B., J.C., K.L.E., C.dF., R.G.N., B.C.S., J.A.S.,  
349 J.S.R.C.W. and S.G.W collected frass data, K.L. provided oak leafing data, and D.L and  
350 J.W.P-H. provided bird data. All authors commented on and edited the manuscript.

351

### 352 **Competing financial interests**

353

354 The authors declare no competing financial interests.

355

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357

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515

## 516 **Figure legends**

517

518 **Fig. 1 | Number of years of data for each 50km grid cell used for each trophic level**  
519 **and bird species. a** for oak, **b** for frass, with trapping locations indicated by dots, **c** for  
520 blue tit, **d** for great tit and **e** for pied flycatcher.

521

522 **Fig. 2 | The relationship between latitude and the phenology of oak leafing and**  
523 **peak caterpillar abundance (a) and the among year relationship between the**  
524 **timing of the two trophic levels (b).** In both panels the solid lines correspond to the  
525 mean prediction and the shaded areas correspond to the posterior distribution of  
526 predictions under type I regression (a) and major axis regression (b). In **a**, dark green  
527 shaded area shows oak leafing and light green shaded area shows the caterpillar peak.  
528 In **b**, data points represent the posterior means for the best linear unbiased predictions  
529 for years that have observations for both trophic levels. Dashed line corresponds to  
530 unity; this is plotted to illustrate the relative slopes. An offset intercept is expected  
531 owing to the growth and development of caterpillars.

532

533 **Fig. 3 | The relationship between latitude and mismatch (a – c) and the timing of**  
534 **peak frass versus first egg date among years (d – f),** with **a** and **d** for blue tits, **b** and **e**  
535 for great tits and **c** and **f** pied flycatchers. In panels a – c mismatch is defined as the  
536 timing of peak avian demand minus the timing of peak frass availability, with peak  
537 nestling demand calculated as being when nestlings are predicted to be 14 days old (see  
538 methods). In panels d – f datapoints represent the posterior means for the best linear  
539 unbiased predictions for years that have observations for both birds and caterpillars.

540 Dashed line corresponds to unity. In d – f the black line is the among year mean major  
 541 axis slope and the red line is the predicted relationship between peak resource  
 542 availability and peak demand. Transparent gray lines represent the posterior  
 543 distribution of predictions.

544

545 **Table 1 | Correlation (a) and major axis slopes (b) of the phenology of higher**  
 546 **trophic level on lower trophic level in time (bold, upper right) and de-trended**  
 547 **space ( lower left). 95% credible intervals in parentheses.**

548

549 (a)

	Oak leafing	Peak caterpillar	Blue tit FED	Great tit FED	Pied flycatcher FED
Oak leafing	-	<b>0.69 (0.295 - 0.963)</b>	<b>0.754 (0.537 - 0.918)</b>	<b>0.808 (0.62 - 0.95)</b>	<b>0.719 (0.409 - 0.934)</b>
Peak caterpillar	0.415 (-0.153 - 0.945)	-	<b>0.724 (0.388 - 0.949)</b>	<b>0.691 (0.297 - 0.951)</b>	<b>0.834 (0.54 - 0.984)</b>
Blue tit FED	0.665 (0.463 - 0.86)	0.485 (-0.028 - 0.963)	-	-	-
Great tit FED	0.713 (0.49 - 0.907)	0.534 (-0.012 - 0.966)	-	-	-
Pied flycatcher FED	0.547 (0.147 - 0.913)	0.306 (-0.498 - 0.959)	-	-	-

550

551 (b)

	Oak leafing	Peak caterpillar	Blue tit FED	Great tit FED	Pied flycatcher FED
Oak leafing	-	<b>1.788 (0.497 - 3.896)</b>	<b>0.667 (0.409 - 0.935)</b>	<b>0.744 (0.485 - 1.023)</b>	<b>0.413 (0.228 - 0.621)</b>
Peak caterpillar	3.008 (-13.635 - 20.407)	-	<b>0.498 (0.189 - 0.775)</b>	<b>0.527 (0.154 - 0.88)</b>	<b>0.343 (0.2 - 0.521)</b>
Blue tit FED	1.126 (0.675 - 1.626)	1.061 (-0.55 - 3.452)	-	-	-
Great tit FED	1.128 (0.7 - 1.639)	0.778 (-0.391 - 2.905)	-	-	-
Pied flycatcher FED	1.113 (0.174 - 2.814)	2.471 (-3.121 - 5.03)	-	-	-

552