Tritrophic phenological match-mismatch in space and time

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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[1], prompting concern that previously

53   synchronous trophic interactions may be disrupted and lead to negative impacts on

54   consumer fitness and demography[2-4]. Trophic asynchrony or mismatch appears to be

55   most prevalent in the food webs of seasonal habitats, such as deciduous forests and

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56 aquatic systems[5], 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[6] 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[7].

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[8], 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[9], 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[6]. With gene flow, spatial

80 variation in the direction of selection may oppose the adaption of mismatched

81 populations to their local optima[8].

3

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[10,11], causing bird-caterpillar mismatch to be most pronounced

87   in warm springs and associated with strong directional selection for earlier laying[12].

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[13] (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[14] and all three bird species[7] 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[15]. 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

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110   latitude provides a major temperature cline along which phenology varies at large

111   scales[16], 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[17]. 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

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137   represent an adaptation of the life cycle of Lepidoptera species to the shorter spring and

138   summer period in the north[6].

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[18,19], 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^{-1} and

154   the point estimates for the equivalent latitudinal trend in birds are from 1.67 – 1.93 days

155   °N^{-1} (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

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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[20] and all three species

179   in the Netherlands[15] 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[13], 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[21-24].

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[25], 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

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193   populations when selection pressures are spatially consistent compared to being

194   spatially variable[8]. 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[26-28] or constraints en-route[29], 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 [30]. However, pied flycatchers provision nestlings

208   with fewer caterpillars and more winged invertebrates compared to blue tit and great

209   tit[31], 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[32]. 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 ± 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

8

220   caterpillar resource[33], 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[34],

228   but the spatial relationship between mismatch and population trends remains largely

229   unstudied[35]. 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[36].

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[37].

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 ≤ leafing date ≥ 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[14,38], but we do not have the data to rule out the third source of bias.

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249 Arboreal caterpillar biomass was monitored by collecting frass fall from traps set

250 beneath oak trees at 47 sites across Britain[13]. 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 g square m^{-1} 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[32]. For these estimates we assumed that the interval was the peak date ± 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[7,39]. 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 psuedoreplication of observations we

273 generated a smaller grid structure corresponding to 5km x 5km.

274

275   **Analysis.** All analyses were conducted in R[40]. 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[41] with the

278   phenology of the two interacting species included as a bivariate Gaussian response[6,42].

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[43]. 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 [44]. The effective sample sizes for all

300   focal parameters exceeded 1000.

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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[45], 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[46], 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[47,48]. 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**

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331   Example R code is available at the following repository:

332   https://github.com/allyphillimore/birds_frass_oak.

333

334   **Acknowledgments**

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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**

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354   The authors declare no competing financial interests.

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356   **References**

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358   1   Thackeray, S. J. *et al.* Phenological sensitivity to climate across taxa and
359   trophic levels. *Nature* **535**, 241-245, doi:10.1038/nature18608 (2016).
360   2   Cushing, D. Plankton production and year-class strength in fish
361   populations: an update of the match/mismatch hypothesis. *Advances in*
362   *Marine Biology* **26**, 249-293 (1990).
363   3   Durant, J. M., Hjermann, D. Ø., Ottersen, G. & Stenseth, N. C. Climate and
364   the match or mismatch between predator requirements and resource
365   availability. *Climate Research* **33**, 271-283 (2007).
366   4   Edwards, M. & Richardson, A. J. Impact of climate change on marine
367   pelagic phenology and trophic mismatch. *Nature* **430**, 881-884 (2004).
368   5   Donnelly, A., Caffarra, A. & O'Neill, B. F. A review of climate-driven
369   mismatches between interdependent phenophases in terrestrial and
370   aquatic ecosystems. *International Journal of Biometeorology* **55**, 805-817
371   (2011).
372   6   Phillimore, A. B., Stålhandske, S., Smithers, R. J. & Bernard, R. Dissecting
373   the contributions of plasticity and local adaptation to the phenology of a
374   butterfly and its host plants. *American Naturalist* **180**, 655 (2012).
375   7   Phillimore, A. B., Leech, D. I., Pearce-Higgins, J. W. & Hadfield, J. D.
376   Passerines may be sufficiently plastic to track temperature-mediated
377   shifts in optimum lay date. *Global Change Biology* **22**, 3259-3272,
378   doi:10.1111/gcb.13302 (2016).
379   8   Bourne, E. C. *et al.* Between migration load and evolutionary rescue:
380   dispersal, adaptation and the response of spatially structured populations
381   to environmental change. *Proceedings of the Royal Society of London B:*
382   *Biological Sciences* **281**, 20132795 (2014).
383   9   Thackeray, S. J. *et al.* Trophic level asynchrony in rates of phenological
384   change for marine, freshwater and terrestrial environments. *Global*
385   *Change Biology* **16**, 3304-3313 (2010).
386   10   Both, C., Asch, M., Bijlsma, R. G., van den Burg, A. B. & Visser, M. E. Climate
387   change and unequal phenological changes across four trophic levels:
388   constraints or adaptations? *Journal of Animal Ecology* **78**, 73-83,
389   doi:10.1111/j.1365-2656.2008.01458.x (2009).
390   11   Vatka, E., Orell, M. & Rytkönen, S. Warming climate advances breeding
391   and improves synchrony of food demand and food availability in a boreal
392   passerine. *Global Change Biology* **17**, 3002-3009, doi:10.1111/j.1365-
393   2486.2011.02430.x (2011).
394   12   Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. Warmer
395   springs lead to mistimed reproduction in great tits (*Parus major*).
396   *Proceedings of the Royal Society B: Biological Sciences* **265**, 1867-1870
397   (1998).
398   13   Smith, K. W. *et al.* Large-scale variation in the temporal patterns of the
399   frass fall of defoliating caterpillars in oak woodlands in Britain:
400   implications for nesting woodland birds. *Bird Study* **58**, 506-511,
401   doi:10.1080/00063657.2011.616186 (2011).
402   14   Tansey, C. J., Hadfield, J. D. & Phillimore, A. B. Estimating the ability of
403   plants to plastically track temperature-mediated shifts in the spring
404   phenological optimum. *Global Change Biology* **23**, 3321–3334 (2017).
405   15   Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B. & Visser, M. E.
406   Climate change and unequal phenological changes across four trophic
407   levels: constraints or adaptations? *Journal of Animal Ecology* **78**, 73-83,
408   doi:10.1111/j.1365-2656.2008.01458.x (2009).

14

409   16   Phillimore, A. B., Leech, D. I., Pearce-Higgins, J. W. & Hadfield, J. D.
410   Plasticity may be sufficient to track temperature-mediated shifts in
411   passerine optimum lay date. *Global Change Biology* **22**, 3259-3272
412   (2016).
413   17   Buse, A., Dury, S., Woodburn, R., Perrins, C. & Good, J. Effects of elevated
414   temperature on multi-species interactions: the case of Pedunculate Oak,
415   Winter Moth and Tits. *Functional Ecology* **13**, 74-82 (1999).
416   18   Lundberg, A. & Alatalo, R. V. *The Pied Flycatcher*. (T & A D Poyser, 1992).
417   19   Perrins, C. M. Tits and their caterpillar food supply. *Ibis* **133**, 49-54,
418   doi:10.1111/j.1474-919X.1991.tb07668.x (1991).
419   20   Charmantier, A. *et al.* Adaptive phenotypic plasticity in response to
420   climate change in a wild bird population. *Science* **320**, 800-803 (2008).
421   21   Cresswell, W. & McCleery, R. How great tits maintain synchronization of
422   their hatch date with food supply in response to long-term variability in
423   temperature. *Journal of Animal Ecology* **72**, 356-366, doi:10.1046/j.1365-
424   2656.2003.00701.x (2003).
425   22   Eeva, T. & Lehikoinen, E. Polluted environment and cold weather induce
426   laying gaps in great tit and pied flycatcher. *Oecologia* **162**, 533-539
427   (2010).
428   23   Sanz, J. J. Effect of food availability on incubation period in the Pied
429   flycatcher (*Ficedula hypoleuca*). *Auk* **113**, 249-253 (1996).
430   24   Tomás, G. Hatching date vs laying date: what should we look at to study
431   avian optimal timing of reproduction? *Journal of Avian Biology* **46**, 107-
432   112, doi:10.1111/jav.00499 (2015).
433   25   Morrison, C. A., Robinson, R. A., Butler, S. J., Clark, J. A. & Gill, J. A.
434   Demographic drivers of decline and recovery in an Afro-Palaearctic
435   migratory bird population. *Proceedings of the Royal Society B: Biological
436   Sciences* **283**, doi:10.1098/rspb.2016.1387 (2016).
437   26   Both, C., G Bijlsma, R. & E Visser, M. Climatic effects on timing of spring
438   migration and breeding in a long-distance migrant, the pied flycatcher
439   *Ficedula hypoleuca. Journal of Avian Biology* **36**, 368-373 (2005).
440   27   Ouwehand, J. *et al.* Light-level geolocators reveal migratory connectivity
441   in European populations of pied flycatchers Ficedula hypoleuca. *Journal of
442   Avian Biology* **47**, 69-83, doi:10.1111/jav.00721 (2016).
443   28   Ouwehand, J. & Both, C. African departure rather than migration speed
444   determines variation in spring arrival in Pied flycatchers. *Journal of
445   Animal Ecology* **86**, 88-97, doi:10.1111/1365-2656.12599 (2017).
446   29   Both, C. & te Marvelde, L. Climate change and timing of avian breeding and
447   migration throughout Europe. *Climate Research* **35**, 93-105,
448   doi:10.3354/cr00716 (2007).
449   30   Ockendon, N., Leech, D. & Pearce-Higgins, J. W. Climatic effects on
450   breeding grounds are more important drivers of breeding phenology in
451   migrant birds than carry-over effects from wintering grounds. *Biology
452   Letters* **9**, doi:10.1098/rsbl.2013.0669 (2013).
453   31   Cholewa, M. & Wesolowski, T. Nestling food of European hole-nesting
454   passerines: do we know enough to test the adaptive hypotheses on
455   breeding seasons? *Acta Ornithologica* **46**, 105-116,
456   doi:10.3161/000164511x625874 (2011).
457   32   Hinks, A. E. *et al.* Scale-dependent phenological synchrony between
458   songbirds and their caterpillar food source. *The American Naturalist* **186**,
459   84-97, doi:10.1086/681572 (2015).

460   33   Burger, C. *et al.* Climate change, breeding date and nestling diet: how
461   temperature differentially affects seasonal changes in pied flycatcher diet
462   depending on habitat variation. *Journal of Animal Ecology* **81**, 926-936,
463   doi:10.1111/j.1365-2656.2012.01968.x (2012).
464   34   Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. Climate change and
465   population declines in a long-distance migratory bird. *Nature* **44**, 81-83
466   (2006).
467   35   McLean, N., Lawson, C., Leech, D. I. & van de Pol, M. Predicting when
468   climate-driven phenotypic changes affects population dynamics. *Ecology*
469   *Letters* **19**, 595-608 (2016).
470   36   Morrison, C. A., Robinson, R. A., Clark, J. A. & Gill, J. A. Spatial and temporal
471   variation in population trends in a long-distance migratory bird. *Diversity*
472   *and Distributions* **16**, 620-627, doi:10.1111/j.1472-4642.2010.00663.x
473   (2010).
474   37   Morrison, C. A., Robinson, R. A., Clark, J. A., Risely, K. & Gill, J. A. Recent
475   population declines in Afro-Palaearctic migratory birds: the influence of
476   breeding and non-breeding seasons. *Diversity and Distributions* **19**, 1051-
477   1058, doi:10.1111/ddi.12084 (2013).
478   38   Phillimore, A. B., Stålhandske, S., Smithers, R. J. & Bernard, R. Dissecting
479   the contributions of plasticity and local adaptation to the phenology of a
480   butterfly and its host plants. *American Naturalist* **180**, 655-670 (2012).
481   39   Crick, H. Q., Baillie, S. R. & Leech, D. I. The UK Nest Record Scheme: its
482   value for science and conservation. *Bird Study* **50**, 254-270 (2003).
483   40   R: A language and environment for statistical computing (R Foundation
484   for Statistical Computing. URL http://www.R-project.org, Vienna, Austria,
485   2015).
486   41   Hadfield, J. D. MCMC methods for multi-response generalized linear mixed
487   models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1-
488   22 (2010).
489   42   Phillimore, A. B., Hadfield, J. D., Jones, O. R. & Smithers, R. J. Differences in
490   spawning date between populations of common frog reveal local
491   adaptation. *Proceedings of the National Academy of Sciences* **107**, 8292-
492   8297 (2010).
493   43   Hadfield, J. D., Heap, E. A., Bayer, F., Mittell, E. A. & Crouch, N. M. A.
494   Intraclutch differences in egg characteristics mitigate the consequences of
495   age-related hierarchies in a wild passerine. *Evolution* **67**, 2688-2700,
496   doi:10.1111/evo.12143 (2013).
497   44   Brooks, S. P. & Gelman, A. General methods for monitoring convergence of
498   iterative simulations. *Journal of computational and graphical statistics* **7**,
499   434-455 (1998).
500   45   Warton, D. I., Wright, I. J., Falster, D. S. & Westoby, M. Bivariate line-fitting
501   methods for allometry. *Biological Reviews* **81**, 259-291 (2006).
502   46   Evans, K. L., Leech, D. I., Crick, H. Q. P., Greenwood, J. J. D. & Gaston, K. J.
503   Latitudinal and seasonal patterns in clutch size of some single-brooded
504   British birds. *Bird Study* **56**, 75-85, doi:10.1080/00063650802648291
505   (2009).
506   47   Naef-Daenzer, B. & Keller, L. F. The foraging performance of great and
507   blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar
508   development, and its consequences for nestling growth and fledging
509   weight. *Journal of Animal Ecology* **68**, 708-718, doi:10.1046/j.1365-
510   2656.1999.00318.x (1999).

16

511   48   Royama, T. Factors governing feeding rate, food requirement and brood
512   size of nestling Great tits *Parus major. Ibis* **108**, 313-347 (1966).

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Figure legends

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

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

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

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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	-	**0.69 (0.295 - 0.963)**	**0.754 (0.537 - 0.918)**	**0.808 (0.62 - 0.95)**	**0.719 (0.409 - 0.934)**
Peak caterpillar	0.415 (-0.153 - 0.945)	-	**0.724 (0.388 - 0.949)**	**0.691 (0.297 - 0.951)**	**0.834 (0.54 - 0.984)**
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	-	**1.788 (0.497 - 3.896)**	**0.667 (0.409 - 0.935)**	**0.744 (0.485 - 1.023)**	**0.413 (0.228 - 0.621)**
Peak caterpillar	3.008 (-13.635 - 20.407)	-	**0.498 (0.189 - 0.775)**	**0.527 (0.154 - 0.88)**	**0.343 (0.2 - 0.521)**
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)	-	-	-

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