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1 **Title: The environmental predictors of spatiotemporal variation in**
2 **the breeding phenology of a passerine bird**

3
4 Jack D Shutt ^{1*}, Irene Benedicto Cabello ¹, Katharine Keogan ¹, Dave I Leech ², Jelmer M
5 Samplonius ¹, Lorient Whittle ³, Malcolm D Burgess ^{4,5}, Albert B Phillimore ¹

6
7 1. Institute of Evolutionary Biology, The University of Edinburgh, The King's Buildings, Edinburgh,
8 EH9 3FL, UK

9 2. British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK

10 3. Woodland Trust, Kempton Way, Grantham, Lincolnshire, NG31 6LL, UK

11 4. RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

12 5. Centre for Research in Animal Behaviour, The University of Exeter, Exeter, Devon, EX4 4QG, UK

13
14 * Corresponding author: jackshutt8@gmail.com, Orcid ID: 0000-0002-4146-8748

15
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17 mismatch

18
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21
22 **Data:** Freely available on Data Dryad (<https://datadryad.org/review?doi=doi:10.5061/dryad.814vb1b>)

23 **Abstract**

24

25 Establishing the cues or constraints that influence avian timing of breeding is key to accurate prediction
26 of future phenology. This study aims to identify the aspects of the environment that predict the timing
27 of two measures of breeding phenology (nest initiation and egg laying date) in an insectivorous
28 woodland passerine, the blue tit (*Cyanistes caeruleus*). We analyse data collected from a 220km, 40-
29 site transect over three years and consider spring temperatures, tree leafing phenology, invertebrate
30 availability and photoperiod as predictors of breeding phenology. We find that mean night-time
31 temperature in early spring is the strongest predictor of both nest initiation and lay date and suggest this
32 finding is most consistent with temperature acting as a constraint on breeding activity. Birch budburst
33 phenology significantly predicts lay date additionally to temperature, either as a direct cue or indirectly
34 via a correlated variable. We use cross-validation to show that our model accurately predicts lay date
35 in two further years, and find that similar variables predict lay date well across the UK national nest
36 record scheme. This work refines our understanding of the principal factors influencing the timing of
37 tit reproductive phenology, and suggests that temperature may have both a direct and indirect effect.

38 **Introduction**

39

40 Global climate change is leading to increased ambient air temperatures and causing an advance of spring
41 phenological events (seasonal natural phenomena) [1,2] across the northern hemisphere, by an average
42 of 2.6 days per °C in the UK [3]. The timing of phenological events is often critical to the organisms
43 involved, influencing whether key life history stages (e.g. reproduction) coincide with favourable
44 environmental conditions. These conditions could be purely abiotic, such as temperature, but often
45 involve temporal synchrony with organisms at other trophic levels, be they resources or consumers
46 [4,5]. Individuals that mistime such phenological events may incur considerable fitness costs [6,7]. Not
47 all organisms or trophic levels are advancing their phenologies at the same pace in relation to climate
48 change, however, as each may respond to different environmental cues or to similar cues dissimilarly
49 [3,8,9]. This variation in response can cause trophic mismatch, whereby consumer phenology becomes
50 asynchronous with an important resource [4,5].

51

52 Predicting how phenology will affect populations in the future requires detailed knowledge of the
53 aspect(s) of the environment that species use to schedule their phenological events, and the magnitude
54 of their responses to these environmental variables [10]. These environmental predictors might act as
55 cues, signalling favourable future conditions, or constraints, prohibiting advancing phenology until
56 certain conditions are met. A model terrestrial system for studying phenology and trophic mismatch is
57 the deciduous tree – folivorous caterpillar – insectivorous passerine bird (e.g. tits *Paridae*) food chain
58 [4,11,12], hereafter referred to as the focal system. In this system, there is an ephemeral superabundance
59 of caterpillars in late spring, which consume young leaves before the trees impart defensive chemicals
60 [13]. Adult birds that synchronise the peak demand of their offspring to coincide with this caterpillar
61 peak fledge more young of higher quality [7,12]. Initiation of nest building occurs over a month before
62 peak offspring resource demand; in the intervening period a clutch is laid, incubated and the chicks are
63 partially reared [4,14]. Birds must therefore determine the timing of egg-laying in response to aspects
64 of the environment that are informative of the timing of the future resource peak [15].

65

66 Despite the popularity of the focal system among researchers, the environmental variables that affect
67 the reproductive phenology of the birds are only partially understood. One contributing predictor is
68 photoperiod, whereby increasing daylight hours indicate approaching favourable breeding conditions
69 [16]. The role of photoperiod has been demonstrated experimentally, as sustained exposure of blue tits
70 (*Cyanistes caeruleus*) to artificially inflated photostimulation caused them to breed three months early
71 when supplied with unlimited food [17]. Photostimulation operates through rapidly stimulating gonadal
72 and follicular growth and signalling song production [18,19]. While there is an interval of
73 approximately eight weeks between the onset of gonadal development and egg laying in wild tits, this
74 can be reduced to five weeks under artificial photostimulation [17,19]. Such plasticity indicates that,
75 while photostimulation is necessary to initiate reproduction, it is not in itself sufficient, and other stimuli
76 act to fine-tune timing [20]. In addition, whilst variable laying dates among populations can be
77 explained by locally adapted photoperiodic responses [21], photoperiod is consistent inter-annually and
78 therefore cannot be responsible for substantial *in situ* variation in phenology (which can be several
79 weeks) [22].

80

81 The average temperature during a period of spring has been shown to be a strong negative correlate of
82 clutch initiation in woodland passerines [10,11,23]. For tit species a rise of 1°C elicits a 3.5-5 day
83 advancement in clutch initiation [4,22,24], but the mechanism whereby average temperature affects
84 birds is unknown [25]. A direct effect of temperature on breeding phenology is often interpreted as
85 being a cue that predicts the timing of the peak caterpillar resource several weeks later [26].
86 Alternatively, low temperatures might act as a constraint, limiting the onset of energetically costly
87 processes such as egg production and incubation [27], although cue and constraint scenarios need not
88 be mutually exclusive. In the space of about two weeks a female blue tit can lay a clutch of eggs
89 weighing in excess of 150% of her body weight [14]. In support of the temperature constraint
90 hypothesis, cooling nestboxes delays egg formation in starlings (*Sturnus vulgaris*) [28], and reduces
91 egg volume in blue tits [29,30]. All previous observational studies have used daily average
92 temperatures, but it is possible that temperatures at different times of day may act via different

93 mechanisms. For instance, rising daytime temperatures may provide a cue of advancing conditions,
94 whereas thermoregulation costs associated with low night-time temperatures may act as a constraint on
95 egg-laying or a short-term cue of the predicted costs of incubation.

96
97 Whether temperature acts directly or via an indirect pathway, such as tree phenology or invertebrate
98 abundance, is yet to be fully established. Tree leafing phenology, most frequently oak (*Quercus* sp) or
99 birch (*Betula* sp), correlates positively with forest passerine lay date over time [31,32] and across space
100 at the site [33] and UK-wide level [34]. As some of these studies omitted temperature as a predictor, it
101 is possible that such phenological correlations arise because plants, invertebrates and birds all respond
102 directly to temperature. A clear mechanism whereby vegetation phenology would affect bird breeding
103 phenology has not been established, although it is possible that birds derive chemical cues from buds
104 or visually assess tree phenology. Bud consumption is minimal and temporally consistent however [35]
105 and inserting leafing branches into aviaries has no effect on lay date [36]. Artificial supplementary
106 feeding of passerines has been found to advance lay dates by a few days to a week [37,38], including
107 in woodland insectivores [39]. Manipulation of resources has been found to elicit greater responses in
108 years [39] and territories [40] with lower food resource levels, indicating a possible alleviation of an
109 environmental nutrient/energy constraint [41]. As far as we are aware no previous analysis has tested
110 the role of natural food resource availability as a phenological driver of breeding phenology in the focal
111 system.

112
113 The aim of this study is to separate the effects of different putative predictors of breeding phenology
114 (temperature, tree phenology, food availability and photoperiod), establishing which factors are most
115 important in generating spatiotemporal variation in blue tit reproductive phenology. We analyse data
116 collected from a 220km transect of 40 woodlands across Scotland [42]. In contrast to typical single-site
117 approaches to studying woodland bird phenology, by considering spatial and temporal variation this
118 study design somewhat uncouples covariation between the putative predictors. In addition, whilst
119 previous studies primarily focus solely on lay date as a measure of avian reproductive phenology, we
120 also examine the predictors of an earlier phenological phase, nest building initiation date, as different

121 environmental aspects may control the timing of each and permit fine-tuning of phenology throughout
122 the breeding season [43,44]. We then assess the robustness of our predictions in two ways. Firstly, we
123 conduct a cross-validation in which we test the performance of our model in predicting lay dates in two
124 subsequent years. Secondly, we examine the generality of our predictions by combining three national
125 datasets to test the performance of two key predictors with respect to blue tit lay dates across a long-
126 term (47-year) UK-wide dataset incorporating 36,839 records.

127

128 **Methods**

129 **Study system**

130

131 This study was conducted along a 220km transect from Edinburgh (55°98'N, 3°40'W) to Dornoch
132 (57°89'N, 4°08'E) in Scotland, incorporating 40 deciduous woodland sites (Fig A1) which varied in
133 elevation (8 – 440 m.a.s.l) [42]. Each site had six nestboxes (26mm hole Schwegler 1B) used by
134 breeding blue tits during 2014-2018. All dates used in this study are ordinal dates counted from January
135 1st. Temperature was monitored by two Thermachron iButtons (DS1922L-F5), which were installed at
136 opposite ends of each site from mid-February until mid-June every year. They were secured 1.5m high
137 on the north side of a tree, to avoid direct sunlight, in a waterproof white plastic film cartridge with a
138 20mm-diameter hole in the bottom to allow ambient air circulation and temperatures were recorded
139 every hour on the hour to a sensitivity of 0.0625°C. Invertebrate availability was monitored over four
140 day intervals using two caged, double-sided yellow sticky traps (245 x 100 mm) at each site, hung at ca
141 1.75m [42]. Invertebrates over 3mm in length were counted [42] and flying invertebrates captured using
142 this technique are important dietary items during early spring [45,46].

143

144 Habitat surveys were conducted at all 40 sites as detailed in [42]. Tree phenology was studied on 6 –
145 10 locally representative focal trees per site per year, with the focal tree selection protocol detailed in
146 Appendix A and focal tree taxa and coverage in Table A1. On each visit (every other day), each focal
147 tree was visually inspected using binoculars. The phenology of each focal tree was tracked, recording

148 the dates of: (i) budburst – when the green leaf first emerges from the earliest bud on any part of the
149 tree, and (ii) leafing – when the first leaf on any part of the tree is fully unfurled and looks to be the
150 correct shape, if not eventual full size, for the leaf of that tree species [33].

151

152 All nestboxes at intensively studied sites were checked every other day throughout the breeding season.
153 The nest initiation date reflected the earliest day on which either the entire floor of the nestbox was
154 covered with nesting material, or the nesting material had built up to ≥ 45 mm depth at the front of the
155 nestbox (measured from the bottom of the exterior of the nestbox to the top of the nesting material
156 bulk). Lay date was defined as the date at which the first egg was laid in a lined nest, calculated as the
157 previous day if two eggs were found as blue tits lay one egg per day, generally early morning [14]. One
158 second brood occurred and was excluded from analyses.

159

160 **Statistical Analyses**

161 **Individual predictor models**

162

163 To establish the best predictor belonging to each putative predictor block (temperature, tree phenology,
164 invertebrate availability) of blue tit reproductive phenology, each measure of each predictor (detailed
165 below) was first modelled individually in a linear mixed model (LMM) [47], with site and year as
166 random effects, using maximum likelihood. We assume that the effects of all variables on phenology
167 are similar across space and time [22], meaning that we interpret the slope as indicative of plasticity
168 with respect to the environmental predictor. Akaike Information Criteria (AIC) were then used for
169 model comparison [48], and the model with the lowest AIC within each predictor block was selected.
170 All models were also compared with a null model which included all random terms but only the
171 intercept as a fixed effect, and marginal R^2 values (representing the variance explained by fixed factors)
172 and conditional R^2 values (representing the variance explained by the entire model) were calculated for
173 each model [49].

174

175 We considered five measures of temperature as predictors of blue tit phenology (24hr, day-time, night-
176 time, daily maximum and daily minimum) to examine whether bird phenology is sensitive to
177 temperatures at particular times of the day or temperature extremes. Each temperature predictor was
178 calculated as a mean over a thermal sensitivity period, which was different for nest initiation and lay
179 date. The use of a sliding window [10,22] to identify this thermal sensitivity period proved to be
180 ineffective with our dataset due to the very high among-day correlation between mean temperatures
181 estimated over different sliding windows, a consequence of most of our replication being spatial rather
182 than temporal (i.e. high elevation sites are typically colder than low elevation sites). We therefore used
183 the sensitivity period for lay date (days 75-128) estimated by an earlier study for blue tits across the UK
184 [22]. As there are no published estimates of the sensitivity period available for nest initiation, we
185 subtracted the mean lag between nest initiation and lay date in our dataset ($n = 20$ days) from the period
186 used for lay date (days 55 – 108). Day-time was defined as those hours after sunrise and before sunset
187 throughout the entire sensitivity period (0800 – 1700hrs for nest initiation, 0700 – 1800hrs for lay date),
188 with night-time the hours always after sunset and prior to sunrise (2000 – 0500hrs for nest initiation,
189 2100 – 0400hrs for lay date). In a *post-hoc* test of the importance of day-time versus night-time
190 temperature, we included both fixed terms in a single LMM and report these results in Appendix A Fig
191 A2.

192

193 We considered six measures of tree phenology (mean budburst/leafing, foliage-weighted
194 budburst/leafing, birch budburst/leafing). Firstly, the mean budburst of all focal trees was calculated for
195 each site in each year. Secondly, a weighted budburst was calculated using Equation A1 that considered
196 the composition of the habitat at each site given the coverage offered by the focal trees. Thirdly, mean
197 birch budburst was calculated for each site containing birch in each year, as birch is the commonest tree
198 genus on the transect [42], has early phenology, and has been previously linked to bird phenology [32].
199 Where we lacked birch phenology data ($n = 4$), birch budburst was taken from the geographically
200 nearest site. Identical measures as detailed above were also taken to create mean leafing, weighted
201 leafing and birch leafing per site per year. Leafing was not considered as a predictor of nest initiation
202 as it occurred on average 19 days later.

203

204 To establish the measure of invertebrate availability, total invertebrate numbers were logged ($\log x+1$)
205 for each sticky trap due to the log normal distribution of abundances and mean totals per site collection
206 day were calculated. To obtain a number per day the exponent ($\exp x-1$) of these totals was then divided
207 by four (as sticky traps were collected every four days) and logged again ($\log x+1$). A sliding window
208 approach [10,22] was then used to identify the time period during which mean invertebrate availability
209 best predicted nest initiation and lay date across all sites and years. For the sliding window, starting
210 dates 82-100 and durations of 10-60 days were considered, with a cut-off end date representing the
211 mean of the respective blue tit phenology.

212

213 **Combined predictor models**

214

215 A full model (lmer) was generated [47] to analyse the predictors of blue tit reproductive phenology
216 simultaneously. Nest initiation and lay date were the responses, in separate models, with the best
217 temperature measure predictor, the best tree phenology predictor, the best invertebrate availability
218 predictor (all respective for each response) and latitude (as a proxy for photoperiod) included as fixed
219 effects, and site and year as random effects. The same models were run using the spaMM package [50],
220 with the inclusion of a Matern spatial autocorrelation term to a) determine the extent of spatial
221 autocorrelation and b) assess the sensitivity of results to the effects of spatial autocorrelation, allowing
222 for an exponential decay ($\nu = 0.5$). A null model, containing no fixed predictors of each response and
223 site and year as random effects, was also created for comparison.

224

225 **Robustness of predictions**

226

227 The predictive performance of the significant terms from the full lay date model were assessed in two
228 ways (nest initiation predictions were not assessed due to poor model performance). First, we employed
229 a cross-validation approach and tested the ability of our estimated model coefficients to predict lay date
230 in two subsequent years (2017-18) at the same sites. For this, a new full model was created identical to

231 that described above (lmer), but without invertebrate availability, as these data were not collected in
232 2017-18. Based on latitude, mean night-time temperature (days 75-128) and mean birch budburst, this
233 model predicted lay date for each nestbox in 2017-18. This prediction was then compared with the
234 observed lay date at each nestbox during each year and the root-mean-square-error and out of sample
235 cross-validated R^2 were calculated.

236

237 To assess whether the drivers we identified are able to predict phenology on a considerably larger spatial
238 and temporal scale we combined three national databases. We used blue tit lay date from the British
239 Trust for Ornithology nest record scheme [51], including records from the period 1970-2016 for which
240 the uncertainty in lay date was ≤ 10 days ($n = 36,839$). Our temperature measure was mean 24hr
241 temperature for days 75-128 for each matched 5km grid square in each year, derived from daily
242 interpolations from UK weather stations [52]. We used birch leafing dates from across the UK as
243 recorded by the Woodland Trust's Nature's Calendar citizen science scheme for the period 1998–2014
244 ($n = 14,892$), using leafing rather than budburst as these are subject to less measurement error by citizen
245 scientists [53]. We analysed these data as a trivariate response in a Bayesian GLMM [54], treating lay
246 date as censored Gaussian [55] and the other variables as Gaussian. We included 50km grid cell, year,
247 50km grid cell: year interaction, 5km grid cell and residual as random terms, using parameter expanded
248 priors except for the residual (inverse Wishart, $\nu = 0.002$) [56]. For each random term other than the
249 residual we can estimate the variance-covariance of lay date, temperature and birch phenology
250 (Appendix A: trivariate model matrix) and from this coefficients of bird phenology regressed on tree
251 phenology and temperature can be calculated (see Appendix A, [56]); for the residual we only estimated
252 the variance of each of the response terms. Model convergence was assessed via inspection of trace
253 files and all effective sample sizes for focal parameters exceeded 1000.

254

255 **Results**

256 **Individual predictor models**

257

258 All temperature predictors for blue tit reproductive phenology returned a negative slope, and all but one
259 were a significant improvement on their respective null models ($\Delta\text{AIC} > 2$, Table A2). The best
260 temperature predictor for both nest initiation and lay date was mean night-time temperature over their
261 respective time sensitivity periods, which significantly outperformed all other temperature predictors
262 (Table A2) and showed similar responses for both nest initiation (-2.43 ± 0.83 days/ $^{\circ}\text{C}$) and lay date ($-$
263 2.87 ± 0.56 days/ $^{\circ}\text{C}$). In a *post-hoc* test that included both mean day-time and mean night-time
264 temperate predictors, the slope for mean night-time temperature was consistent with the slope in the
265 original model, whereas the slope for mean day-time temperature was far shallower, consistent with
266 night-time temperature being the stronger predictor (Fig A2). Temperature predictor models for lay date
267 consistently captured more variance (Table A2, marginal $R^2 = 0.19$) than those for nest initiation (Table
268 A2, marginal $R^2 = 0.05$). For nest initiation, site variance was much more pronounced than year
269 variance, and mean night-time temperature explained approximately a third of each (Table A2). For lay
270 date, site and year variance were more similar in magnitude and mean night-time temperature explained
271 more than four-fifths of inter-annual variance, and over a third of site variance (Table A2).

272

273 The slopes of all models using tree phenology as a predictor of blue tit reproductive phenology reveal
274 that later tree phenology predicts later reproductive phenology (Table A3). The best tree phenology
275 predictor of both nest initiation and lay date was birch budburst (Table A3). Whilst birch budburst was
276 not a significant predictor of nest initiation ($b = 0.17 \pm 0.11$, $\Delta\text{AIC} = 0.4$, marginal $R^2 = 0.01$), it was a
277 significant predictor of lay date ($b = 0.35 \pm 0.07$, $\Delta\text{AIC} = 18.6$, marginal $R^2 = 0.11$).

278

279 Using sliding windows we found the best mean invertebrate availability predictors of blue tit phenology
280 were between days 82 and 95 for nest initiation and days 93-123 for lay date. Invertebrate availability
281 significantly predicted nest initiation (Table A4), but captured very little variance in either nest initiation
282 or lay date (marginal $R^2 = 0.01 - 0.03$), and the effect sizes were small, such that nest initiation and lay
283 date were predicted to occur just four and five days earlier, respectively, when invertebrate availability
284 was at its highest value compared to its lowest (Fig 1C & 1F).

285

286 **Combined predictor models**

287

288 In the full models, that included the best predictor from each single predictor model and latitude as a
289 proxy for photoperiod, nest initiation was not significantly predicted by any single predictor variable
290 and the full model performs rather poorly in explaining the variance (Table 1, marginal $R^2 = 0.06$,
291 conditional $R^2 = 0.25$). In comparison, lay date was significantly predicted by both night-time
292 temperature ($b = -1.65 \pm 0.69$) and birch budburst ($b = 0.22 \pm 0.09$), explaining a substantial proportion
293 of the variance (marginal $R^2 = 0.20$, conditional $R^2 = 0.44$), capturing approximately 39% of site
294 variance and 93% of inter-annual variance (Table 1). Latitude was a non-significant predictor of both
295 responses. Models that estimated spatial autocorrelation returned very similar results and revealed
296 spatial autocorrelation to be negligible, with the range at which autocorrelation drops to 0.1 being less
297 than 0.01° for both nest initiation and lay date, equating to distances within a site [42].

298

299 **Robustness of predictions**

300

301 The cross-validation model using data collected in the subsequent two years was found to provide an
302 accurate (root-mean-square-error = 6.05 days) and unbiased (Fig 2) prediction of lay date, with the
303 explanatory power very similar to that of the original model (out-of-sample cross-validated $R^2 = 0.21$).

304

305 Across the UK (50x50km grid cells) the regression coefficients for mean 24hr temperature as a predictor
306 of lay date were negative but non-significant ($b = -2.070$, 95% credible interval [CI] = $-7.186 - 3.550$),
307 whereas over time the equivalent slope was significant ($b = -2.059$, 95% CI = $-3.370 - -0.858$) (Fig A3).
308 Similarly, birch leafing was a positive but non-significant predictor of lay date across the UK but
309 significant across years ($b = 0.311$, CI = $0.092 - 0.516$), with the slope similar to that obtained for our
310 transect (Fig A3). On average birch leafing occurred 11.7 days (95% CI = $11.08 - 12.33$) before blue
311 tit lay date in the UK. The slope estimates obtained for temperature and birch as predictors of lay date
312 do not differ significantly over space versus time and are similar to those obtained for our transect.

313

314 **Discussion**

315

316 In this study, we aimed to gain a clearer understanding of the proximate environmental drivers of the
317 breeding phenology of a passerine bird by testing multiple putative drivers (temperature, tree
318 phenology, prey abundance and photoperiod) both independently and then together. Mean night-time
319 temperature in early spring and the budburst phenology of birch trees are the most important predictors
320 of blue tit breeding phenology, with elevated night-time temperatures and earlier birch budburst
321 significantly predicting earlier lay dates across sites and years. These predictors performed well in cross-
322 validation using data for two additional years, and using variants on these predictors we found that they
323 generalise to a considerably larger spatial scale (UK) and over a much longer timescale. These results
324 concur with previous studies suggesting that temperature is a strong causal predictor of lay dates in
325 woodland passerines [22,23], but advance our understanding by identifying night-time temperatures as
326 most predictive. From this we infer that warmer night-time conditions may remove a constraint on
327 breeding rather than providing a cue [27]. A striking result emerging from our work is that birch
328 phenology outperformed both mean tree phenology, and mean tree phenology weighted for local tree
329 abundance, indicating that blue tits may be sensitive to the seasonality of particular tree species within
330 the landscape.

331

332 Spring temperatures are well known to be a strong negative correlate of woodland passerine laying
333 dates, though the mechanism through which it acts is unknown [25]. The multiple regression slope we
334 estimate is shallower than that we obtain in the single predictor models and estimates from other blue
335 tit studies [22,24] and this discrepancy arises because analyses that consider temperature as the sole
336 driver of breeding phenology will estimate a slope that combines both direct and indirect effects of
337 temperature, whereas our analyses include variables that represent proximate drivers arising via two
338 indirect pathways (birch phenology and invertebrate availability). This is the first study to identify
339 night-time temperatures as the most important temperature predictor and we suggest that increasing
340 night-time temperatures may lift a thermal energetic constraint on producing and incubating eggs

341 [27,57]. This would also explain why female yolk development [58] – but not male gonadal
342 development [59] – correlates with laying dates. It remains possible that our finding that night-time
343 temperatures are more important than day-time temperatures arises due to instances of direct sunlight
344 contributing to measurement error of the latter. Nonetheless we suggest that the hypothesis that night-
345 time temperatures are a constraint warrants further exploration.

346

347 Tree phenology was a poor predictor of nest initiation, both in individual and combined predictor
348 models, but birch budburst was a strong and significant predictor of lay date in all models. This is
349 consistent with birds responding to certain tree genera more than others, as has been suggested for birch
350 in northern Europe previously [32]. In the UK national dataset used in this study, birch leafing is
351 strongly positively correlated with the more widely reported and reliable oak leafing across both space
352 ($r = 0.973$) and time ($r = 0.909$) but occurs on average 13.8 days earlier (see Appendix A for further
353 details). We suggest that this early phenology of birch provides an indicator of future environments
354 earlier in the year than other genera, coinciding with the bird's requirement for information; this is
355 supported by budburst predicting lay date better than later leafing. As tree phenology was a very poor
356 predictor of nest initiation but a significant predictor of first egg date, this could indicate that it provides
357 a supplementary cue between the two phenological phases allowing for fine-tuning of the timing of egg
358 laying after nest building. Such a cue could be visual or chemical [35], or possibly indirect through
359 invertebrate availability on, or in, birch buds, food resources shown via faecal metabarcoding to be
360 heavily utilised by blue tits in Scotland in early spring but not captured by the sticky traps [45]. In
361 addition, if the effect of temperature proves to be indirect via tree phenology or invertebrate availability
362 then the reliability of assuming that temperature has a direct causal effect [22,60] will depend on the
363 linearity of temperature effects on tree and invertebrate phenology. Birch, for instance, is delayed by
364 warmer conditions during a chilling period in the early winter [53], such that a focus only on the spring
365 period may overestimate the advance that this species will show.

366

367 Flying invertebrate abundance was a significant predictor of nest initiation when tested in isolation, but
368 captured relatively little of the variation and was not a significant predictor of either phase of blue tit

369 reproductive phenology in the combined models. We note that the predicted effect size of a few days
370 difference in lay dates between high and low prey availability is of similar magnitude to the responses
371 to artificial feeding observed in other studies [39,40] and could reflect the maximum amount that
372 females can plastically shift laying due to food availability, which would presumably alleviate energetic
373 constraints like increasing night-time temperatures. However, sticky trap derived estimates of food
374 availability may provide an incomplete estimate of the resource available to blue tits, due to the
375 variability inherent in catching insects on sticky traps and not recording non-flying taxa. Thus, we
376 cannot exclude the possibility that average nightly temperature and birch phenology provide a better
377 predictor of the true available prey abundance than our sampling yields.

378

379 Previous research has demonstrated that photostimulation is fundamental in commencing temperate
380 passerine reproductive phenology [17,18], but we found no evidence that it explains the spatial variation
381 observed on the scale of our study. This supports the idea that photostimulation opens a ‘window’ for
382 possible breeding beyond which other supplementary cues refine the exact timing, and these processes
383 give rise to the observed variation.

384

385 The breeding phenology of many avian species across the temperate northern hemisphere is advancing
386 at a similar rate to that noted in this study in response to warming temperatures [24,61] and it is possible
387 that other species in this region utilise a similar set of environmental predictors. In the temperate
388 southern hemisphere avian breeding phenology is also associated with vegetation productivity and food
389 resources, but the productive period extends for longer and its timing is less predictable [62]. Moreover,
390 conversely to the north, physiological stress from high temperatures rather than low appears to constrain
391 breeding, suggesting that our insights may not generalise here [63].

392

393 In summary, mean night-time temperatures and birch budburst phenology are significant predictors of
394 lay date in Scottish blue tits, consistent with temperature having both a direct and indirect effect and
395 acting as a thermal constraint rather than a cue. Our models performed well in cross-validation and as
396 the effects we estimated in Scotland could be generalised to the national scale over a longer time period

397 this gives a degree of confidence in the robustness and generality of our inferences, and highlights their
398 value for predicting future variation in blue tit breeding phenology. This will enable more accurate
399 prediction of the effects of trophic mismatch in this focal system [10,22].

400

401 **Declarations**

402

403 **Ethics** – All birds were handled and ringed by fieldworkers with appropriate British Trust for
404 Ornithology permits.

405 **Data accessibility** – Available freely online, stored with the Dryad Digital Repository
406 (<https://datadryad.org/review?doi=doi:10.5061/dryad.814vb1b>)

407 **Authors' contributions** – JDS participated in the design of the study, collected the transect field data,
408 performed the statistical analyses and drafted the manuscript. IBC, KK and JMS helped collect transect
409 field data. DL and LW provided national datasets. MDB participated in the design of the study. ABP
410 conceived, designed and supervised the study and assisted in collecting field data and performing
411 statistical analyses. All authors contributed manuscript comments and gave final approval for
412 publication.

413 **Competing interests** – We declare no competing interests.

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420

421 **References**

422

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- 587

Tables and figures

Table 1 Summary of model outputs from LMM's incorporating all predictors of nest initiation and lay date. Significance asterisks show p values (0.05 * 0.01 ** 0.001 ***). Temperature shows the slope for the best temperature predictor found for each response in Table A2 (mean night-time temperature for both responses), tree phenology shows the slope for the best tree phenology predictor for each response in Table A3 (birch budburst for both responses), invertebrate availability shows the slope for the best invertebrate availability predictor for each response in Table A4 (mean availability between days 82-95 for nest initiation, days 93-123 for lay date) and photoperiod shows the slope for latitude as a proxy for photoperiod. Random effect variances for each model are also shown (site, year and residual). In spaMM models nu was fixed at 0.5 to constrain the spatial autocorrelation to follow an exponential decay.

Response	Model	Intercept	Temperature	Tree phenology	Invertebrate availability	Photoperiod proxy	Site variance	Year variance	Residual variance	R ² marginal	R ² conditional
Nest initiation	Null	104.5 ± 1.5					28.2	4.1	97.9	0.00	0.25
	lmer	139.8 ± 102.7	-2.00 ± 1.27	0.07 ± 0.14	-1.18 ± 1.63	-0.59 ± 1.74	22.9	3.1	98.3	0.06	0.25
	spaMM	127.6 ± 99.6	-1.86 ± 1.16	0.07 ± 0.14	-1.25 ± 1.57	-0.39 ± 1.69	28.7	1.7	89.8		rho = 283.5
Lay date	Null	123.2 ± 2.4					17.2	16.2	34.2	0.00	0.49
	lmer	139.7 ± 67.2	-1.65 ± 0.69 *	0.22 ± 0.09 *	-1.50 ± 1.07	-0.50 ± 1.15	10.5	1.2	33.6	0.20	0.44
	spaMM	129.0 ± 67.9	-1.48 ± 0.69 *	0.23 ± 0.08 *	-1.29 ± 1.04	-0.37 ± 1.16	14.3	1.4	29.7		rho = 267.3

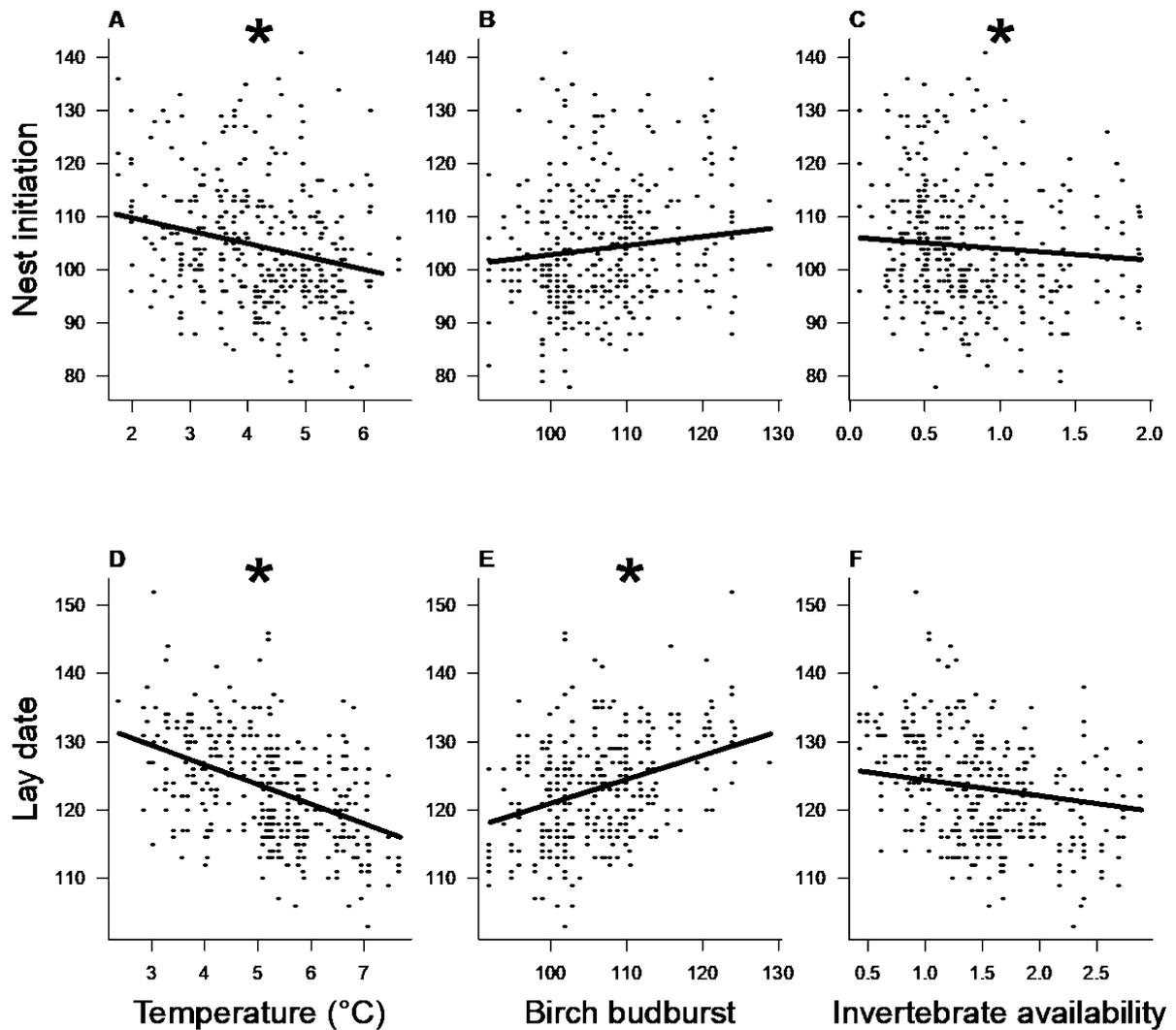


Fig 1 Relationship between the best individual environmental predictor variables and two measures of blue tit reproductive phenology (**A-C**: nest initiation, **D-F**: lay date). **A** Mean night-time (2000 – 0500 hrs) temperature during the period 24th February – 18th April **B** Mean birch budburst date **C** Mean invertebrate availability during the period 23rd March – 5th April **D** Mean night-time (2100 – 0400 hrs) temperature during the period 16th March – 8th May **E** Mean birch budburst date **F** Mean invertebrate availability during the period 3rd April – 3rd May. All slopes shown are taken from the best predicting models summarised in Tables A2-A4 and significant slopes are marked with an asterisk.

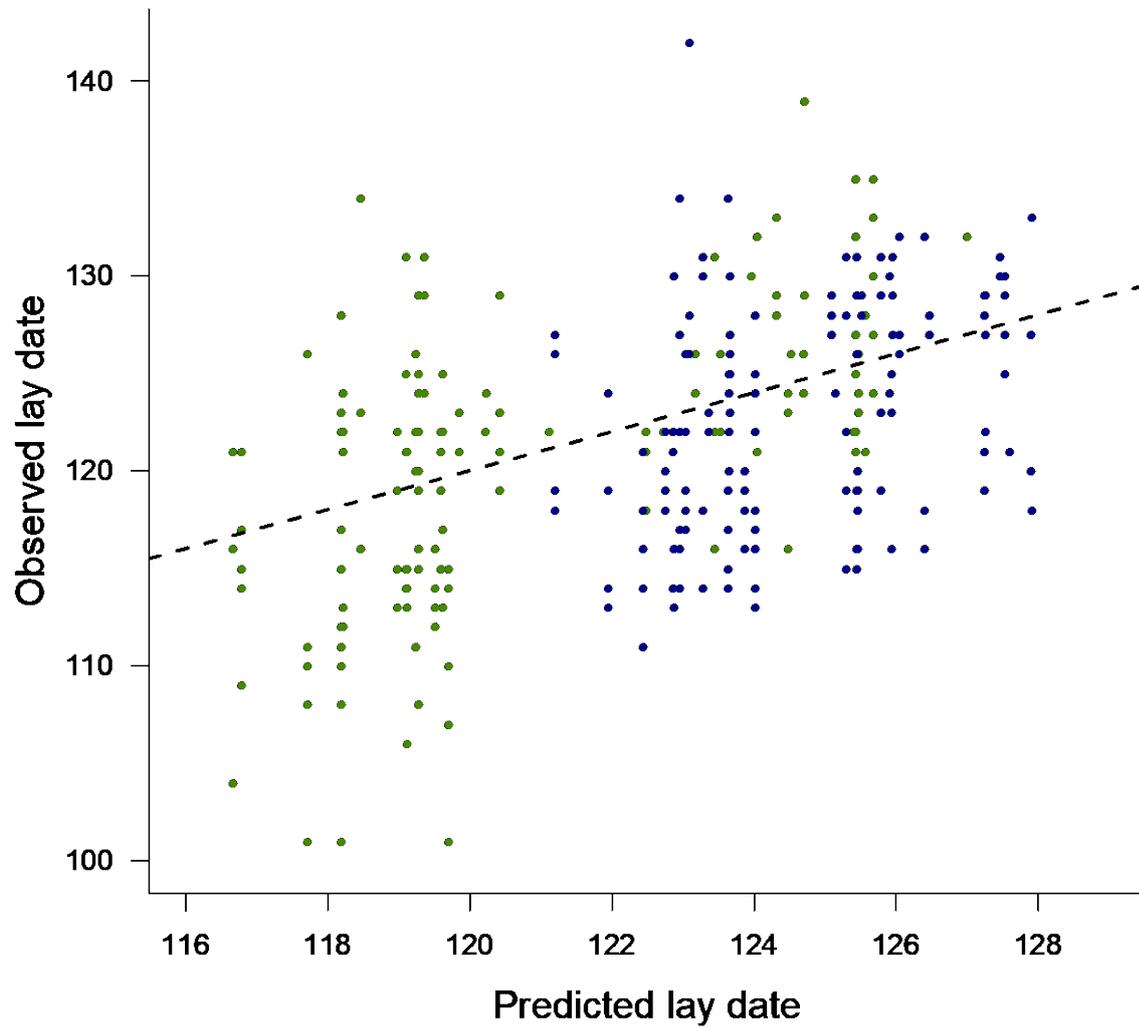


Fig 2 The relationship between predicted and observed lay dates during the validation years 2017 (green points) and 2018 (blue points) on the Scottish transect. The dashed line is the 1:1 relationship. Note that observed lay date varies more than predicted lay date because predictions are made for site means.

Supplementary Material for Shutt *et al* “The environmental predictors of spatiotemporal variation in the breeding phenology of a passerine bird”, Proceedings of the Royal Society B (DOI: 10.1098/rspb.2019.0952)

Appendix A

Contents:

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7. Correlation of birch leafing phenology to oak leafing phenology
7. Literature cited in the supplementary material

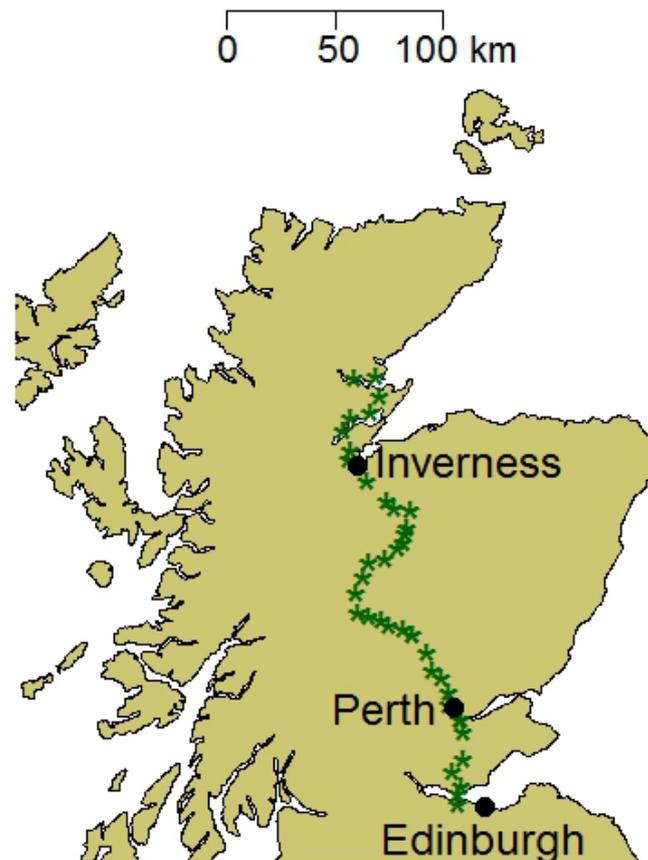


Fig A1 Map of Scotland illustrating the locations of all 40 sites along the transect (green stars) with selected cities as location indicators.

Focal tree selection protocol

In 2014, six focal trees were selected (the nearest deciduous tree with a trunk diameter $\geq 20\text{cm}$ to each nestbox) and identified to genus level at each site. If oak (*Quercus* sp) or birch (*Betula* sp) were present at a site but not represented in this selection, up to six of each relevant species present were numbered and one of each present selected by the random roll of a die, resulting in six to eight focal trees per site. In subsequent years (2015-16) the same individual focal trees were used wherever possible (consistency 2014-15 = 80%, 2015-16 = 97%), and additional trees were added so that each site contained 8-10 focal trees. These extra trees were selected by using the method described above for oak and birch but extending this to sycamore (*Acer pseudoplatanus*) and willow (*Salix* sp). If there were fewer than eight focal trees at the site by this stage, the selection method described above was used on randomly selected deciduous trees of species typical of the surrounding habitat, leaving each site with at least eight locally representative focal trees.

Table A1 Detailing the number of focal trees studied of each taxon each year, with the percentage of intensively studied sites (2014 n=30, 2015 n=35, 2016 n=37) with at least one focal tree of this taxon (site coverage), ordered by focal tree number in 2016, followed by site coverage in 2016. Total focal tree n=186 in 2014 (mean 6.2/site), 293 in 2015 (mean 8.4/site) and 313 in 2016 (mean 8.5/site). Species within each tree taxon along the transect are detailed in [1].

Tree Taxon (<i>Genus</i>)	2014		2015		2016	
	Focal Trees	Sites (%)	Focal Trees	Sites (%)	Focal Trees	Sites (%)
Birch (<i>Betula</i>)	85	93	118	97	123	97
Oak (<i>Quercus</i>)	19	40	48	57	53	57
Sycamore (<i>Acer</i>)	29	47	30	37	33	38
Willow (<i>Salix</i>)	7	13	20	31	22	32
Alder (<i>Alnus</i>)	15	30	22	31	22	30
Beech (<i>Fagus</i>)	13	27	17	23	17	22
Ash (<i>Fraxinus</i>)	7	20	10	20	11	19
Elm (<i>Ulmus</i>)	2	3	7	17	8	19
Rowan (<i>Sorbus</i>)	6	17	8	14	8	14
Aspen (<i>Populus</i>)	2	3	6	9	7	11
Hazel (<i>Corylus</i>)	3	10	5	14	4	11
Cherry (<i>Prunus</i>)	0	-	2	3	2	3
Chestnut (<i>Castanea</i>)	0	-	0	-	2	3
Lime (<i>Tilia</i>)	0	-	0	-	1	3

Equation A1 Calculation to obtain weighted site mean budburst at a single site in a single year, where f = frequency of tree at site (percentage), b = mean budburst of tree species at site per year and 1-14 denote tree taxa. Weighted site mean leafing was calculated identically.

$$\frac{\sum_{i=1}^{n=14} f_i b_i}{\sum_{i=1}^{n=14} f_i}$$

Trivariate model matrix in space and time

Blue tit first egg date (F), temperature (T) and birch phenology (P) from across the UK were included in a mixed model with a trivariate response. Then for each random term included in the model we were able to estimate a 3 x 3 variance-covariance matrix:

$$\begin{bmatrix} \sigma_F^2 & \sigma_{F,T} & \sigma_{F,P} \\ \sigma_{F,T} & \sigma_T^2 & \sigma_{T,P} \\ \sigma_{F,P} & \sigma_{T,P} & \sigma_P^2 \end{bmatrix}$$

From this matrix we can define \mathbf{A} as the 2 x 2 variance-covariance matrix of predictors (T and P) and \mathbf{B} as a vector of the covariance of predictors and response. Then $\mathbf{A}^{-1}\mathbf{B}$ returns the equivalent to the multiple regression coefficients across levels of a focal random term [2]. We use this approach to obtain separate estimates of the effect of temperature and birch leafing on blue tit lay date over space (50km grid cells) and time (years). If the predictor variables are causative and there is no local adaptation we predict that responses over space and time should be the same [3].

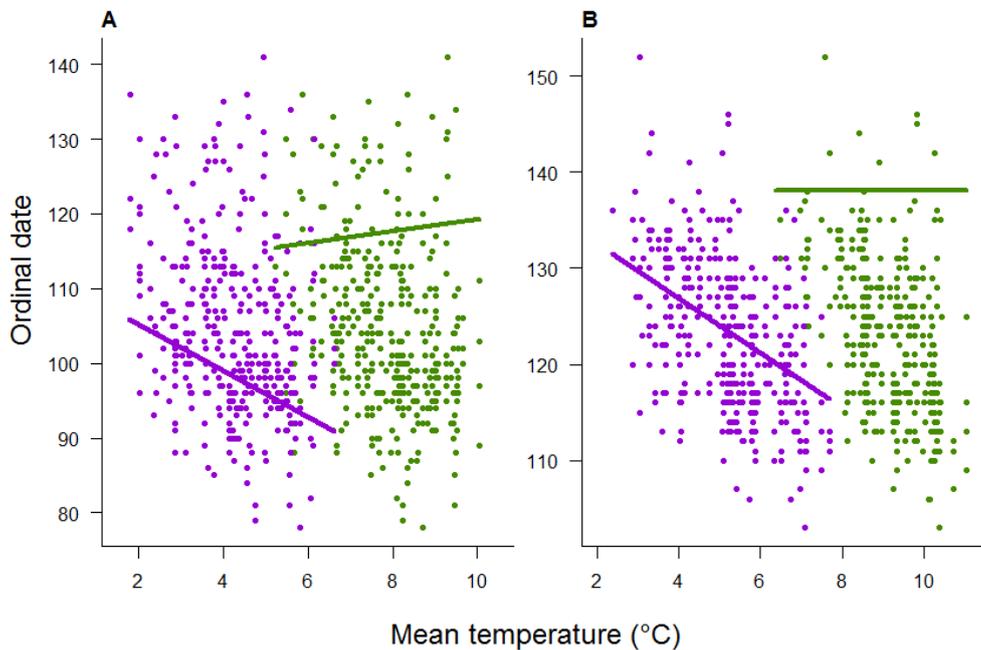


Fig A2 The slopes of a linear model with **A** nest initiation and **B** lay date as the response variable and both mean day-time (green) and mean night-time (purple) temperatures as the predictor variables, with site and year as random effects. Whilst the slope for night-time temperature remains consistent with that when it is used a single predictor (Table A2), the slope for day-time temperature is much reduced (Table A2), highlighting night-time temperature as the better predictor of both nest initiation and lay date.

Table A2 Temperature predictors of nest initiation and lay date, with slopes (b) and their associated standard errors (se) estimated from LMM's (see methods), together with the AIC value of each for comparison, and the random effect variances (site, year and residual). The best temperature predictors of nest initiation and lay date respectively are presented in bold.

Response	Predictor	Intercept ± se	b ± se	AIC	Site variance	Year variance	Residual variance	R² marginal	R² conditional
Nest initiation	Null	104.5 ± 1.4		3145.6	28.3	3.0	96.2	0.00	0.25
	24hr	118.2 ± 5.2	-2.33 ± 0.86	3141.1	21.6	1.9	96.6	0.04	0.23
	Mean day-time	118.2 ± 6.5	-1.75 ± 0.82	3143.7	22.7	2.0	96.9	0.03	0.22
	Mean night-time	114.7 ± 3.7	-2.43 ± 0.83	3139.9	21.9	2.0	96.2	0.05	0.24
	Mean maximum	111.4 ± 7.5	-0.65 ± 0.70	3146.9	26.2	2.4	96.6	0.00	0.23
	Mean minimum	109.4 ± 1.9	-2.21 ± 0.74	3140.7	23.6	0.7	96.3	0.05	0.24
Lay date	Null	123.3 ± 2.1		2464.5	18.1	11.6	33.9	0.00	0.47
	24hr	146.8 ± 4.6	-3.23 ± 0.62	2440.2	11.2	1.6	34.5	0.17	0.40
	Mean day-time	142.7 ± 6.4	-2.14 ± 0.69	2448.3	13.1	4.0	34.7	0.07	0.38
	Mean night-time	138.1 ± 3.1	-2.87 ± 0.56	2437.2	11.3	2.3	34.1	0.19	0.42
	Mean maximum	128.3 ± 6.9	-0.40 ± 0.53	2454.2	17.2	9.8	34.2	0.00	0.44
	Mean minimum	130.3 ± 2.1	-2.21 ± 0.52	2440.9	11.8	3.9	34.2	0.15	0.42

Table A3 Tree phenology predictors of nest initiation and lay date, with their slopes (b) and associated standard errors (se) estimated from LMM's (see methods), together with the AIC value of each for comparison, and the random effect variances (site, year and residual). The best tree phenology predictors of nest initiation and lay date respectively are presented in bold. BB = budburst, LF = leafing.

Response	Predictor	Intercept \pm se	b \pm se	AIC	Site variance	Year variance	Residual variance	R ² marginal	R ² conditional
Nest initiation	Null	103.7 \pm 1.2		2698.6	24.6	1.8	91.8	0.00	0.22
	Mean BB	89.4 \pm 12.6	0.13 \pm 0.11	2699.3	22.6	2.0	92.0	0.01	0.22
	Weighted BB	91.1 \pm 11.0	0.11 \pm 0.10	2699.3	22.4	1.9	92.1	0.01	0.22
	Birch BB	85.9 \pm 11.4	0.17 \pm 0.11	2698.2	22.9	1.7	91.7	0.01	0.22
Lay date	Null	123.2 \pm 2.0		2367.9	18.5	10.6	33.9	0.00	0.46
	Mean BB	97.2 \pm 9.1	0.23 \pm 0.08	2362.7	13.8	7.4	34.2	0.05	0.41
	Weighted BB	98.9 \pm 7.8	0.21 \pm 0.07	2360.8	14.3	7.8	33.9	0.05	0.43
	Birch BB	86.0 \pm 7.9	0.35 \pm 0.07	2349.3	13.3	5.8	33.0	0.11	0.44
	Mean LF	103.0 \pm 8.0	0.16 \pm 0.06	2364.9	13.3	7.0	34.5	0.04	0.40
	Weighted LF	101.2 \pm 7.2	0.18 \pm 0.06	2361.9	13.1	7.0	34.3	0.06	0.41
	Birch LF	99.2 \pm 6.8	0.20 \pm 0.06	2359.2	12.3	6.0	34.2	0.07	0.40

Table A4 Invertebrate abundance predictors of nest initiation and lay date, with slopes (b) and associated standard errors (se) taken from LMM's (see methods), along with null models and AICs for comparison, and the random effect variances (site, year and residual).

Response	Start Date	Intercept \pm se	b \pm se	AIC	Site variance	Year variance	Residual variance	R ² marginal	R ² conditional
Nest initiation	Null	104.5 \pm 1.4		3145.6	28.3	3.0	96.2	0.00	0.25
	82 – 95	106.2 \pm 1.8	-2.16 \pm 1.56	3106.5	24.8	2.4	98.2	0.01	0.22
Lay date	Null	123.3 \pm 2.1		2350.2	17.3	11.3	34.3	0.00	0.45
	93 – 123	126.7 \pm 2.4	-2.30 \pm 1.21	2348.7	15.0	6.8	34.5	0.03	0.41

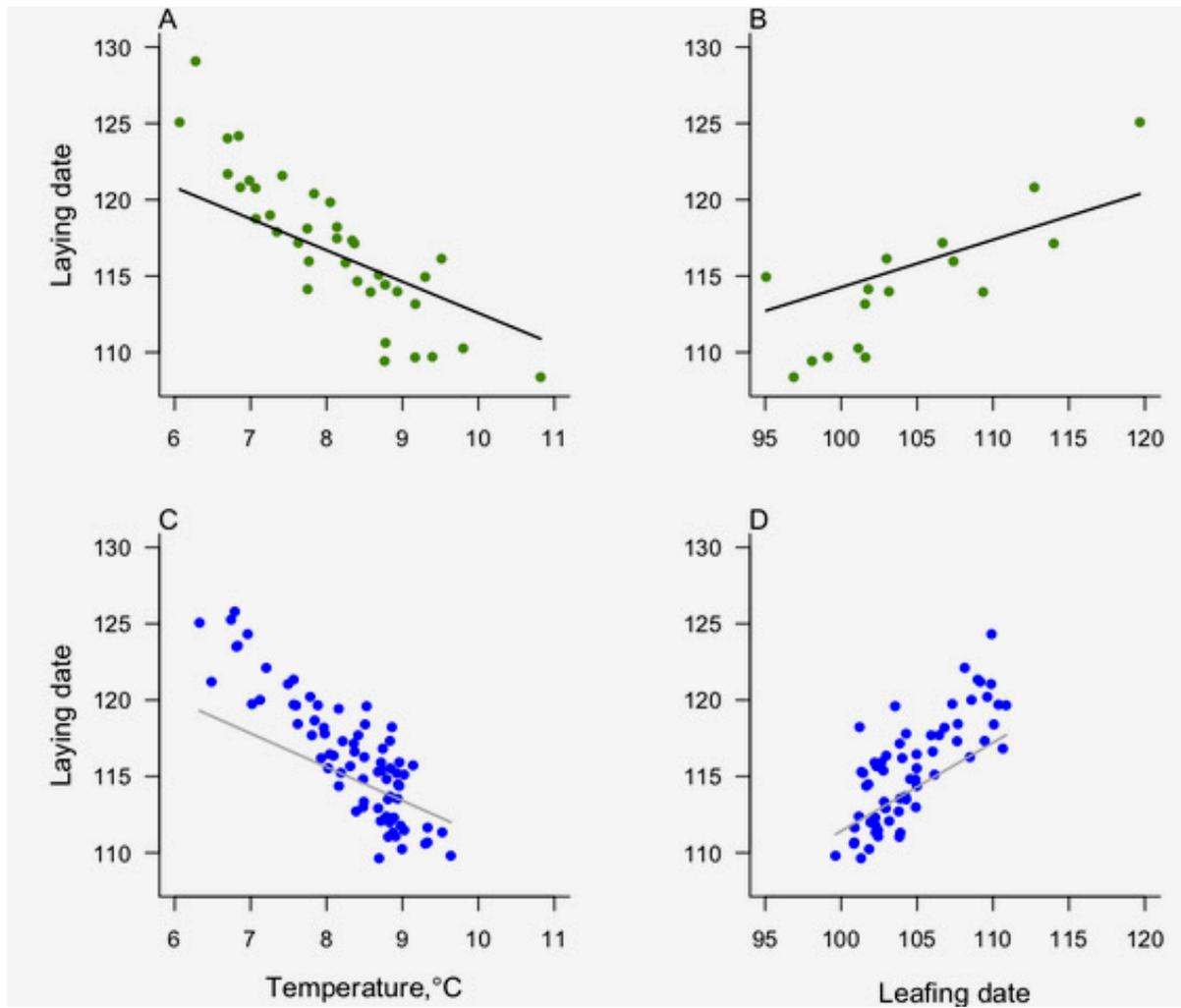


Fig A3 The relationship between lay date and spring temperature (A, C) and birch leafing date (B, D) over time (A, B) and space (C, D) across UK-wide datasets. Predicted slopes correspond to the mean posterior multiple regression slopes, with black and grey lines corresponding to significant and non-significant slopes, respectively. Green points are mean values in a year and blue points are mean values in a grid cell (over space). Only years and grid cells with a minimum of 50 observations are included as points.

Correlation of birch leafing phenology to oak leafing phenology

Methods

First leafing data for pedunculate oak (*Quercus robur*, $n = 11285$) and silver birch (*Betula pendula*, $n = 14892$) for the period 1998 – 2014 were obtained from the Woodland Trust's Nature's Calendar citizen science scheme. The two phenological measures were included as a bivariate response in a general linear mixed model with 50km grid cell, year and 5km grid cell included as random terms. Models were fit using MCMCglmm [4] and run for 110,000 iterations with the first 10,000 removed as burn-in. Priors were inverse-Wishart for the residual term and parameter-expanded for the other random terms. Based on the model posteriors we assessed the correlation and major axis regression between birch and oak over space and time.

Results

Across the UK silver birch leafing is strongly positively correlated with pedunculate oak leafing across 50km grid cells ($r = 0.973$, 95% HPD = 0.946 – 0.992) and years ($r = 0.909$, 0.783 – 0.977). On average oak leafing occurs 13.803 days (11.121 – 14.438) after birch. Across grid cells the major axis slope reveals that for every days delay in oak leafing there is a smaller delay in birch leafing ($b = 0.657$, 0.594 – 0.728). Across years phenology of birch and oak leafing is not significantly different from a 1:1 relationship ($b = 0.999$, 0.748 – 1.250).

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