

**This item is the archived peer-reviewed author-version of:**

Great and blue tit laying dates vary with fine-scale variation in local tree composition but not tree budburst

**Reference:**

Matthysen Erik, Adriaensen Frank, Van de Kerckhove Peter, Vandekerckhove Kris.- Great and blue tit laying dates vary with fine-scale variation in local tree composition but not tree budburst  
Journal of ornithology - ISSN 2193-7192 - Heidelberg, Springer heidelberg, 162:3(2021), p. 709-722  
Full text (Publisher's DOI): <https://doi.org/10.1007/S10336-021-01872-2>  
To cite this reference: <https://hdl.handle.net/10067/1767240151162165141>

1 **Great and Blue Tit laying dates vary with fine-scale**  
2 **variation in local tree composition but not tree budburst**

3  
4 Running head: linking bird phenology with individual trees

5  
6 Erik Matthysen<sup>1</sup>, Frank Adriaensen<sup>1</sup>, Peter Van de Kerckhove<sup>2</sup> &  
7 Kris Vandekerckhove<sup>2</sup>

8  
9 <sup>1</sup>Evolutionary Ecology Group, Department of Biology, University of Antwerp,  
10 B-2610 Wilrijk, Belgium

11 <sup>2</sup>Research Group on Forest Ecology and Management, Research Institute for  
12 Nature and Forest (INBO), Gaverstraat 4, B-9500 Geraardsbergen.

13  
14 Corresponding author: Erik Matthysen, [erik.matthysen@uantwerpen.be](mailto:erik.matthysen@uantwerpen.be) +32 3  
15 265 3464

16  
17  
18  
19 Author contributions: EM and FA conceived the study. FA provided the long-  
20 term bird data. FA, PVK and KV provided tree data. EM performed all analyses  
21 and wrote the manuscript. All authors provided input on the interpretation of the  
22 results and on the draft manuscript.

25 **Abstract**

26 Many studies have investigated how spring temperature affects laying dates and how this in  
27 turn affects the synchrony between nestling food demands and the insect food peak that  
28 follows tree budburst. While there is strong evidence that temperature itself acts as a cue for  
29 this plasticity in annual timing, the exact nature of the cue and response remain to be  
30 elucidated. Here we use long-term data on Great and Blue Tits and an unprecedented dataset  
31 on the location and phenology of 1396 trees to investigate whether small-scale variation in  
32 laying date can be explained by local tree phenology, and/or by tree species composition  
33 around nestboxes. Individual trees maintained their relative timing of budburst between years,  
34 while differences among tree species were more variable between springs. Contrary to  
35 expectation, we found no relation between first-egg dates and average budburst date at  
36 different distances around the nestbox. This can at least partly be explained by the very low  
37 degree of spatial autocorrelation in tree budburst. We did find an effect of local tree  
38 composition whereby Blue Tits, but not Great Tits, laid earlier in nestboxes surrounded by  
39 more oaks and fewer beeches. Although Blue Tit nest failure rate was higher in territories  
40 with more beech trees, independently of laying date, we found no evidence for preferential  
41 occupation of oak-dominated territories. Thus although we found some evidence for fine-  
42 scale effects of tree species on timing of breeding, the underlying mechanism remains unclear.

43 Key words: phenology, synchrony, breeding success, *Parus*, *Cyanistes*

44

## 45 **Introduction**

46 Over the past few decades, evidence has accumulated for changes in the timing of bird  
47 breeding seasons in response to global warming, and this has become one of the best-studied  
48 ecological systems documenting climate change effects in natural populations (Crick et al.  
49 1997; Parmesan 2007; Charmantier and Gienapp 2014; Radchuk et al. 2019). In particular,  
50 effects of increasing spring temperature have been documented to lead to advances in  
51 budburst of trees, emergence of caterpillars, and timing of breeding in forest-dwelling  
52 insectivores that largely depend on these caterpillars as staple food for their nestlings. The  
53 close link between spring temperature and the timing of these different trophic levels had  
54 already been well documented before the impact of climate warming became visible  
55 (Slagsvold 1976; Van Noordwijk et al. 1995).

56 In the past few decades, many studies have investigated how bird species and populations  
57 may or may not be able to maintain synchrony between the timing of egg-laying and  
58 subsequent hatching of nestlings, and the increasingly early insect food peak (Torti and Dunn  
59 2005; Visser 2008), which in turn may affect population trends and even population  
60 persistence (Both et al. 2006; Møller et al. 2008; Miller-Rushing et al. 2010). Mean laying  
61 dates in temperate environments generally covary with spring temperatures (Dunn 2004;  
62 Parmesan 2007), in interaction with photoperiod (Lambrechts and Perret 2000; Gienapp et al.  
63 2010). Indoor experiments on Great Tits have suggested that temperature itself, rather than  
64 exposure to leafing trees, acts as a direct cue triggering egg-laying (Visser et al. 2009;  
65 Schaper et al. 2011). Other studies have shown that temperature Nevertheless, our  
66 understanding of how exactly temperature affects timing of egg-laying in the wild remains  
67 incomplete (Schaper et al. 2012; Caro et al. 2013). Given that neither temperature nor tree  
68 budburst are amenable to large-scale experimentation in the field, and given the high degree  
69 of temporal correlation between the two processes, the study of temporal variation has  
70 obvious limitations in further elucidating how birds finetune their timing of breeding in  
71 relation to lower trophic level phenologies (Caro et al. 2013). Moreover, remarkable  
72 differences in response to spring temperatures have been shown among populations of the  
73 same species in similar environments (Visser et al. 2003; Matthysen et al. 2011; Samplonius  
74 et al. 2018), and even among individuals within a population (Nussey et al. 2005). Thus, it  
75 seems likely that birds may use additional cues besides temperature to modulate their decision  
76 to start laying (Bison et al. 2020).

77 As an alternative to temporal variation, the study of spatial variation in synchrony between  
78 timing of breeding and tree budburst can provide valuable complementary information.  
79 Several studies have examined spatial variation in bird phenology across geographic gradients  
80 (Slagsvold 1976; Visser et al. 2003; Both et al. 2004; Møller et al. 2008; Grimm et al. 2015),  
81 but comparatively few studies have examined spatial variation in phenology at smaller scales  
82 within regions experiencing similar climates (Nilsson and Kallander 2006; Møller 2008;  
83 Bourgault et al. 2010; Dekeukeleire et al. 2019; Shutt et al. 2019). Even fewer studies have  
84 examined phenological variation within heterogeneous study sites and linked this to variation  
85 in microclimate and/or tree composition (Nager and Van Noordwijk 1995; Cole et al. 2015;  
86 Germain et al. 2015; Hinks et al. 2015; Amininasab et al. 2016). Understanding such fine-  
87 scale variation in reproductive timing is not only valuable to further our understanding of the  
88 phenological cues used by birds as well as timing constraints, but also to properly assess other  
89 sources of variation, notably estimates of additive genetic variation (Germain et al. 2016).

90 Several studies have already demonstrated that within the same forest, individual trees show  
91 consistent year-to-year variation in their relative timing of budburst (Crawley and  
92 Akhteruzzaman 1988; Van Dongen et al. 1997; Wesolowski and Rowinski 2006; Cole and  
93 Sheldon 2017; Delpierre et al. 2017) even though this may be modulated by variation in tree  
94 age (Augsburger and Bartlett 2003) and consistency may vary among species (Wesolowski  
95 and Rowinski 2006). Given this consistency and the longevity of individual trees, this implies  
96 that past variation in tree phenology can be reconstructed from present observations, allowing  
97 to link repeated observations of bird phenology over long time periods to tree phenology  
98 (Hinks et al. 2015).

99 Thus, given the importance of synchronization for breeding success (Hinks et al. 2015), we  
100 may expect birds to finetune their timing of breeding to local variation in tree phenology.  
101 Even though onset of egg laying often precedes actual budburst, making it unlikely that this is  
102 used as a direct cue (Nilsson and Kallander 2006; Schaper et al. 2011; Wesolowski and  
103 Rowinski 2014) multiple cues may be available for birds to predict local variation in  
104 budburst. For example, bud swelling may precede actual budburst by one to two weeks (Sass-  
105 Klaassen et al. 2011; Puchalka et al. 2017). Timing of individual trees can be predicted by  
106 phenology in the previous autumn (leaf senescence) (Marchand et al. 2020) when breeders  
107 may already be present on their territories. Birds might even detect volatiles emitted by  
108 developing buds (Piskorski and Dorn 2010) as they are able to do for caterpillar-infested trees  
109 (Amo et al. 2013) or birds may cue on the development of herbivores synchronized to

110 individual trees (Van Dongen et al. 1997). Finally, birds may simply use their own experience  
111 from the past breeding season (Grieco et al. 2002) or use social information from neighbours  
112 (Helm et al. 2006).

113 So far, very few studies have examined the link between bird and tree phenology at small  
114 spatial scales. The only study we are aware of is the one by Hinks et al. (2015) who found a  
115 strong correlation between Great Tit (*Parus major*) laying dates and budburst of nearby  
116 pedunculate oak trees (*Quercus robur*) in Marley Wood, UK. This area is characterized by  
117 strong spatial autocorrelation in budburst creating clusters of early and late trees. Since these  
118 clusters are of similar size as or even larger than the birds' territories, this system is highly  
119 suitable to detect synchronization of birds and trees at the local scale (Hinks et al. 2015). In  
120 the same study area, bird phenology also correlated with remote-sensing derived vegetation  
121 phenology (including multiple tree species) at a larger scale (240m resolution compared to  
122 20m) (Cole et al. 2015). However, such spatial clustering of early and late trees is not  
123 necessarily characteristic for forests in general (Wesolowski and Rowinski 2006), and the  
124 mechanisms behind individual variation in tree phenology often remain little understood  
125 (Polgar and Primack 2011; Hinks et al. 2015). Thus, more studies are required to assess the  
126 general validity of spatial synchronization between timing of bird breeding and tree budburst.

127 In this paper we present results from a long-term dataset of timing of clutch initiation in Great  
128 and Blue Tits (*Cyanistes caeruleus*) in a study plot where data are available for all mature  
129 trees on tree location (in relation to nestboxes), tree species, size and timing of budburst. We  
130 first show how tree budburst varies among tree species and show that budburst is repeatable  
131 between years at individual tree level. Secondly, we investigate whether variation in first-egg  
132 dates is explained by tree species composition (Cole et al. 2015; Szulkin et al. 2015;  
133 Amininasab et al. 2016) and/or by the timing of budburst of surrounding trees at multiple  
134 spatial scales. For this we use budburst data collected in a single year, assuming that this  
135 reflects relative tree phenology throughout the study period. Thirdly, we explore whether such  
136 effects of tree composition and/or budburst variation are reflected in habitat preference (age of  
137 birds, occupation rate, and between-year shifts in nestbox use) and ultimately in variation in  
138 nest success rates and numbers of fledged young.

139

## 140 **Materials and Methods**

### 141 ***Study area and methods***

#### 142 ***Study area and tree composition***

143 Data were collected in a study plot in northern Belgium used for a long-term population study  
144 of Blue and Great Tits since 1979. The 12-ha plot (in previous studies referred to as plot B or  
145 ‘Boswachter’; 51°16’N, 4°29’E) is part of a larger forested area of ca. 300 ha in size. It is a  
146 mixed mature broadleaved stand dominated by pedunculate oak (henceforth ‘oak’) and beech  
147 (*Fagus sylvatica*), with smaller numbers of other broadleaved trees and a few conifers. A  
148 sparse subcanopy is present, mostly consisting of black alder (*Alnus glutinosa*), rowan  
149 (*Sorbus aucuparia*), hazel (*Coryllus avellana*) and black cherry (*Prunus serotina*). The herbal  
150 layer is patchy and primarily consists of bracken (*Pteridium aquilinum*) and bramble (*Rubus*  
151 spp.). In 2010, all large trees (diameter  $\geq$  20 cm) in the plot were labelled, their diameter at  
152 breast height (DBH) measured and tree species and tree condition noted. In 2017, a full  
153 resurvey of all labelled trees in the plot, with detailed tree positioning was performed using  
154 Field-Map™ technology (www.fieldmap.cz, Kovacsova and Antalova 2010). All tree  
155 diameters were also remeasured. The final dataset included 1558 individual standing trees  
156 (alive or dead) in 2017. Of these 1558 trees the majority were oak (73%) and beech (17%),  
157 with small numbers of northern red oak *Quercus rubra* (2.7%), silver birch *Betula pendula*  
158 (2.0%), black alder (1.3%), hornbeam *Carpinus betulus* (0.8%), Norway spruce *Picea abies*  
159 (0.7%) and larch *Larix decidua* (0.7%), none of the remaining species accounting for more  
160 than 0.3% (Fig. 1, Online Resource Table S1).

#### 161 ***Budburst data***

162 Budburst data were collected for all deciduous trees in 2010, and for a selection of trees in  
163 2009 and 2017. In 2010, all trees were visited 5-6 times between 23 March and 19 May, with  
164 most frequent observations (three visits per tree) between 22 April and 6 May. Leaving out  
165 dead trees and conifers, the dataset comprised 1396 individual trees. One overall score was  
166 given per tree, on a scale from 0 to 6 (Online Resource Fig. S2). After inspection of the data,  
167 we chose to define budburst date as the first observation day when the tree reached score 4.  
168 For trees where score 4 was missing we interpolated between the dates when the nearest  
169 scores were recorded (e.g. when scores 3 and 5 were recorded but not 4, we used the middle

170 date between them). For the earliest trees where the first observed score was 5, we arbitrarily  
171 assigned budburst date two days earlier; for very late trees that had 3.5 as the maximum score,  
172 two days later. Six trees that reached a maximum score of 1 or 2 or showed no budburst at all,  
173 were given a missing value; four of these trees were probably already in very poor condition  
174 as they turned out to be dead in 2017. In 2009 we recorded budburst on a single date and only  
175 for a subset of trees holding nestboxes (20 april, 117 trees). On 21 april 2017 budburst was  
176 recorded again for most of these trees (N = 100).

177 Since results indicated that the relative timing of oak and beech trees differed between years,  
178 we consulted an external dataset for information on the relative timing of oak and beech over  
179 a larger span of years (Demolder et al. 2017). This information was used to test whether  
180 annual variation in the relative timing of oak versus beech could affect the relative timing of  
181 bird phenology in territories with more oak or beech trees. The data were collected since 2003  
182 for ca. 40 trees of each species in two large forested areas (Meerdaalbos and Zoniënwood)  
183 both at ca. 50km from the study area. From these data we derived for each year a value for the  
184 relative onset of leaf development of oak versus beech, which varied between 14 days in 2006  
185 and minus 7 days in 2012 (a negative value indicates that oaks were earlier than beech).

### 186 ***Bird breeding data***

187 From 1997 to 2017, a constant set of 118 nestboxes were operational in the study plot. A third  
188 of these had small (26mm) entrances (evenly spaced across the plot) allowing access to Blue  
189 Tits only (Dhondt and Adriaensen 1999) (Fig. 1). Due to irregular spacing of the boxes, the  
190 minimum distance between neighbouring boxes varied between 5 and 44m. Nestboxes were  
191 visited approximately weekly from the onset of nest-building. First-egg dates were estimated  
192 from the first observation of a partially laid clutch, assuming one egg was laid per day. Only  
193 first clutches were included in the study, discarding second clutches or replacement clutches.  
194 All laying dates are expressed as days since the 1<sup>st</sup> of March. Occupation rates (disregarding  
195 nestbox type) were rather low with on average 25% for Great Tits and 28% for Blue Tits,  
196 based on all first clutches, including unidentified females. Occupation rates of the two types  
197 were very similar (51 and 53% for small and large entrances, respectively) reflecting the high  
198 proportion of Blue Tits breeding in large-entrance holes. We captured 80 to 90% of all parents  
199 on the nest when feeding 8-day old nestlings, but also recorded the identities of many females  
200 while incubating. Their age (first breeding season, or older) was derived from lifetime capture  
201 histories and/or based on plumage. Nestlings were ringed close to fledging when they were

202 approximately two weeks old and their body mass was measured to the nearest 0.1g (either  
203 individually, or total brood mass divided by number of nestlings). The majority of females  
204 (75% of individuals used in this study, N = 778) used only a single nestbox for breeding in  
205 their lifetime; for others this ranged from two to five. Clutches laid by unknown females were  
206 excluded from the study (19.1% and 16.4% of Blue and Great Tits, respectively). Most of  
207 these were deserted or otherwise did not hatch any young (64 and 69% respectively); the  
208 proportion of unknown females among nests with hatched young was therefore much lower  
209 (6.9 and 5.1% respectively). There was no significant difference in laying dates between  
210 known and unknown females (model with fixed species and random year effect,  $t_{1269} = 1.76$ ,  $P$   
211  $= 0.08$ ) with unknown females laying on average 0.68 ( $\pm$  SE 0.39) days later. The final dataset  
212 contained 553 first clutches of Blue Tit, and 509 of Great Tit. The total number of first  
213 clutches per nestbox over the study period varied between 2 and 17. Basic breeding and  
214 population data for each species are reported in Table 1.

### 215 ***Tree characteristics around focal nestboxes***

216 Since we had no data on actual territory boundaries, we used two different approaches to link  
217 breeding data with characteristics of nearby trees (species, size and budburst date), in line  
218 with earlier studies (Wilkin et al. 2007; Hinks et al. 2015). In the first approach we linked  
219 nestboxes with the surrounding trees regardless of the position of nearby occupied nests,  
220 assuming that birds would time their breeding to the characteristics of surrounding trees, and  
221 not necessarily trees inside their own territory. We considered three different distances: 15, 25  
222 and 35m. We chose this distance range because most nestboxes had only a few trees within  
223 10m distance. On the other hand, nests were typically between 25 and 75m from the nearest  
224 occupied nest of the same species. This approach resulted, for each radius, in a single set of  
225 tree characteristics for each nestbox throughout the study ('nestbox variables'). However, this  
226 approach neglects the fact that occupation rates varied strongly throughout the study, and thus  
227 both the size and position of territories used by the breeding pair could differ substantially  
228 between years. Therefore, in a second approach we assigned trees to putative territories  
229 approximated by Thiessen polygons, in line with previous studies (Wilkin et al. 2007;  
230 Schlicht et al. 2014; Hinks et al. 2015). Here we assume that timing of breeding is influenced  
231 by trees within the pair's estimated territory. Within each year, all trees were allocated to the  
232 nearest occupied nestbox. We did this allocation independently for Great Tits and Blue Tits as  
233 these do not show interspecific aggression when territories overlap, even though there is some

234 exploitative competition for food affecting reproductive success (Dhondt 2012; Gamelon et  
235 al. 2019). In order to avoid unrealistically large territories in low-density years and/or parts of  
236 the area with low occupation, we set a maximum cut-off distance at either 25 or 35m  
237 (Schlicht et al. 2014)). We did not include a lower cut-off distance (e.g. 15m) because at this  
238 short distance there was hardly any difference with tree characteristics within a fixed 15m  
239 radius. This approach resulted in different values for tree composition per nestbox and year  
240 ('territory variables').

241 In both approaches, we characterized tree composition by summing basal area (calculated  
242 from tree diameter at breast height) per tree species (including the nestbox tree) and expressed  
243 this relative to the total basal area summed across all tree species. The latter was done to  
244 allow comparison between the 'territory' and 'nestbox' approaches, and because we were  
245 interested in the role of tree species composition and phenology rather than overall tree  
246 density. We included all trees recorded in 2010, regardless of their condition in 2017 (dead or  
247 alive) since most tree deaths occurred in the last third of the study period (i.e. after 2010).  
248 Since relative basal areas of the most common tree species were significantly correlated, we  
249 performed a Principal Component Analysis on basal areas for the four most common tree  
250 species (oak, beech, red oak and alder) as well as the combined values for birch (*Betula spp.*)  
251 and conifers (several species). This was done at the three scales mentioned above for the  
252 nestbox approach and for the two cut-off distances for the territory approach. Results were  
253 very similar for all five PCA analyses (Online Resource section S3), with a first axis  
254 contrasting the abundance of oak versus beech, the second mostly reflecting the abundance of  
255 birch and/or conifers versus other tree species, and the third reflecting the abundance of red  
256 oak. Since the latter had an eigenvalue only slightly above one and represented a single and  
257 not very abundant tree species, we did not consider it further.

258 For budburst data, we similarly calculated the mean budburst date of all trees within the  
259 radius (nestbox-level) or within the putative territory (territory-level) as we did for tree  
260 species composition. For this we only used the data of 2010, assuming that these reflect the  
261 relative timing of trees throughout the study period. We also calculated the mean for oak and  
262 beech trees separately. In addition, we calculated the percentage of early trees, to test the  
263 hypothesis that laying date would be affected by the earliest trees rather than by average  
264 budburst. 'Early trees' were identified based on the frequency distribution of budburst for all  
265 trees (Online Resource Fig. S4). This showed that a large number of trees (about one third) all  
266 had their budburst within a few days (from 27 to 30 April) while before this date there was

267 more variation. Therefore we considered early trees as those having budburst up until 26  
268 April. These represented 26% of all trees, but only 10% of oaks (Online Resource Fig. S4).  
269 Overall, correlations between the nestbox-level and territory-level characteristics were high  
270 (Pearson's  $r$  from 0.86 to 0.98,  $N = 1355$ ). As expected, correlations were somewhat higher  
271 for the 25m distance comparisons, than for the 35m comparisons (details not shown).

## 272 ***Statistical analysis***

273 All analyses were performed in SAS v9.4 (SAS Institute, Cary, NC). Principal Component  
274 Analysis was performed using proc PRINCOMP and spatial autocorrelation of tree budburst  
275 with proc VARIOGRAM.

276 We used generalized linear mixed models (proc MIXED) to model variation in laying date in  
277 relation to local tree composition and mean budburst. All linear models were run with normal  
278 error structure, and residuals were checked for normality. We ran separate models using either  
279 tree variables at nestbox level (one value per nestbox) or at territory level (one value per  
280 nestbox per year; see above) (overview in Online Resource Table S5). Species were analysed  
281 separately but to verify differences in outcomes we ran additional models on the joint dataset  
282 to test for interactions between species and the variable of interest. All models included age  
283 of female (first-year or older; cf. Jarvinen 1991; Reed et al. 2013) as fixed effect, and year,  
284 nestbox and female ID as random effects. For tree composition we always included the first  
285 two axes of the PCA.

286 Inspection of the data showed that the first axis of tree composition was highly correlated  
287 with mean budburst date of all trees, for all distances considered (Pearson's  $r = 0.55$  to  $0.63$ ,  
288  $N = 118$  nestboxes; see also Online Resource Table S6). Therefore we did not include these  
289 variables in the same model. In a first set of models (1-6; Online Resource Table S5) we  
290 included all nestboxes and analyzed laying date in relation to either local tree composition or  
291 mean budburst date, and repeated this at three different scales (15m, 25m, 35m). In the  
292 second set of models (7-9) we focused on territories dominated by oak trees, since these are  
293 by far the most common trees in the study area. Here we only included nestboxes if at least  
294 50% of the basal area (within the relevant distance class) consisted of oaks. In these models  
295 we used mean budburst of oak trees as explanatory variable, as well as the two tree  
296 composition variables, since these were not correlated (all  $r$  between  $0.05$  and  $-0.13$ ). All  
297 previously described models were run again at the territory level instead of nestbox level,

298 with cut-off distances of 25m and 35m (see above) (models 10-15). Model results were  
299 compared with a null model without any data on tree composition or budburst (but containing  
300 female age as well as the above mentioned random effects).

301 We also tested alternative models using data from older birds only (not in Table S5), to test  
302 the hypothesis that birds would need a learning phase to adjust their timing to local tree  
303 phenology (Nager and Van Noordwijk 1995; Grieco et al. 2002), and hence the influence of  
304 tree phenology might be only or more clearly expressed in older birds. We also re-ran all  
305 models using the percentage of early trees (defined as above) instead of mean budburst date.  
306 Since neither of these models showed any substantial difference with the outcomes of the  
307 main models, we will not report any of the details.

308 For additional analyses we also used linear models either using PROC MIXED or PROC  
309 GLIMMIX for non-normal error distributions, as explained in the results.

310

## 311 **Results**

### 312 ***Variation in budburst***

313 In 2010, trees reached a budburst score of 4 on average on 29 April (i.e. day 58; SD = 7.7, N  
314 = 1396) with an estimated range from 31 March to 21 May (Online Resource Fig. S4). There  
315 were significant differences among tree species ( $F_{4,1356} = 163.4$ ,  $P < 0.001$ ) with birches being  
316 earliest (16 April on average), followed by red oaks (20 April), alders (24 April), beeches (25  
317 April) and oaks, the latter being considerably later than all others (on average 3 May; all  
318 species comparisons  $P < 0.05$  except red oak – alder and alder - beech) (Online Resource Fig.  
319 S7).

320 Relative timing of budburst of individual trees was repeatable among years, as shown by  
321 highly significant correlations between the estimated budburst date in 2010 and the budburst  
322 score on a single date in either 2009 or 2017 (Table 1). Fig. 2 illustrates this with the  
323 correlation for oak trees between 2009 and 2010. Correlations were substantially stronger for  
324 oak trees only than for all tree species combined, reflecting that timing of tree species differed  
325 among years (Table 1). Notably, beech trees were on average earlier than oaks in 2009 and  
326 2010, but later in 2017 (details not shown).

327 Spatial autocorrelation in budburst date was weak for all tree species combined (Moran's I =  
328 0.05, Geary's c = 0.96; both  $P < 0.001$ ) and close to non-existent when only considering oaks  
329 (Moran's I = 0.017,  $P < 0.01$ ; Geary's c = 0.986,  $P > 0.3$ ) (Online Resource Table S8).

### 330 ***Variation in laying date***

331 Annual laying dates varied between 2 and 28 April per year and species with an overall mean  
332 of 13 April for Blue Tits, and 16 April for Great Tits (Table 2). Within a year and species,  
333 laying dates typically ranged over a period of two to three weeks. In 2010, the year when  
334 detailed budburst data were collected, mean laying dates were 14 and 15 April, respectively.  
335 At that time most trees were still in the initial stages of budburst or had not yet commenced,  
336 as the proportion of trees with a score of at least one (visible bud swelling) was only 20% on  
337 8 April and still only 66% on the next scoring visit on 22 April (n = 600 and 469 trees  
338 scored).

339 While a long-term advancement of laying date has been documented in this population for  
340 both species since 1979 (Visser et al. 2003; Matthysen et al. 2011), there was no significant  
341 change over the time period in this study (Matthysen, unpubl. data).

342 All models of laying date showed highly significant effects of female age ( $P < 0.001$  in nearly  
343 all models; see Table 3 for estimates in the best model). As expected from earlier work on the  
344 same population (Matthysen et al. 2011) older females started laying on average one to one  
345 and a half day earlier in both species.

346

### 347 ***Correlations between laying date, tree composition and budburst***

348 In the Great Tit, none of the models showed any significant contribution of tree composition  
349 or mean budburst date at any of the specified scales, neither at the nestbox level or at the  
350 territory level (all  $P$ -values  $> 0.5$ ). Consequently, the best model for Great Tits with the lowest  
351 AICc value was the null model with age as the only fixed effect (Online Resource Table S9).

352 For Blue Tits, none of the models showed any significant contribution of mean budburst date  
353 (all  $P > 0.1$ ). Most models showed significant contributions of the first principal component of  
354 tree composition (Online Resource Table S9); not surprisingly, these were in particular the  
355 models that included all nestboxes (i.e. not restricted to nestboxes surrounded by oaks). A few  
356 models showed a weak but non-significant contribution of the second principal component of  
357 tree composition ( $P = 0.06$  to  $0.07$ ). Regression coefficients for tree composition were  
358 negative in all cases, showing overall strong support for earlier laying in nestboxes  
359 surrounded by more oak trees (PC1) and much weaker support for earlier laying when  
360 surrounded by more birches and conifers (PC2). The best model for Blue Tits included tree  
361 composition in a 25m radius around the nestbox (Online Resource Table S9). This model  
362 performed considerably better than the null model containing only female age as fixed effect  
363 ( $\Delta\text{AICc} = 10.3$ ) and also better than similar models with tree composition within 15 and 35m  
364 ( $\Delta\text{AICc} = 3.3$  and  $2.6$ , respectively). The model was also highly similar to the territory-level  
365 model with 25-m level cut-off ( $\Delta\text{AICc} = 0.6$ ). This is not surprising since the PC1 values at  
366 nestbox and territory level were highly correlated at this distance ( $r = 0.986$ ). Since the  
367 contribution of PC2 was not significant in either model, we removed PC2 and again found  
368 slightly better support for the nestbox-level model than the territory-level model ( $\Delta\text{AICc} =$   
369  $1.6$ ). We thus chose the model with tree composition within a fixed 25m radius as the best

370 model for Blue Tits (details in Table 3). According to this model, laying dates advanced with  
371 about 2.5 days over the entire range of tree composition (Fig. 3). The difference between Blue  
372 and Great Tits was partially confirmed by a joint model which showed a nearly significant  
373 interaction between species and tree composition ( $F_{1,545} = 3.11$ ,  $P = 0.078$ ; this model also  
374 included a random year\*species term). In all further analyses, unless otherwise mentioned,  
375 tree species composition refers to the first principal component in a fixed 25m radius.

### 376 ***Further analyses on tree composition***

377 We explored the effect of tree species composition on Blue Tits in more detail by replacing  
378 tree composition with basal area of either oak or beech within 25m. This showed that either  
379 tree species explained significant variation in laying date (both  $P < 0.001$ ), which is not  
380 surprising given the high correlation ( $r = -0.88$ ). We further tested whether the effect of tree  
381 composition on laying date was modulated by the relative timing of oak versus beech.  
382 Specifically, we predicted that the later laying in beech-dominated territories would be less  
383 pronounced or even reversed in years when beech trees were particularly early. We tested this  
384 by adding the annual timing difference between beech and oak ('beech earliness') from a  
385 different study area (see Methods) to the final Blue Tit model (only for years 2003-2017).  
386 This showed that overall, laying dates were later in years when oaks were relatively late  
387 compared to beeches ( $F_{1,12.9} = 15.2$ ,  $P = 0.002$ ). The main effect of tree composition was also  
388 maintained ( $F_{1,114} = 6.9$ ,  $P = 0.01$ ), but in contrast to our prediction, there was no interaction  
389 between local tree composition and beech earliness ( $F_{1,280} = 0.00$ ,  $P > 0.9$ ). Finally, since  
390 earlier analyses showed that laying dates advanced progressively throughout the study period,  
391 we tested whether the relative timing in oak versus beech territories also changed over the  
392 study period; indeed we found a significant advancement of laying date over time (year  
393 included as continuous variable:  $F_{1,548} = 19.0$ ,  $P < 0.001$ ) but no interaction between tree  
394 composition and time ( $F_{1,548} = 0.9$ ,  $P > 0.3$ ).

### 395 ***Habitat selection and fitness***

396 For additional analyses on habitat selection and fitness in relation to tree composition, we  
397 focused on Blue Tits but will give some results on Great Tits for comparison only. First we  
398 checked whether effects of tree composition could be biased by age-dependent occupation of  
399 territories. This was not the case, as mean tree composition did not differ between young and  
400 older female Blue Tits at the population level (GLMM with tree composition as dependent

401 variable, individual age class (first year or older) as fixed effect, and year and bird identity as  
402 random effects;  $F_{1,385} = 0.0$ ,  $P > 0.9$ ). We also found no preferential shift by individual  
403 females towards nestboxes with more oaks, using a paired test on females that changed their  
404 nestbox location from the first to the second breeding season ( $N = 63$ ; paired t-test,  $t = -0.41$ ,  $P$   
405  $> 0.6$ ). Tree composition also did not predict Blue Tit occupation rate per nestbox (proportion  
406 of years with a first clutch; GLMM with poisson error,  $F_{1,115} = 0.2$ ,  $P = 0.6$ ).

407 Analyses on reproductive success showed that Blue Tit brood loss (i.e. the proportion of nests  
408 without any fledged young) was higher in territories with fewer oaks and more beeches within  
409 25m (Online Resource Table S10). This was largely explained by the effect on losses in the  
410 nestling stage, while for pre-hatching losses there was a weaker and non-significant trend  
411 (Online Resource Table S10). Closer examination of the data with respect to actual tree  
412 composition showed that nests with post-hatching brood loss were surrounded on average by  
413 fewer oaks ( $16.0 \pm 5.5$  versus  $17.3 \pm 5.1$ ;  $n = 34$  and  $515$ ) but in particular by more beech  
414 trees ( $6.0 \pm 4.0$  versus  $3.3 \pm 3.5$ ). We found no effect of tree composition on number of  
415 fledglings or mean fledgling mass, although it did affect clutch size with larger clutches in  
416 territories with more oaks ( $p = 0.03$ ; Online Resource Table S10). For comparison, the same  
417 analyses in Great Tits showed no relationships at all between breeding success and tree  
418 composition (all  $P > 0.7$ ; details not shown).

419 Finally, we tested whether the effect of tree composition on Blue Tit brood loss (post-  
420 hatching) was modulated by nests being early or late, by adding laying date to the model  
421 (centered within years). Early nests had lower failure rates ( $F_{1,545} = 5.09$ ,  $P = 0.02$ ) while the  
422 effect of tree composition remained highly significant ( $P = 0.002$ ) but there was no interaction  
423 with tree composition ( $P > 0.9$ ). Similar results were found for the model on overall nest  
424 failure that included unknown females as well (interaction term  $P > 0.3$ ).

425

426

## 427 **Discussion**

428 In this study we show that fine-scale variation in timing of budburst of individual trees does  
429 not explain variation in laying date in either Great Tits or Blue Tits. However, variation in  
430 local tree composition does explain variation in Blue Tit laying dates, with later first-egg  
431 dates in territories containing fewer oaks and more beech trees.

### 432 ***Tree phenology***

433 While multiple studies have investigated phenology of individual trees, we are aware of few  
434 studies that have mapped budburst timing of individual trees at the level of entire stands. We  
435 found high between-year consistency in the relative timing of budburst of individual trees,  
436 confirming previous studies on pedunculate oak (Crawley and Akhteruzzaman 1988; Hinks et  
437 al. 2015; Delpierre et al. 2017) as well as other tree species (Wesolowski and Rowinski 2006;  
438 Cole and Sheldon 2017). This individual consistency was most pronounced when only oak  
439 trees were considered. The lower repeatability for all tree species combined can be explained  
440 by shifts in relative timing among tree species between years; indeed, beech trees also showed  
441 significant repeatability in budburst between years, but the relative timing of oak and beech  
442 trees varied among years. These findings are in agreement with Delpierre et al. (2017) who  
443 also showed comparable repeatability values for pedunculate oak, red oak and beech, while  
444 Wesolowski and Rowinski (2006) found higher repeatability in oaks than other broadleaved  
445 trees. The fact that we found high repeatabilities of budburst (at least within species) and over  
446 multiple years strongly supports our assumption that relative timing of trees within one study  
447 year may be extrapolated over longer time periods, and allows us to use long-term population  
448 data to examine bird-tree synchrony.

449 In contrast to Hinks et al. (2015), however, we did not find any spatial autocorrelation in  
450 timing of neighbouring trees, thus no clustering of trees with synchronous phenology. This  
451 can be explained by both abiotic and biotic differences between our study area and the Marley  
452 Wood site studied by Hinks et al. (2015). Our study area is comparatively small with a flat  
453 topography and homogeneous soil conditions, while the Wytham Woods of which Marley  
454 Wood is a part, is a larger forest with a complex geology and topography, showing more than  
455 100m difference in elevation between high and low parts (Wilkin et al. 2007). Moreover, oak  
456 tree density in Marley Wood is much lower with few but very large oaks interspersed in other  
457 vegetation; according to Hinks et al. (2015) only 118 trees were monitored in a 28-ha forest,

458 compared to over 1000 trees in our 12-ha study area. Topography and tree density in our  
459 study area are more in line with the study area in Białowieża forest analysed by Wesolowski  
460 et al. (2006) where there was no spatial concordance in the timing of different tree species.  
461 The latter study does not provide details, however, on local patterns of phenology of  
462 neighbouring trees of the same species, particularly oak trees.

463 Finally, there are detailed historic sources confirming that the oak and beech trees at the forest  
464 site in study were originally planted. For the oaks, written sources dating back as far as the  
465 beginning of the 15<sup>th</sup> century mention both local breeding and purchase of oak saplings; for  
466 beech this is the case from the 18<sup>th</sup> century onwards (Adriaenssens and Verheyen 2013). This  
467 may have led to a mixture of trees with different regional provenances and different  
468 phenology.

### 469 ***Variation in laying date***

470 We did not find any evidence for spatial synchrony between laying dates and budburst of  
471 trees surrounding individual nestboxes. This lack of synchrony contrasts with several other  
472 studies (Møller 2008; Bourgault et al. 2010; Cole et al. 2015; Hinks et al. 2015). However, all  
473 of these studies were performed in substantially different conditions from ours. Møller et al.  
474 (2008) examined the relation between barn swallows (*Hirundo rustica*) and local tree and  
475 flower phenology by comparing colonies across farms in a large study area (45 km<sup>2</sup>).  
476 Bourgault et al. (2010) found a strong correlation between oak phenology and Blue Tit laying  
477 dates by comparing forest stands at different elevations in Corsica. The only studies we know  
478 of that have looked at bird-tree synchrony at the level of individual nests were both done on  
479 Great Tits in Wytham Woods (Cole et al. 2015; Hinks et al. 2015). Hinks et al. (2015) found a  
480 significant correlation between laying date and oak budburst at a small scale (20m) in an area  
481 showing strong spatial autocorrelation in oak budburst, as mentioned earlier. In the same  
482 forest and at a somewhat lower resolution (240m), Cole et al. (2015) found that the degree of  
483 phenological matching between Great Tits and tree budburst depended on local tree  
484 composition, being particularly strong in areas dominated by pedunculate oak and hazel.

485 The absence of spatial synchronization in our study may be explained by the near absence of  
486 spatial clustering in phenology; thus, most nestboxes were surrounded by a mixture of early  
487 and late trees, and most breeding birds would be exposed to an intermediate environment in  
488 terms of tree budburst. So both from a proximate (available cues) and ultimate (available trees  
489 for foraging) perspective, we could expect synchronization to be low compared to a forest

490 with clustering of early and late trees. Nevertheless, even if trees are mixed more or less  
491 randomly, there is still variation among territories in average timing of budburst, especially at  
492 small scales. One could argue that birds may not adjust their timing to the average phenology  
493 but, for example, only to the earliest trees. However, we did not find any difference in our  
494 results when replacing average budburst date with a measure of the proportion of early trees  
495 in the territory.

496 An alternative explanation for the lack of spatial synchrony is that birds do not respond  
497 directly to individual tree phenology but to other cues predicting local tree budburst, notably  
498 variation in microclimate. Aviary experiments have indeed shown that an increase in  
499 temperature, but not exposure to leafing branches, induces Great Tits to lay earlier (Visser et  
500 al. 2009; Schaper et al. 2011; Schaper et al. 2012). This would imply that the spatial matching  
501 between bird laying and tree phenology found in other studies may be driven by  
502 microclimatic factors that affect both bird and tree phenology. However, the spatial synchrony  
503 between Great Tit laying and oak budburst in Marley Wood could not be explained by  
504 temperature or elevational differences (Hinks et al. 2015). A study on Blue Tits in deciduous  
505 forest also suggested that vegetation and/or insect phenology, rather than temperature itself,  
506 set the cue for timing of breeding across years (Thomas et al. 2010). Thus, more research is  
507 needed to elucidate the cues driving small-scale variation in phenology at individual nest  
508 level.

509 One general implication of our finding is that within this particular study area, females appear  
510 to have limited options in achieving phenological synchrony by shifting towards sites with  
511 earlier or later phenology. Previous analyses in our population and others (Charmantier et al.  
512 2008; Matthysen et al. 2011; Vedder et al. 2013) have shown considerable among-year  
513 plasticity in individual females that allows them to track annual changes in tree and caterpillar  
514 phenology. Clearly, females at this research plot will not be able to enhance their synchrony  
515 by moving into earlier territories in warm springs.

### 516 ***Laying date and tree composition***

517 Consistent variation in laying date among forest types has been very well documented in hole-  
518 nesters, in relation to factors such as general tree species composition (Nilsson and Kallander  
519 2006; Szulkin et al. 2015), evergreenness (Bourgault et al. 2010; Szulkin et al. 2015),  
520 elevation (Nager and Van Noordwijk 1995) and urbanization (Dhondt et al. 1984;  
521 Chamberlain et al. 2009; Vaugoyeau et al. 2016) but typically this variation has been studied

522 at the between-site rather than the within-site level. Some exceptions are the studies by  
523 Szulkin et al. (2015) who found a correlation between Blue Tit laying and local variation in  
524 evergreen versus deciduous trees, by Wilkin et al. (2007) who found that Great Tits laid  
525 earlier in oak-dominated, more south-facing and low-altitude territories within Wytham  
526 Woods, and by Arriero et al. (2006) showing later laying by Blue Tits in territories with more  
527 immature or degraded oaks. Our finding that Blue Tits started laying earlier in nestboxes with  
528 more mature oak trees nearby is in agreement with at least two other studies in mixed  
529 temperate forests on Blue and Great Tits, respectively (Wilkin et al. 2007; Amininasab et al.  
530 2016). Dekeukeleire et al. (2019) could not demonstrate such an effect of tree composition on  
531 Great and Blue Tit laying dates in similar stands in Belgium as the ones we studied,  
532 dominated by pedunculate oak, red oak and beech; however, their raw data show a similar  
533 pattern as our study, with on average 4-5 days earlier laying in pure pedunculate oak stands  
534 versus pure beech stands, and mixed stands being intermediate. The lack of significant  
535 variation between their stand types may be explained by the inclusion of many different  
536 intermediate stand types in their study (Dekeukeleire et al. 2019) which reduced the statistical  
537 power. The effect size is somewhat larger than in our study, probably because our study are is  
538 more mixed without stands of pure oak or beech.

539 We have no clear explanation of why laying is earlier in oak-dominated versus beech-  
540 dominated territories. This is clearly not explained by species-specific differences in budburst  
541 (cf. Bourgault et al. 2010; Cole et al. 2015), since beech trees were earlier in most years.  
542 Moreover, the difference between oak- and beech-dominated territories was unrelated to the  
543 relative timing of oak versus beech trees in general. We also did not find that later laying in  
544 beech-dominated areas would confer an advantage, since there was no interaction between  
545 effects of laying date and tree composition on breeding success. Thus, we cannot show that  
546 this variation in timing is adaptive.

547 An alternative hypothesis would be that Blue Tit females breed later in beech-dominated  
548 territories because these are sites of intrinsically lower food quality, and therefore attract  
549 females of lower phenotypic quality. This is supported to some extent by the lower failure rate  
550 in territories with more oaks and fewer beech trees. This would agree with other studies  
551 showing higher breeding success in forest stands or territories with a higher proportion of  
552 oaks (Wilkin et al. 2009; Dekeukeleire et al. 2019). However, we note that the actual  
553 difference in number of oak trees between successful and failed territories was rather small,  
554 and that this difference seems to be driven more strongly by the number of beech rather than

555 oak trees. In addition, we found no association between female age and tree composition, nor  
556 preferential shifts towards territories with more oaks by individual females. Moreover,  
557 territories with more beech trees did not have broods with lower fledgling mass, which is  
558 generally accepted as a proxy of food availability and a predictor of brood fitness (Tinbergen  
559 and Boerlijst 1990; Matthysen et al. 2011). It is possible that females in territories with more  
560 beech are constrained to lay early due to lower food availability early in the season, as  
561 suggested by Wilkin et al. (2007) for Great Tits. Some support for this is given by the smaller  
562 clutch size in Blue Tit territories with more beech trees, but it does not explain why such  
563 territories had higher failures in the post- rather than the pre-hatching stage. By lack of data  
564 on female foraging or condition in the egg-laying stage, we cannot test this hypothesis further.  
565 We also have no clear explanation why Blue, but not Great Tits, delayed egg-laying in  
566 territories with more beech trees. The two species are known to differ in foraging ecology  
567 including tree species, tree parts and prey size (Gibb 1954; Betts 1955; Nour et al. 1998;  
568 Slagsvold and Wiebe 2007). A recent study found Blue Tits to be more selective than Great  
569 Tits in their choice of tree species in an urban environment, but neither species favoured oaks  
570 in particular, and there was no clear link with breeding success (Mackenzie et al. 2014). There  
571 is also no clear difference in home range size, although this has rarely been studied  
572 (Naefdaenzer 1994), and if anything Blue Tits may have larger home ranges (Mackenzie et al.  
573 2014).

574 Regardless of its causation, the fact that Great and Blue Tit respond differently to habitat  
575 variation in terms of laying date has been reported earlier based on comparisons among  
576 multiple forest types (Dhondt et al. 1984). Surprisingly, however, and despite the large  
577 number of publications on breeding biology of each species, very few studies have addressed  
578 these differences between Great and Blue Tits in recent decades. Dhondt et al. (1984) found  
579 that Great and Blue Tit varied in the relative order of timing between habitats along a rural to  
580 urban gradient. In an analysis across Europe, Vaugoyeau et al. (2016) also found habitat-  
581 related differences between the species, with Great Tits showing overall stronger variation  
582 and being particularly late in coniferous habitat, while Blue Tits were even later in evergreen  
583 habitat. It should be noted however, that this study included many sites where only one of the  
584 species was reported. Nilsson & Källander (2006) found no differences between the two  
585 species in their relative timing in oak/birch or coastal/inland sites. A few studies have also  
586 reported differential responses over time of the two species in relation to spring temperature  
587 (Wesolowski and Cholewa 2009; Vatka et al. 2014). In our own study population, however,

588 we showed earlier that Great and Blue Tits showed highly similar responses (Matthysen et al.  
589 2011).

## 590 **Acknowledgements**

591 We are grateful to numerous students and field assistants that contributed to the data  
592 collection, with special thanks to Diederik De Bruyn, Frans Fierens and Joris Elst. Marc  
593 Esprit and Stefaan Goessens (INBO) produced the detailed tree positioning map of the  
594 research site, that allowed us to carry out the spatial analysis.

595 Funding was provided by a sabbatical leave grant of the University of Antwerp (BOF)  
596 awarded to EM.

597 The authors declare that they have no conflict of interest.

598

## 599 **References**

- 600 Adriaenssens F, Verheyen K (2013) Oude bossen van de Antwerpse Kempen [Ancient  
601 woodlands of the Antwerp Campine Region]. . Davidsfonds Publishing, Leuven
- 602 Amininasab SM et al. (2016) Influence of fine-scale habitat structure on nest-site occupancy,  
603 laying date and clutch size in Blue Tits *Cyanistes caeruleus*. *Acta Oecologica-*  
604 *International Journal of Ecology* 70:37-44. doi: 10.1016/j.actao.2015.11.006
- 605 Amo L, Jansen JJ, van Dam NM, Dicke M, Visser ME (2013) Birds exploit herbivore-  
606 induced plant volatiles to locate herbivorous prey. *Ecol. Lett.* 16:1348-1355. doi:  
607 10.1111/ele.12177
- 608 Arriero E, Sanz JJ, Romero-Pujante M (2006) Habitat structure in Mediterranean deciduous  
609 oak forests in relation to reproductive success in the Blue Tit *Parus caeruleus*. *Bird*  
610 *Study* 53:12-19. doi: 10.1080/00063650609461411
- 611 Augspurger CK, Bartlett EA (2003) Differences in leaf phenology between juvenile and adult  
612 trees in a temperate deciduous forest. *Tree Physiology* 23:517-525. doi:  
613 10.1093/treephys/23.8.517
- 614 Betts MM (1955) The food of titmice in oak woodland. *J. Anim. Ecol.* 24:282-323. doi:  
615 10.2307/1715
- 616 Bison M et al. (2020) Best environmental predictors of breeding phenology differ with  
617 elevation in a common woodland bird species. *Ecology and Evolution* 10:10219-  
618 10229. doi: 10.1002/ece3.6684
- 619 Both C et al. (2004) Large-scale geographical variation confirms that climate change causes  
620 birds to lay earlier. *Proceedings of the Royal Society of London Series B-Biological*  
621 *Sciences* 271:1657-1662. doi: doi.org/10.1098/rspb.2004.2770

- 622 Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines  
623 in a long-distance migratory bird. *Nature* 441:81-83. doi: doi.org/10.1038/nature04539
- 624 Bourgault P, Thomas D, Perret P, Blondel J (2010) Spring vegetation phenology is a robust  
625 predictor of breeding date across broad landscapes: a multi-site approach using the  
626 Corsican blue tit (*Cyanistes caeruleus*). *Oecologia* 162:885-892. doi: 10.1007/s00442-  
627 009-1545-0
- 628 Caro SP, Schaper SV, Hut RA, Ball GF, Visser ME (2013) The case of the missing  
629 mechanism: how does temperature influence seasonal timing in endotherms? *Plos*  
630 *Biology* 11:8. doi: 10.1371/journal.pbio.1001517
- 631 Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ (2009) Avian  
632 productivity in urban landscapes: a review and meta-analysis. *Ibis* 151:1-18. doi: DOI  
633 10.1111/j.1474-919X.2008.00899.x
- 634 Charmantier A, Gienapp P (2014) Climate change and timing of avian breeding and  
635 migration: evolutionary versus plastic changes. *Evolutionary Applications* 7:15-28.  
636 doi: 10.1111/eva.12126
- 637 Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LEB, Sheldon BC (2008) Adaptive  
638 phenotypic plasticity in response to climate change in a wild bird population. *Science*  
639 320:800-803. doi: 10.1126/science.1157174
- 640 Cole EF, Long PR, Zelazowski P, Szulkin M, Sheldon BC (2015) Predicting bird phenology  
641 from space: satellite-derived vegetation green-up signal uncovers spatial variation in  
642 phenological synchrony between birds and their environment. *Ecology and Evolution*  
643 5:5057-5074. doi: 10.1002/ece3.1745
- 644 Cole EF, Sheldon BC (2017) The shifting phenological landscape: Within- and between-  
645 species variation in leaf emergence in a mixed-deciduous woodland. *Ecology and*  
646 *Evolution* 7:1135-1147. doi: 10.1002/ece3.2718
- 647 Crawley MJ, Akhteruzzaman M (1988) Individual variation in the phenology of oak trees and  
648 its consequences for herbivorous insects. *Functional Ecology* 2:409-415. doi:  
649 10.2307/2389414
- 650 Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier.  
651 *Nature* 388:526-526
- 652 Dekeukeleire D et al. (2019) Forest fragmentation and tree species composition jointly shape  
653 breeding performance of two avian insectivores. *Forest Ecology and Management*  
654 443:95-105. doi: 10.1016/j.foreco.2019.04.023
- 655 Delpierre N, Guillemot J, Dufrene E, Cecchini S, Nicolas M (2017) Tree phenological ranks  
656 repeat from year to year and correlate with growth in temperate deciduous forests.  
657 *Agricultural and Forest Meteorology* 234:1-10. doi: 10.1016/j.agrformet.2016.12.008
- 658 Demolder H et al. (2017) Biodiversity Indicators 2017. State of Nature in Flanders (Belgium).  
659 Mededelingen van het Instituut voor Natuur- en Bosonderzoek (3)
- 660 Dhondt AA (2012) Interspecific competition in birds. Oxford University Press, Oxford
- 661 Dhondt AA, Adriaensen F (1999) Experiments on competition between Great and Blue Tit:  
662 Effects on Blue Tit reproductive success and population processes. In: Adams NJaS,  
663 RH (ed) Proceedings of the 22nd International Ornithological Congress, vol 1.  
664 Ostrich, Durban, pp 39-48

- 665 Dhondt AA, Eyckerman R, Moermans R, Hublé J (1984) Habitat and laying date of Great and  
666 Blue Tit *Parus major* and *P. caeruleus*. *Ibis* 126:388-397
- 667 Dunn P (2004) Breeding dates and reproductive performance. *Advances in Ecological*  
668 *Research* 35:69-87. doi: 10.1016/S0065-2504(04)35004-X
- 669 Gamelon M et al. (2019) Accounting for interspecific competition and age structure in  
670 demographic analyses of density dependence improves predictions of fluctuations in  
671 population size. *Ecology Letters* 22:797-806. doi: 10.1111/ele.13237
- 672 Germain RR, Schuster R, Delmore KE, Arcese P (2015) Habitat preference facilitates  
673 successful early breeding in an open-cup nesting songbird. *Functional Ecology*  
674 29:1522-1532. doi: 10.1111/1365-2435.12461
- 675 Germain RR, Wolak ME, Arcese P, Losdat S, Reid JM (2016) Direct and indirect genetic and  
676 fine-scale location effects on breeding date in song sparrows. *Journal of Animal*  
677 *Ecology* 85:1613-1624. doi: 10.1111/1365-2656.12575
- 678 Gibb J (1954) Feeding ecology of tits, with notes on Treecreeper and Goldcrest. *Ibis* 96:513-  
679 543
- 680 Gienapp P, Vaisanen RA, Brommer JE (2010) Latitudinal variation in breeding time reaction  
681 norms in a passerine bird. *J. Anim. Ecol.* 79:836-842. doi: 10.1111/j.1365-  
682 2656.2010.01693.x
- 683 Grieco F, van Noordwijk AJ, Visser ME (2002) Evidence for the effect of learning on timing  
684 of reproduction in blue tits. *Science* 296:136-138. doi: 10.1126/science.1068287
- 685 Grimm A et al. (2015) Earlier breeding, lower success: does the spatial scale of climatic  
686 conditions matter in a migratory passerine bird? *Ecology and Evolution* 5:5722-5734.  
687 doi: 10.1002/ece3.1824
- 688 Helm B, Piersma T, Van der Jeugd H (2006) Sociable schedules: interplay between avian  
689 seasonal and social behaviour. *Anim. Behav.* 72:245-262. doi:  
690 10.1016/j.anbehav.2005.12.007
- 691 Hinks AE, Cole EF, Daniels KJ, Wilkin TA, Nakagawa S, Sheldon BC (2015) Scale-  
692 Dependent Phenological Synchrony between Songbirds and Their Caterpillar Food  
693 Source. *American Naturalist* 186:84-97. doi: 10.1086/681572
- 694 Jarvinen A (1991) A meta-analytic study of the effects of female age on laying date and  
695 clutch size in the great tit *Parus major* and the pied flycatcher *Ficedula hypoleuca*.  
696 *Ibis* 133:62-66. doi: 10.1111/j.1474-919X.1991.tb04811.x
- 697 Kovacsova P, Antalova M (2010) Precision forestry - definition and technologies. *Sumarski*  
698 *List* 134:603-611
- 699 Lambrechts MM, Perret P (2000) A long photoperiod overrides non-photoperiodic factors in  
700 blue tits' timing of reproduction. *Proc. R. Soc. B-Biol. Sci.* 267:585-588. doi:  
701 10.1098/rspb.2000.1041
- 702 Mackenzie JA, Hinsley SA, Harrison NM (2014) Parid foraging choices in urban habitat and  
703 their consequences for fitness. *Ibis* 156:591-605. doi: 10.1111/ibi.12166
- 704 Marchand LJ et al. (2020) Inter-individual variability in spring phenology of temperate  
705 deciduous trees depends on species, tree size and previous year autumn phenology.  
706 *Agricultural and Forest Meteorology* 290. doi: 10.1016/j.agrformet.2020.108031

- 707 Matthysen E, Adriaensen F, Dhondt AA (2011) Multiple responses to increasing spring  
708 temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus*, *Parus*  
709 *major*). *Global Change Biology* 17:1-16. doi: 10.1111/j.1365-2486.2010.02213.x
- 710 Miller-Rushing AJ, Hoyer TT, Inouye DW, Post E (2010) The effects of phenological  
711 mismatches on demography. *Philosophical Transactions of the Royal Society B-*  
712 *Biological Sciences* 365:3177-3186. doi: 10.1098/rstb.2010.0148
- 713 Møller AP (2008) Climate change and micro-geographic variation in laying date. *Oecologia*  
714 155:845-857. doi: doi: 10.1007/s00442-007-0944-3
- 715 Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did  
716 not show a phenological response to climate change are declining. *Proc. Natl. Acad.*  
717 *Sci. U. S. A.* 105:16195-16200. doi: doi: 10.1073/pnas.0803825105
- 718 Naefdaenzer B (1994) Radiotracking of Great and Blue Tits - new tools to assess territoriality,  
719 home-range use and resource distribution. *Ardea* 82:335-347
- 720 Nager RG, Van Noordwijk AJ (1995) Proximate and ultimate aspects of phenotypic plasticity  
721 in timing of great tit breeding in a heterogeneous environment. *American Naturalist*  
722 146:454-474. doi: 10.1086/285809
- 723 Nilsson JA, Kallander H (2006) Leafing phenology and timing of egg laying in great tits  
724 *Parus major* and blue tits *P. caeruleus*. *J. Avian Biol.* 37:357-363. doi:  
725 10.1111/j.2006.0908-8857.03604.x
- 726 Nour N, Currie D, Matthysen E, Van Damme R, Dhondt AA (1998) Effects of habitat  
727 fragmentation on provisioning rates, diet and breeding success in two species of tit  
728 (great tit and blue tit). *Oecologia* 114:522-530
- 729 Nussey DH, Postma E, Gienapp P, Visser ME (2005) Selection on heritable phenotypic  
730 plasticity in a wild bird population. *Science* 310:304-306. doi:  
731 10.1126/science.1117004
- 732 Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of  
733 phenological response to global warming. *Global Change Biology* 13:1860-1872. doi:  
734 doi.org/10.1111/j.1365-2486.2007.01404.x
- 735 Piskorski R, Dorn S (2010) Early-Season Headspace Volatiles from Apple and Their Effect  
736 on the Apple Blossom Weevil *Anthonomus pomorum*. *Chem. Biodivers.* 7:2254-2260.  
737 doi: 10.1002/cbdv.201000221
- 738 Polgar CA, Primack RB (2011) Leaf-out phenology of temperate woody plants: from trees to  
739 ecosystems. *New Phytol.* 191:926-941. doi: 10.1111/j.1469-8137.2011.03803.x
- 740 Puchalka R, Koprowski M, Gricar J, Przybylak R (2017) Does tree-ring formation follow leaf  
741 phenology in Pedunculate oak (*Quercus robur* L.)? *Eur. J. For. Res.* 136:259-268. doi:  
742 10.1007/s10342-017-1026-7
- 743 Radchuk V et al. (2019) Adaptive responses of animals to climate change are most likely  
744 insufficient. *Nature Communications* 10:14. doi: 10.1038/s41467-019-10924-4
- 745 Reed TE, Jenouvrier S, Visser ME (2013) Phenological mismatch strongly affects individual  
746 fitness but not population demography in a woodland passerine. *Journal of Animal*  
747 *Ecology* 82:131-144. doi: 10.1111/j.1365-2656.2012.02020.x

- 748 Samplonius JM et al. (2018) Phenological sensitivity to climate change is higher in resident  
749 than in migrant bird populations among European cavity breeders. *Global Change*  
750 *Biology* 24:3780-3790. doi: 10.1111/gcb.14160
- 751 Sass-Klaassen U, Sabajo CR, den Ouden J (2011) Vessel formation in relation to leaf  
752 phenology in pedunculate oak and European ash. *Dendrochronologia* 29:171-175. doi:  
753 10.1016/j.dendro.2011.01.002
- 754 Schaper SV, Dawson A, Sharp PJ, Caro SP, Visser ME (2012) Individual variation in avian  
755 reproductive physiology does not reliably predict variation in laying date. *General and*  
756 *Comparative Endocrinology* 179:53-62. doi: 10.1016/j.ygcen.2012.07.021
- 757 Schaper SV, Rueda C, Sharp PJ, Dawson A, Visser ME (2011) Spring phenology does not  
758 affect timing of reproduction in the great tit (*Parus major*). *Journal of Experimental*  
759 *Biology* 214:3664-3671. doi: 10.1242/jeb.059543
- 760 Schlicht L, Valcu M, Kempenaers B (2014) Thiessen polygons as a model for animal territory  
761 estimation. *Ibis* 156:215-219. doi: 10.1111/ibi.12105
- 762 Shutt JD et al. (2019) The environmental predictors of spatio-temporal variation in the  
763 breeding phenology of a passerine bird. *Proceedings of the Royal Society B-*  
764 *Biological Sciences* 286:9. doi: 10.1098/rspb.2019.0952
- 765 Slagsvold T (1976) Annual and geographical variation in time of breeding of great tit *Parus*  
766 *major* and pied flycatcher *Ficedula hypoleuca* in relation to environmental phenology  
767 and spring temperature. *Ornis Scandinavica* 7:127-145. doi: 10.2307/3676183
- 768 Slagsvold T, Wiebe KL (2007) Learning the ecological niche. *Proc. R. Soc. B-Biol. Sci.*  
769 274:19-23. doi: 10.1098/rspb.2006.3663
- 770 Szulkin M, Zelazowski P, Marrot P, Charmantier A (2015) Application of High Resolution  
771 Satellite Imagery to Characterize Individual-Based Environmental Heterogeneity in a  
772 Wild Blue Tit Population. *Remote Sensing* 7:13319-13336. doi: 10.3390/rs71013319
- 773 Thomas DW, Bourgault P, Shipley B, Perret P, Blondel J (2010) Context-dependent changes  
774 in the weighting of environmental cues that initiate breeding in a temperate passerine,  
775 the Corsican blue tit (*Cyanistes caeruleus*). *Auk* 127:129-139. doi:  
776 10.1525/auk.2009.09141
- 777 Tinbergen JM, Boerlijst MC (1990) Nestling weight and survival in individual great tits  
778 (*Parus major*). *Journal of Animal Ecology* 59:1113-1127
- 779 Torti VM, Dunn PO (2005) Variable effects of climate change on six species of North  
780 American birds. *Oecologia* 145:486-495. doi: 10.1007/s00442-005-0175-4
- 781 Van Dongen S, Backeljau T, Matthysen E, Dhondt AA (1997) Synchronization of hatching  
782 date with budburst of individual host trees (*Quercus robur*) in the winter moth  
783 (*Operophtera brumata*) and its fitness consequences. *Journal of Animal Ecology*  
784 66:113-121
- 785 Van Noordwijk AJ, McCleery RH, Perrins CM (1995) Selection for the timing of Great Tit  
786 breeding in relation to caterpillar growth and temperature. *Journal of Animal Ecology*  
787 64:451-458
- 788 Vatka E, Rytkonen S, Orell M (2014) Does the temporal mismatch hypothesis match in boreal  
789 populations? *Oecologia* 176:595-605. doi: 10.1007/s00442-014-3022-7

790 Vaugoyeau M et al. (2016) Interspecific variation in the relationship between clutch size,  
791 laying date and intensity of urbanization in four species of hole-nesting birds. *Ecology*  
792 and *Evolution* 6:5907-5920. doi: 10.1002/ece3.2335

793 Vedder O, Bouwhuis S, Sheldon BC (2013) Quantitative Assessment of the Importance of  
794 Phenotypic Plasticity in Adaptation to Climate Change in Wild Bird Populations. *Plos*  
795 *Biology* 11. doi: 10.1371/journal.pbio.1001605

796 Visser ME (2008) Keeping up with a warming world; assessing the rate of adaptation to  
797 climate change. *Proceedings of the Royal Society B-Biological Sciences* 275:649-659.  
798 doi: 10.1098/rspb.2007.0997

799 Visser ME et al. (2003) Variable responses to large-scale climate change in European *Parus*  
800 populations. *Proceedings of the Royal Society of London Series B-Biological*  
801 *Sciences* 270:367-372. doi: 10.1098/rspb.2002.2244

802 Visser ME, Holleman LJM, Caro SP (2009) Temperature has a causal effect on avian timing  
803 of reproduction. *Proceedings of the Royal Society B-Biological Sciences* 276:2323-  
804 2331. doi: DOI: 10.1098/rspb.2009.0213

805 Wesolowski T, Cholewa M (2009) Climate variation and bird breeding seasons in a primeval  
806 temperate forest. *Climate Research* 38:199-208. doi: 10.3354/cr00789

807 Wesolowski T, Rowinski P (2006) Timing of bud burst and tree-leaf development in a  
808 multispecies temperate forest. *Forest Ecology and Management* 237:387-393. doi:  
809 10.1016/j.foreco.2006.09.061

810 Wesolowski T, Rowinski P (2014) Do Blue Tits *Cyanistes caeruleus* synchronize  
811 reproduction with caterpillar peaks in a primeval forest? *Bird Study* 61:231-245. doi:  
812 10.1080/00063657.2014.899307

813 Wilkin TA, King LE, Sheldon BC (2009) Habitat quality, nestling diet, and provisioning  
814 behaviour in great tits *Parus major*. *J. Avian Biol.* 40:135-145. doi: 10.1111/j.1600-  
815 048X.2009.04362.x

816 Wilkin TA, Perrins CM, Sheldon BC (2007) The use of GIS in estimating spatial variation in  
817 habitat quality: a case study of lay-date in the Great Tit *Parus major*. *Ibis* 149:110-  
818 118. doi: 10.1111/j.1474-919X.2007.00757.x

819

820

821

822 **Tables**

823 Table 1. Between-year repeatability of budburst date of individual trees ( $r_s$  = Spearman rank  
 824 correlation). Note that in 2009 and 2017 budburst scores were assessed on a single day, while  
 825 in 2010 multiple visits were made and used to estimate the date of reaching budscore 4. Thus,  
 826 negative correlation signs indicate that an earlier budburst in 2010 corresponds with a higher  
 827 budburst score on a fixed day in either 2009 or 2017.

828

	2009 vs 2010			2010 vs 2017		
	$r_s$	<b>P</b>	<b>N</b>	$r_s$	<b>P</b>	<b>N</b>
All trees	-0.69	< 0.001	116	-0.42	< 0.001	100
Oak	-0.81	< 0.001	89	-0.61	< 0.001	73
Beech	-0.53	0.02	20	-0.47	0.03	20

829

830

831 Table 2. Baseline breeding data of the two study species (first broods only). All values are  
 832 based on annual means, subsequently averaged over the study period (N = 21 years). The  
 833 range of annual means is given between parentheses. Data are given for all females, as well as  
 834 for known females only (data used for the actual analyses).

	Great Tit		Blue Tit	
	all females	known females only	all females	known females only
Laying date (April)	16 (2 – 29)	16 (2 – 28)	13 (2 – 27)	13 (2 – 25)
S.D. in laying date	4.92 (2.5 – 8.1)	4.88 (2.5-8.5)	4.72 (2.9 – 7.9)	4.41 (2.5 – 8.2)
Clutch size	8.64 (6.8 – 11.0)	8.98 (7.5 – 11.0)	10.7 (8.4 – 12.0)	11.3 (9.9 – 12.8)
Nest success rate	76.5 (38 – 100)	89.7 (60 – 100)	77.0 (61 – 91)	92.9 (81 – 100)
Proportion 1 <sup>st</sup> year females	/	61.0 (34 – 79)	/	59.9 (39 – 81)
Number of first clutches	29.0 (17 – 40)	24.2 (13 – 37)	32.6 (21 – 53)	26.3 (15 – 47)

835

836

837 Table 3. Parameter estimates for fixed effects in the best model explaining laying date  
 838 variation of Great and Blue Tits. In the Blue Tit model, tree composition represents the  
 839 relative amount of oak versus beech trees in a 25m radius around the nestbox (first axis of a  
 840 Principal Component Analysis, see methods). Variance estimates for random effects were  
 841 41.7 (year), 14.5 (female identity), 1.02 (nestbox) and 12.0 (residual) for Great Tits. For Blue  
 842 Tits these were 32.1 (year), 10.8 (female identity), 0.8 (nestbox) and 9.8 (residual).  
 843

<b>Effect</b>	<b>Estimate</b>	<b>Estimate refers to</b>	<b>DF</b>	<b>F</b>	<b>P</b>
<b>Great Tit:</b>					
Female age	1.12 ± 0.43	First-year versus older	1; 281	6.86	<0.01
<b>Blue Tit:</b>					
Female age	1.66 ± 0.38	First-year versus older	1; 411	19.5	< 0.001
Tree composition	-0.54 ± 0.16		1; 99.7	12.1	< 0.001

844

845

## 846 **Figure Legends**

847 Figure 1. Overview of the study area. The left panel shows how the plot is divided into six  
848 parcels bordered by lanes with predominantly oak trees. Symbols represent nestboxes as they  
849 were present from 1997 to 2017, with either large (32mm; circles; N = 78) or small (26mm;  
850 triangles; N =40) entrances. The right panel shows individual trees (N = 1558) by species  
851 (green = oak, red = beech, orange = red oak, yellow = birch, grey = conifer, black = alder,  
852 pink = other).

853

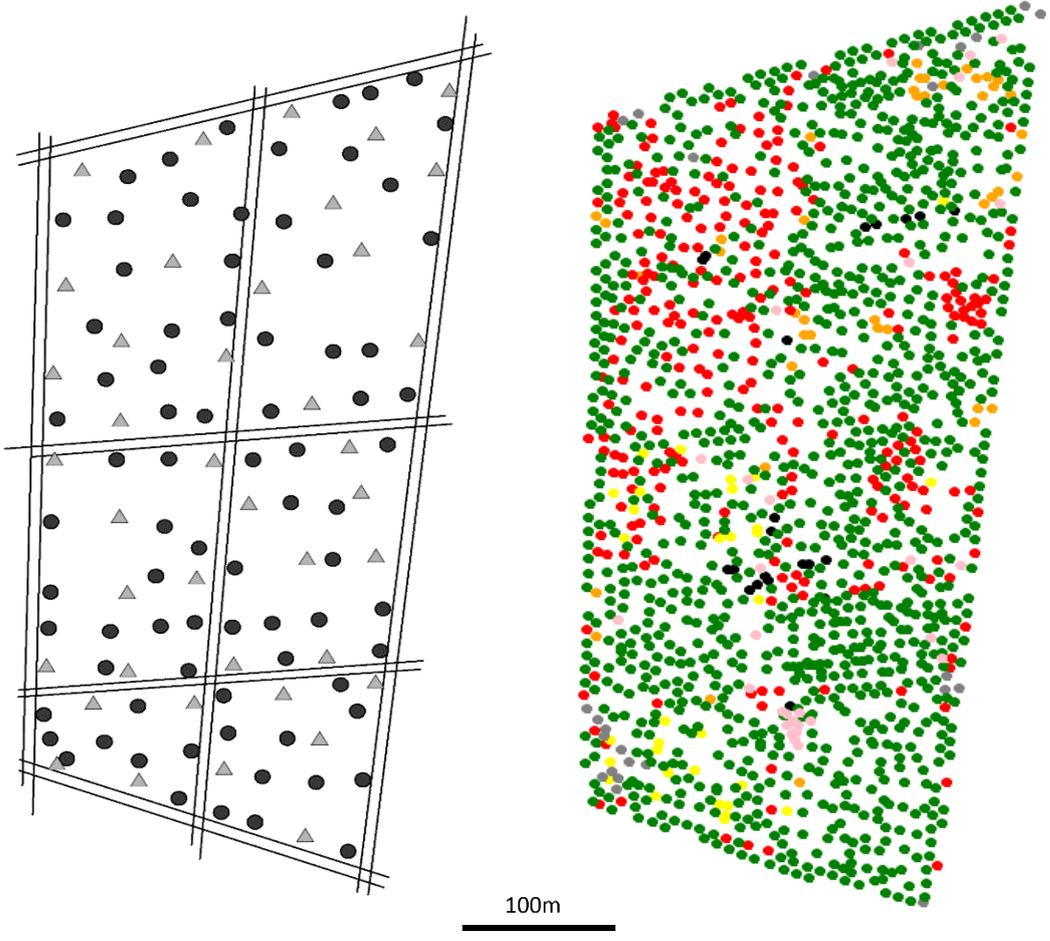
854 Figure 2. Repeatability of budburst for oak (black) and beech (white) trees between 2009 and  
855 2010. Note that in 2009 all trees were scored on the same day, while in 2010 budburst date  
856 (estimated time of reaching budburst score 4) was extrapolated from multiple observation  
857 days. Bubble sizes reflect number of trees (from 1 to 7). Data points for beech are slightly  
858 offset for clarity. Note that beech was markedly earlier in 2010, but much less so in 2009.

859

860 Figure 3. Relation between Blue Tit laying date and tree species composition (first principal  
861 component axis at 25m scale; higher values mean an increasing number of oaks, and fewer  
862 beech trees). The regression line and confidence interval are plotted through the raw data for  
863 visual purposes, not taking into account random effects or age variation.

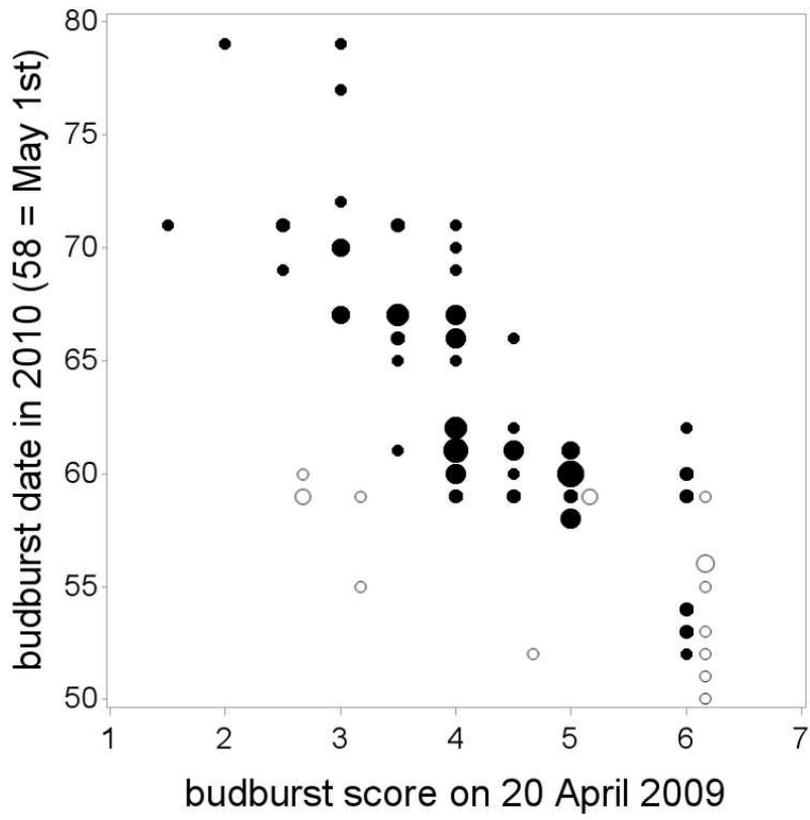
864 **Figure 1**

865



866 **Figure 2**

867



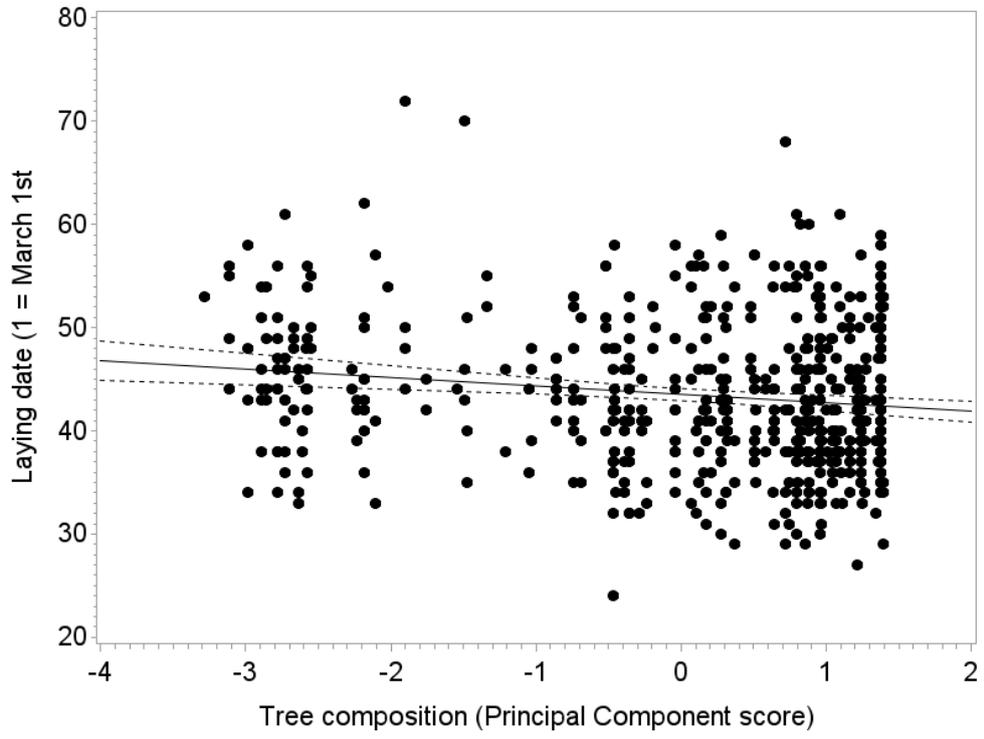
868

869

870

871 **Figure 3**

872



873