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1 **The sensitivity of breeding songbirds to changes in seasonal timing is linked**
2 **to population change but cannot be directly attributed to the effects of**
3 **trophic asynchrony on productivity**

4
5 Running head: Breeding phenology and population change

6
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SF, JPH, DL, SA, JB, MB and RH provided data; SF performed the analyses; SF, JPH and
DL wrote the manuscript; other authors provided editorial advice.

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21 ABSTRACT

22 A consequence of climate change has been an advance in the timing of seasonal events.
23 Differences in the rate of advance between trophic levels may result in predators becoming
24 mismatched with prey availability, reducing fitness and potentially driving population
25 declines. Such “trophic asynchrony” is hypothesised to have contributed to recent population
26 declines of long-distance migratory birds in particular. Using spatially extensive survey data
27 from 1983 to 2010 to estimate variation in spring phenology from 280 plant and insect
28 species and the egg-laying phenology of 21 British songbird species, we explored the effects
29 of trophic asynchrony on avian population trends and potential underlying demographic
30 mechanisms. Species which advanced their laying dates least over the last three decades, and
31 were therefore at greatest risk of asynchrony, exhibited the most negative population trends.
32 We expressed asynchrony as the annual variation in bird phenology relative to spring
33 phenology, and related asynchrony to annual avian productivity. In warmer springs, birds
34 were more asynchronous, but productivity was only marginally reduced; long-distance
35 migrants, short-distance migrants and resident bird species all exhibited effects of similar
36 magnitude. Population, but not productivity declines were greatest among those species
37 whose productivity was most greatly reduced by asynchrony. This suggests that population
38 change is not mechanistically driven by the negative effects of asynchrony on productivity.
39 The apparent effects of asynchrony are therefore either more likely to be strongly expressed
40 via other demographic pathways, or alternatively, are a surrogate for a species’ sensitivity to
41 other environmental pressures which are the ultimate cause of decline.

42 KEYWORDS

43 citizen science, climate change, demography, migration, mismatch hypothesis, phenology,
44 population change, trophic asynchrony

45 INTRODUCTION

46 Climate warming has been linked to advancing seasonal timing (phenology) in many
47 organisms (Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2007; Thackeray *et al.*,
48 2016), but variable responses to temperature change across taxa have led to differing rates of
49 seasonal advancement between trophic levels (Stenseth *et al.*, 2002; Thackeray *et al.*, 2010).
50 Primary producers have generally advanced timing more rapidly than primary consumers,
51 which in turn have advanced more quickly than secondary and higher consumers (Both *et al.*,
52 2009; Thackeray *et al.*, 2010, 2016). This phenological trophic asynchrony can result in
53 predator breeding cycles becoming mismatched with seasonal peaks in prey availability
54 (Harrington *et al.*, 1999; Visser & Both, 2005), the negative fitness consequences incurred
55 potentially contributing to subsequent population declines (Both *et al.*, 2006, 2010; Visser *et*
56 *al.*, 2012).

57 In birds, the ability to advance timing of breeding may be dependent on responsiveness to the
58 seasonal cues that act as a proxy for changes in food abundance (reviewed in Visser *et al.*,
59 2012). Additionally, selection for advanced breeding may be constrained, either by the costs
60 of breeding too early (e.g. increased risk of cold temperatures and/or insufficient food
61 resources) or by events outside of the breeding season (Jones & Cresswell, 2010; Rubolini *et*
62 *al.*, 2010; Visser *et al.*, 2012; Finch *et al.*, 2014). Long-distance migratory birds are
63 hypothesised to be at greater risk of seasonal asynchrony in breeding phenology than either
64 short-distance migrants or resident species due to 1) phenology cues experienced at distant
65 wintering sites inadequately reflecting seasonal advancement on breeding grounds (although
66 see Saino & Ambrosini, 2008); and/or 2) direct constraints imposed on their ability to
67 advance breeding phenology as a result of their migratory behaviour. While migrant laying
68 dates have advanced in response to climate change over recent decades (Crick *et al.*, 1997;
69 Dunn & Winkler, 2010; Møller *et al.*, 2010; Ockendon *et al.*, 2013), this shift may be

70 insufficient to match advancement of seasonal food peaks (e.g. in the case of Dutch pied
71 flycatcher *Ficedula hypoleuca* populations: Both *et al.*, 2006). Onset of breeding may be
72 constrained by timing of arrival, influenced by environmental conditions away from the
73 breeding grounds (Both & Visser, 2001; Both *et al.*, 2005; Both, 2010; Finch *et al.*, 2014),
74 and there is evidence that arrival dates of European migrants wintering in sub-Saharan Africa
75 have advanced less rapidly than those of short-distance migrants (Rubolini *et al.*, 2007; but
76 see Pearce-Higgins & Green, 2014 Fig. 2.3). If long-distance migrants are more constrained
77 in their ability to track changes in their breeding environment, the temporal overlap between
78 peak prey availability and offspring demand may be reduced relative to that experienced by
79 short-distance migrants and residents; consequently, long-distance migrants may be more
80 sensitive to further increases in asynchrony. This hypothesis has been suggested as a potential
81 explanation for the more rapid population declines observed in long-distance migratory
82 species (Robbins *et al.*, 1989; Sanderson *et al.*, 2006; Møller *et al.*, 2008; Salido *et al.*, 2012;
83 Vickery *et al.*, 2013).

84 However, there remains uncertainty about the extent to which asynchrony might influence the
85 population dynamics of birds (reviewed in Knudsen *et al.*, 2011; Pearce-Higgins & Green,
86 2014). To date, much of the evidence relating migrant declines to mismatch has been indirect
87 (e.g. Jones & Cresswell, 2010; Cormont *et al.*, 2011; Saino *et al.*, 2011) and a more recent,
88 comparative study found no evidence of an influence of asynchrony on population trends of a
89 wide range of European and North American bird species (Dunn & Møller, 2014).
90 Furthermore, several recent mechanistic studies identifying relationships between avian
91 phenology and productivity have failed to find any resultant impact on population size (Reed
92 *et al.*, 2013a; McLean *et al.*, 2016). It could therefore be possible that confounding variables
93 related to both laying date and population trends are responsible for the observed

94 relationships; teasing apart such relationships highlights the need for further mechanistic
95 studies.

96 Only a few studies have directly investigated the relationship between asynchrony and either
97 demography or population change, and these too have demonstrated mixed results (e.g. see
98 Table 3 in Dunn *et al.*, 2011). While some have identified a negative relationship (e.g. pied
99 flycatcher Both *et al.*, 2006; black grouse *Tetrao tetrix* Ludwig *et al.*, 2006), the strength of
100 the effect has been variable and other studies have found little evidence of impacts (e.g.
101 European golden plover *Pluvialis apricaria* Pearce-Higgins *et al.*, 2010; tree swallow
102 *Tachycineta bicolor* Dunn *et al.*, 2011; great tit Reed *et al.*, 2013b). As yet, there is no robust
103 evidence linking changes in the relative phenology of birds and their prey to broad-scale
104 variation in productivity or population trends.

105 It is perhaps unsurprising that studies predicting a general effect of climate change-induced
106 asynchrony on population-level processes have produced conflicting evidence, as there is
107 likely to be considerable variation in the extent of asynchrony between individuals,
108 populations and species. The magnitude of asynchrony observed is likely to depend on many
109 factors, including, but not limited to: spatial variability in spring phenology and peaks in prey
110 abundance; seasonal variation in the rate of warming, should species respond to differently
111 timed cues; habitat (strongly versus less seasonal habitats); the strength of seasonality in local
112 prey abundance (sharp versus broad or no peak); the proportion of the population that
113 produces multiple broods; and constraints on the ability of individuals to shift reproductive
114 timing due to events outside of the breeding season (Cresswell & McCleery, 2003; e.g. Visser
115 *et al.*, 2003; Both *et al.*, 2006, 2010; Durant *et al.*, 2007; Charmantier *et al.*, 2008; Møller,
116 2008; Burger *et al.*, 2012; Cole *et al.*, 2015; Hinks *et al.*, 2015; Mayor *et al.*, 2017). While
117 single-population or single-species studies make it difficult to generalise the impacts of
118 seasonal asynchrony, a multi-species, broad-scale approach can produce a more robust

119 assessment of the broad effects of climate change-induced asynchrony on avian population
120 dynamics. Furthermore, any variation between species may help to identify the ecological
121 and demographic mechanisms by which asynchrony may influence abundance.

122 We use UK-wide survey data from taxa at three different trophic levels to estimate annual,
123 population-level variation in the reproductive timing of 21 common bird species relative to
124 the seasonal phenology of primary producers and invertebrate primary consumers. We first
125 relate long-term changes in avian reproductive timing to national population trends, and then
126 examine the evidence supporting the effect of asynchrony on avian productivity as a plausible
127 underlying demographic mechanism. We use first event (first leaf/flower/flight date)
128 phenology of 280 plant and invertebrate species as an overall index of spring phenology.
129 Given the large number of species, similarity of phenological trends observed for lower
130 trophic levels (Thackeray *et al.*, 2010), and recent evidence that indirect measures of spring
131 phenology are likely to be indicative of the seasonal availability of functionally relevant
132 invertebrate taxa (e.g. Cole *et al.*, 2015; Hinks *et al.*, 2015; Mayor *et al.*, 2017), this index of
133 spring phenology is likely to represent broader temperature-mediated changes in the
134 phenology of prey species available to the breeding bird species in our study.

135 Using this mechanistic approach, we predict that those species which have advanced egg-
136 laying dates the most over time will exhibit more positive population trends (Hypothesis 1).
137 If the mechanism underlying this relationship is indeed attributable to increasing asynchrony
138 with climate warming, we further predict that a) asynchrony will increase with warmer
139 temperatures; b) in years of greatest asynchrony, avian productivity will be reduced, and c)
140 the most negative consequences will be exhibited by long-distance migrants (Hypothesis 2).
141 We expect that those species demonstrating the greatest reductions in productivity as a result
142 of trophic asynchrony are most likely to have experienced the greatest declines in both
143 population size and productivity over the study period (Hypothesis 3). Finally, we expect the

144 associations predicted above to be the result of a causal mechanistic pathway (the
145 asynchrony-productivity pathway; Hypothesis 4).

146 **MATERIALS AND METHODS**

147 **Bird phenology**

148 The British Trust for Ornithology's (BTO's) Nest Record Scheme (NRS) uses volunteer-
149 collected data to quantify the annual breeding performance of a broad range of bird species
150 across Britain (see Crick *et al.*, 2003 for full methods). Observers monitor individual nesting
151 attempts and record location, visit date, and the number and developmental stage of any eggs
152 or chicks present. Very few nests are found during laying so clutch initiation (first egg) dates
153 are rarely known with certainty. Instead, they are back-calculated to produce a minimum and
154 maximum lay date estimate (Crick *et al.* 2003), with the mid-point of this range taken as the
155 nest-specific first egg date estimate, excluding any records where the range is greater than 10
156 days. In our dataset of 80,495 nests found between 1983-2010, the mean value of this range is
157 5.4 days. Using these nest data, we developed an annual lay date metric for 21 common UK-
158 breeding terrestrial passerines (see Table S1) that represents the peak in initiation of first
159 broods and, consequently, the onset of the breeding season (Fig. 1; see Appendix S1 for lay
160 date calculation method and Figs. S1-S3 for examples). We only calculated a lay date metric
161 for a species in a given year if at least 10 nests of that species were monitored. The
162 robustness of these estimates was assessed by bootstrapping (Appendix S1; Fig S4-S5)

163 **Spring phenology**

164 We derived a spring phenology metric for primary consumers and producers by modelling
165 first event dates in each year (1983–2010) using survey data from the UK Phenology
166 Network (plants: first flowering and/or leaf dates; www.naturescalendar.org.uk), Rothamsted
167 Research suction traps (aphids: first flight dates; see Bell *et al.*, 2015 for methods) and light

168 traps (moths: fifth percentile of catch date; see Conrad *et al.*, 2006 for methods), and the UK
169 Butterfly Monitoring Scheme (butterflies: first appearance on survey transects; see
170 www.ukbms.org for methods). Annual metrics from all taxonomic groups were correlated
171 with each other (Fig S7) and averaged to create a single, annual index of spring phenology
172 (Fig. 1; see Appendix S1 for a complete description of methods and Figs. S6 and S8 for the
173 annual and seasonal variation in phenology across taxonomic groups; Table S2 gives all
174 species included in the spring phenology metric calculations).

175 **Relative asynchrony**

176 Direct estimates of the seasonal variation in abundance of avian prey that can be directly
177 matched (i.e. functionally linked) to bird phenology (e.g. as for Visser *et al.*, 1998, 2015;
178 Burger *et al.*, 2012; Reed *et al.*, 2013a) were not available at a national scale. We therefore
179 cannot explicitly say whether a species is ‘matched’ or ‘mismatched’ with the peak
180 abundance of its prey. Instead, we derived a measure of *relative asynchrony* for each species
181 by relating our measure of spring phenology to the timing of bird egg laying. Specifically, we
182 subtracted the annual spring phenology metric derived from plants and invertebrates above,
183 from the estimated annual lay date metric for each bird species to derive an annual index of
184 the timing of breeding relative to spring phenology (i.e. an index of **annual asynchrony**; Fig.
185 1). Because we do not know the actual degree of temporal matching between the bird species
186 featured in this study and the phenology of their prey, the absolute annual asynchrony values
187 are unimportant; for one species, breeding 30 days before the spring phenology metric may
188 be optimal, whilst for another optimal breeding may occur 20 days afterwards. Instead, we
189 focus on comparing species-specific variation in annual asynchrony values *relative to* the
190 species-specific mean over the study period. To permit comparison of this relative change
191 across species, we centred annual asynchrony values by taking the difference between each
192 annual value and the mean value (**mean asynchrony**) for each species across the study

193 period. The resulting scaled metric (hereafter referred to simply as **relative asynchrony**; Fig.
194 1) represents apparent asynchrony, or divergence from average levels of asynchrony for that
195 species: positive values occur in years when birds breed relatively later than average for the
196 species with respect to spring phenology; negative values occur in years where birds breed
197 earlier than average.

198 **Bird productivity**

199 Annual productivity indices (ratio of juveniles to adults) were generated from capture data
200 collected during standardised mist-netting and ringing activities of volunteers at ~130 sites
201 across Britain operated as part of the BTO's Constant Effort Sites (CES) scheme (Peach *et al.*,
202 1996; Robinson *et al.*, 2009). The CES productivity estimate integrates productivity
203 across the full season (i.e. the number of young raised to independence across all broods),
204 which is likely to be representative of full-season productivity for multi-brooded species, and
205 also incorporates a component of post-fledging mortality. The CES productivity estimate thus
206 provides a better estimate of the annual production of potential recruits (Streby *et al.*, 2014)
207 than simply using the number of fledglings produced per nesting attempt derived from
208 individual nesting attempts recorded under the Nest Record Scheme. Previous analyses of
209 these data show associations with population trends or temperature (e.g. Eglington *et al.*,
210 2014; Robinson *et al.*, 2014; Morrison *et al.*, 2016), so they are likely to be a robust estimate
211 of true productivity.

212 **Migratory strategy**

213 To determine whether the effects of variation in relative phenology are dependent on
214 migratory strategy, species were classified as long-distance (sub-Saharan) migrants (n=5),
215 short-distance (intra-European) migrants (n=6), and residents (where over-wintering range in
216 the UK is approximately the same as the breeding range, n=10; see Table S1). Classification

217 followed Wernham *et al.* (2002) and Thaxter *et al.* (2010), but chiffchaff *Phylloscopus*
218 *collybita* was classified as a predominantly short-distance migrant given the relative paucity
219 of sub-Saharan ringing recoveries for this species (Robinson *et al.*, 2015a).

220 **Weather effects on productivity**

221 As temperature and precipitation during the nestling stage may directly direct influence
222 annual productivity, we calculated average daily values of both variables during the peak
223 nestling phase of each species across all years using the UK Met Office's Central England
224 Temperature (Parker *et al.*, 1992) and England and Wales Precipitation (Alexander & Jones,
225 2000) datasets. We defined the peak nestling phase as starting on the peak hatch date and
226 ending on the peak fledging date. Peak hatch date was derived by adding the durations of the
227 laying period (using species-specific clutch size means and assuming eggs are laid on
228 successive days) and the incubation period (assuming incubation begins with the penultimate
229 egg) to the peak lay date, while peak fledging date was derived by further adding the duration
230 of the fledging period (using species-specific mean fledging times); all species-specific
231 values are based on published literature and originate from standard parameter files for use in
232 Nest Record Scheme data validation and processing (Crick *et al.*, 2003). Although wind may
233 also be an important driver of avian breeding success, it is most likely to affect pelagic
234 seabirds or aerial insectivores (Weimerskirch *et al.* 2012; Møller *et al.* 2013), rather than the
235 primarily surface or foliage gleaning species studied here, and so is not considered further.

236 **Conceptual framework for testing predictions**

237 We use a conceptual framework analogous to that of McLean *et al.* (2016) to test our
238 predictions that increasing asynchrony is related to reduced annual productivity, resulting in
239 long-term productivity declines that are likely to in turn drive population declines. We
240 present the linear effects of x on y as dy/dx , with the productivity-asynchrony relationship

241 given as dP/dA , and laying date, asynchrony, long-term productivity and long-term
 242 population trends given as dL/dT , dA/dT , dP/dT and dN/dT , respectively.

243 **Statistical analyses**

244 *Analysis 1: The relationship between rate of change in laying date and long-term population*
 245 *change*

246 We tested our prediction that those species which have advanced egg-laying dates the most
 247 over time will exhibit more positive population trends (Hypothesis 1; Fig. 1) by first
 248 modelling lay dates for each species in each year of the study. For all equations, categorical
 249 variable beta coefficients are given in bold type:

$$250 \text{ Lay date} = \alpha + \beta_1 \cdot \text{year} + \boldsymbol{\beta_2} \cdot \text{species} + \boldsymbol{\beta_3} \cdot \text{year} \cdot \text{species} + \varepsilon \quad (1)$$

251 Next, for each individual species we calculated linear population change (dN/dT) in England
 252 between 1983 and 2010 using long-term population index data from the BTO's Common
 253 Bird Census and BTO/JNCC/RSPB Breeding Bird Survey joint trends analysis (Robinson *et*
 254 *al.*, 2015b). For each individual species, we modelled its annual population index as a
 255 function of year:

$$256 \text{ Annual population index} = \alpha + \beta_1 \cdot \text{year} + \varepsilon \quad (2)$$

257 We then modelled species-specific population change (dN/dT) against rate of change in lay
 258 date (dL/dT) for that individual species (β_3 from model (1) above), including the species'
 259 migration strategy as a covariate to control for differences in population trends between
 260 species with different strategies:

$$261 \text{ } dN/dT = \alpha + \beta_1 \cdot dL/dT + \boldsymbol{\beta_2} \cdot \text{migratory strategy} + \varepsilon \quad (3)$$

262 *Analysis 2: The relationship between relative asynchrony and productivity*

263 Next, we tested whether the mechanism underlying the above relationship between the rate of
264 change in lay date and population trend could be attributed to the potential effects of
265 increasing asynchrony on productivity as a consequence of climate warming (Hypothesis 2).
266 We used a general linear model to first test whether a) asynchrony increases with warmer
267 spring temperatures, and then used general linear mixed effects models to test whether b) in a
268 given year, avian productivity is associated with relative asynchrony; and whether c) the
269 nature of this relationship varies with migratory strategy.

270 For b) and c) above, we modelled annual productivity across all species and years as a
271 function of model covariates which we identified *a priori* as those specifically of interest
272 (relative asynchrony, migratory strategy and their interaction) or potential nuisance weather
273 variables (temperature and precipitation; Fig. 1). Our aim was not to explain as much
274 variation in productivity as possible but to explicitly test for any relationship between relative
275 asynchrony and annual productivity estimates, and the extent to which this relationship varies
276 with migratory distance. To derive the optimal random effects structure for all models, we
277 fitted models in R with the *lme* function in the *nlme* package (Pinheiro *et al.*, 2015; R Core
278 Team, 2015) following the methods in Zuur *et al.* (2009). We used the restricted maximum
279 likelihood method to fit models with different random effects structures: no random effects,
280 random intercept allowed to vary by species (1|species), random intercept and slope of
281 relative asynchrony allowed to vary by species (1 + asynchrony|species). The optimal
282 structure included a random intercept effect of species (1|species, b_1).

283 We also tested whether differences in the relationship between productivity and relative
284 asynchrony according to migratory strategy were influenced by relatedness between species.
285 Using a likelihood ratio test, we found that the species effect alone produced a more optimal
286 random effects structure than when species was nested within family (1|family/species ; $\chi^2 =$

287 0.050, $P = 0.82$) or within genus (1|genus/species; $\chi^2 = 1.18$, $P = 0.27$). This indicates that
 288 responses exhibited by individual species were independent of phylogenetic relatedness.

289 To evaluate the significance of individual covariates and interactions, we used likelihood
 290 ratio tests to compare models with and without the relevant term, with the global model given
 291 as:

$$292 \text{ Annual productivity} = \alpha + \beta_1 \cdot \text{relative asynchrony} + \beta_2 \cdot \text{migration strategy} + \beta_3 \cdot \text{relative} \\ 293 \text{ asynchrony} \cdot \text{migration strategy} + \beta_4 \cdot \text{temperature} + \beta_5 \cdot \text{precipitation} + b_1 + \varepsilon \quad (4)$$

294 We also tested the significance of a quadratic relative asynchrony term in addition to a linear
 295 term in a model without the migratory strategy interaction, as it is possible that average
 296 relative asynchrony is optimal for productivity:

$$297 \text{ Annual productivity} = \alpha + \beta_1 \cdot \text{relative asynchrony} + \beta_2 \cdot \text{relative asynchrony}^2 + \beta_3 \cdot \\ 298 \text{ migration strategy} + \beta_4 \cdot \text{temperature} + \beta_5 \cdot \text{precipitation} + b_1 + \varepsilon \quad (5)$$

299 However, the quadratic term was non-significant ($\chi^2 = 0.485$, $df=1$, $P = 0.49$). Models testing
 300 different fixed effects were fitted using the maximum likelihood method with the *lme*
 301 function.

302 We also explored the potential for species-specific habitat preferences to confound a
 303 relationship between relative asynchrony and migratory strategy, given that negative effects
 304 of asynchrony may be greater in more seasonal habitats such as woodland (Both *et al.*, 2010).
 305 However, we found no indication that the effect of relative asynchrony on productivity was
 306 related to nesting habitat type (see Appendix S1).

307 *Analysis 3: The relationship between the sensitivity of productivity to asynchrony and long-*
 308 *term population and productivity trends*

309 In Analysis 2 above, we tested predictions regarding the relationship between relative
 310 asynchrony and annual productivity at a multi-species level. In Analysis 3, we tested whether
 311 the species exhibiting the greatest reductions in annual productivity in relation to increasing
 312 trophic asynchrony (i.e. the most ‘sensitive’ species) were those most likely to demonstrate
 313 the greatest long-term declines in both abundance and productivity over the study period
 314 (Hypothesis 3; Fig. 1).

315 We first derived a species-specific **productivity-asynchrony sensitivity metric** (hereafter
 316 simply ‘sensitivity’ or dP/dA ; Fig. 1) by calculating the absolute slope of the productivity-
 317 asynchrony relationship for each individual species ($\beta_1 + \beta_3$) in the model:

$$318 \text{ Annual productivity} = \alpha + \beta_1 \cdot \text{relative asynchrony} + \beta_2 \cdot \text{species} + \beta_3 \cdot \text{relative asynchrony} \cdot \\ 319 \text{ species} + \beta_4 \cdot \text{temperature} + \beta_5 \cdot \text{precipitation} + \varepsilon \quad (6)$$

320 Negative values of the sensitivity metric indicate that for that species, productivity decreases
 321 with increasing relative asynchrony; positive values of the metric indicate that productivity
 322 increases with relative asynchrony.

323 Next, we modelled both long-term population (dN/dT ; model (7); Analysis 3a) and
 324 productivity (dP/dT ; model (8); Analysis 3b) trends for each species as a function of their
 325 sensitivity, dP/dA , including migration strategy as a covariate:

$$326 \text{ Analysis 3a: } dN/dT = \alpha + \beta_1 \cdot dP/dA + \beta_2 \cdot \text{migratory strategy} + \varepsilon \quad (7)$$

$$327 \text{ Analysis 3b: } dP/dT = \alpha + \beta_1 \cdot dP/dA + \beta_2 \cdot \text{migratory strategy} + \varepsilon \quad (8)$$

328 In models (3) and (7,8), we weighted observations according to the inverse of the standard
 329 error of the species-specific interaction coefficients from models (1) and (6), respectively, to
 330 account for uncertainty in these derived estimates.

331 *Analysis 4: Testing for a proposed causal pathway between asynchrony and productivity*

332 Finally, using a similar methodology to that proposed by McLean *et al.* (2016), we tested
 333 predictions arising from the hypothesis that the relationship between asynchrony and
 334 productivity is the result of a causal mechanistic pathway (the asynchrony-productivity
 335 pathway). We first tested for an association between productivity trend (dP/dT) and
 336 asynchrony trend (dA/dT), predicting that species which had experienced the greatest rates of
 337 increasing asynchrony over time (dA/dT) would have exhibited the greatest decreases in
 338 productivity over time (dP/dT). We tested for this negative association using the model:

$$339 \quad dP/dT = \alpha + \beta_1 \cdot dA/dT + \varepsilon \quad (9)$$

340 Secondly, if the relationship between productivity trends over time (dP/dT) and the
 341 sensitivity of productivity to asynchrony (dP/dA) is the product of a causal pathway, then
 342 dP/dT can be decomposed as:

$$343 \quad dP/dT = dA/dT \times dP/dA \quad (10)$$

344 We therefore calculated predicted dP/dT as the product of $dA/dT \times dP/dA$ and examined the
 345 correlation of predicted dP/dT with observed dP/dT . If productivity trends are a product
 346 solely of the focal pathway being considered (i.e. the effects of increasing asynchrony on
 347 productivity), then we would expect a strong correlation between these values. If the two are
 348 poorly correlated, then other traits and/or demographic pathways which we have not directly
 349 investigated in this study must have a greater effect on long-term productivity trends, and/or
 350 may be counteracting or masking any effect of asynchrony on productivity.

351 **RESULTS**

352 **Analysis 1: The relationship between rate of change in laying date and long-term** 353 **population change**

354 On average, birds in the UK have advanced their timing of breeding by 0.28 days per year
 355 since 1983 ($F_{1,540} = 49.1$, $P < 0.001$). Population trend (dN/dT) showed a significant negative
 356 relationship with rate of change in lay date (dL/dT ; $F_{1,17} = 7.26$, $P = 0.016$). Species that have
 357 advanced laying the least, and which are consequently experiencing the greatest increases in
 358 asynchrony, exhibit more negative population trends (Fig. 2).

359

360 **Analysis 2: The relationship between relative asynchrony and productivity**

361 Relative asynchrony was positively related to mean spring temperature; in warmer springs,
 362 bird phenology was later than average relative to the timing of lower trophic level taxa (Fig.
 363 3; $F_{1,580} = 71.9$, $P < 0.001$).

364 We then investigated the relationship between productivity and relative asynchrony using the
 365 model:

$$366 \text{ Annual productivity} = \alpha + \beta_1 \cdot \text{relative asynchrony} + \beta_2 \cdot \text{migration strategy} + \beta_3 \cdot \\ 367 \text{ temperature} + \beta_4 \cdot \text{precipitation} + b_1 + \varepsilon \quad (11)$$

368 We initially tested whether this relationship was dependent on migratory strategy in the
 369 global model (model (4)), but the interaction between asynchrony and migratory strategy was
 370 found to be non-significant ($\chi^2 = 3.03$, $df=2$, $P = 0.22$) and therefore removed. There was a
 371 significant negative relationship between productivity and relative asynchrony in model (11);
 372 none of the other terms were significant (Fig. 4; Table 1). Productivity was significantly
 373 lower in years where breeding was later than average relative to the phenology of lower
 374 trophic level taxa, although the marginal R^2 value (calculated after Nakagawa & Schielzeth,
 375 2013) suggests that the model explains a relatively small amount of variation in productivity
 376 (marginal $R^2 = 0.05$).

377 **Analysis 3: The relationship between the sensitivity of productivity to asynchrony and**
378 **long-term population and productivity trends**

379 Population trend (dN/dT) exhibited a significant positive relationship with the species-
380 specific productivity-asynchrony sensitivity metric (dP/dA ; Fig. 5a; Table 2), when
381 controlling for the effect of migratory strategy. Species displaying greater reductions in their
382 annual productivity as relative asynchrony increased (i.e. more negative dP/dA values) had
383 populations that were either declining or increasing at a slower rate (e.g. linnet *Carduelis*
384 *cannabina*, blue tit *Cyanistes caeruleus*). In contrast, species which showed a weaker
385 negative relationship, or even a positive association between relative asynchrony and
386 productivity, displayed more positive population trends (e.g. long-tailed tit *Aegithalos*
387 *caudatus*, whitethroat *Sylvia communis*).

388 While we would predict that long-term productivity declines (dP/dT) are the demographic
389 mechanism mediating the above association between sensitivity and population trend, when
390 we regressed sensitivity against the long-term productivity trend between 1983 and 2010,
391 controlling for the effect of migratory strategy, we found no significant relationship (Fig. 5b;
392 Table 2).

393 **Analysis 4: Testing for a proposed causal pathway between asynchrony and**
394 **productivity**

395 We first tested for an association between productivity trend (dP/dT) and asynchrony trend
396 (dA/dT). We found no support for our prediction that species which had experienced
397 increasing asynchrony over time would have more negative productivity trends ($F_{1,17} = 0.96$,
398 $P = 0.34$). We further tested for a proposed causal pathway between productivity and
399 asynchrony by decomposing productivity change (dP/dT) as the product of asynchrony
400 change and sensitivity to asynchrony ($dA/dT \times dP/dA$). Observed productivity change was

401 only weakly correlated with predicted productivity change ($dA/dT \times dP/dA$; $r = 0.088$; Fig. 6),
402 with predicted productivity values indicating that insufficient variation in productivity change
403 is predicted by the proposed pathway.

404 **DISCUSSION**

405 Previous studies have identified a significant advance in mean lay dates of British birds since
406 the 1960s in response to increasing spring temperatures (Crick *et al.*, 1997; Crick & Sparks,
407 1999). This relationship is largely mirrored in this study by advances in peak lay dates
408 between 1983 and 2010. Furthermore, we show that the population trends of common,
409 British-breeding passerines are correlated with their rate of lay date advance. Species which
410 have advanced their lay dates most substantially exhibit more positive population trends over
411 the last three decades. Advances in spring migration arrival dates have similarly been found
412 to correlate with population trends (Møller *et al.*, 2008; Newson *et al.*, 2016).

413 We attempted to identify the mechanism underlying the relationship between population
414 change and breeding phenology across a suite of bird species at a large spatial scale by
415 investigating the demographic consequences of changes in reproductive timing relative to an
416 index of spring phenology, which we use as a proxy for seasonal prey availability and
417 potential trophic asynchrony. We predicted that increasing asynchrony would be associated
418 with reduced annual productivity, resulting in long-term productivity declines that are
419 consequently the likely demographic mechanism underlying population declines.

420 We found that, as predicted by the more marked response of lower trophic levels to
421 temperature change (Thackeray *et al.*, 2016), relative asynchrony between breeding birds and
422 spring phenology increased in warmer springs. This increase in asynchrony was associated
423 with a significant but comparatively small reduction in avian productivity, accounting for
424 only 5% of the observed inter-annual variation in national productivity estimates. The

425 relationship between relative asynchrony and productivity for individual species gives a
426 measure of their sensitivity to asynchrony, which we found to be significantly related to long-
427 term population trend. Those species displaying a more negative productivity response in
428 relation to greater asynchrony exhibited more negative population trends over the study
429 period than species exhibiting less negative, or positive, responses.

430 However, despite the above associations, we found no evidence to support the hypothesis that
431 the observed relationships between asynchrony and population trends were driven by any
432 negative impact of asynchrony on productivity. Species experiencing the greatest increases in
433 asynchrony did not systematically exhibit the greatest declines in productivity over time. We
434 also found no support for the prediction that the most ‘asynchrony-sensitive’ species (defined
435 here as those whose productivity was most greatly reduced by asynchrony) would display the
436 greatest declines in productivity over time. Finally, by using a conceptual framework after
437 McLean *et al.* (2016), we demonstrated that long-term productivity change is poorly
438 explained by a direct asynchrony-productivity pathway.

439 In combination, this evidence strongly suggests that increasing asynchrony is unlikely to be
440 the main mechanism driving long-term productivity change. Our results suggest that the
441 observed positive association between long-term population change and sensitivity to
442 asynchrony is likely to be non-causal, and the product of another mechanistic pathway than
443 one operating directly via the effects of asynchrony on productivity.

444 Also, contrary to the hypothesis that the breeding success of long-distance migrants may be
445 more sensitive to asynchrony than other species and consequently driving their faster
446 population declines (Robbins *et al.*, 1989; Sanderson *et al.*, 2006; Møller *et al.*, 2008; Salido
447 *et al.*, 2012; Vickery *et al.*, 2013), we found no evidence that the relationship between
448 productivity and relative asynchrony varied with migratory distance. This is in keeping with

449 the interpretation of our other results, concluding that the negative effects of asynchrony on
450 productivity are unlikely to be a direct demographic driver of observed population declines in
451 long-distance migrants. The absence of the predicted relationship may be because
452 hypothesised constraints imposed by migratory strategies are not realised, or because the
453 effects of asynchrony on population change operate via other mechanistic pathways, as
454 discussed above. Also, other events on the breeding grounds and at passage and wintering
455 sites, such as hunting, habitat loss and degradation, and climatic variation may be much
456 stronger drivers of population change in long-distance migrants, obscuring any potential
457 impacts of asynchrony (reviewed in Vickery *et al.*, 2013). Ascertaining the primary
458 environmental drivers of population declines in long-distance migrants will first require
459 identification of demographic drivers (e.g. Johnston *et al.*, 2016; Morrison *et al.*, 2016).

460 **The relationship between relative asynchrony and productivity**

461 Evidence for a relationship between asynchrony and productivity was much weaker than
462 initially predicted. It is of course possible that our index of spring phenology may be a
463 relatively poor proxy for the temporal patterns of food availability experienced by bird
464 populations. While our study makes use of the best phenological datasets available for
465 primary producers and consumers at extensive spatial scales, there may not be a direct
466 functional link between the taxa we use as a proxy of food availability and the avian
467 consumers included in the analyses. While avian diets have been studied in detail in several
468 localised systems (e.g. Perrins, 1991; Naef-Daenzer *et al.*, 2000; Burger *et al.*, 2012), the
469 degree to which these relationships are representative of more extensive spatial scales is
470 currently unclear. Our findings are thus based upon the assumption that the spring phenology
471 index is related to broader patterns of phenology in more functionally relevant taxa.
472 However, evidence from recent studies suggests that indirect measures of spring phenology
473 (e.g. spring green-up) are likely to be indicative of the seasonal availability of functionally

474 relevant invertebrate taxa (e.g. Cole *et al.*, 2015; Hinks *et al.*, 2015; Mayor *et al.*, 2017), and
475 previous analyses of ours and other datasets have identified consistent advances in phenology
476 across a wide range of invertebrate taxa over time and in response to climate warming (e.g.
477 Roy & Sparks, 2000; Pearce-Higgins *et al.*, 2005; Hassall *et al.*, 2007; Thackeray *et al.*,
478 2010). What we are not able to account for, due to a lack of invertebrate census data, are any
479 confounding impacts of climate change on prey abundance. If warmer springs lead to both
480 greater asynchrony with prey and increased prey numbers, any negative impacts of the former
481 may be offset by the latter. This appears unlikely for many of the species considered given
482 the relative importance of moth caterpillars in their diet (Krištín & Patočka, 1997), and the
483 apparent negative effect of warming upon moth populations in the UK (Martay *et al.*, 2016).

484 Scale-dependent effects of asynchrony offer an alternative explanation for the relatively weak
485 association between relative asynchrony and productivity. They may also explain the lack of
486 a relationship between sensitivity to asynchrony and long-term productivity trends. As our
487 aim was to document the broader relationships between asynchrony and productivity across
488 large spatial scales and habitats, we evaluated relationships at the population, not the
489 individual, level. Asynchrony could have a negative impact on breeding success of some
490 individuals within the population, but others may be able to track changes in prey phenology,
491 maintaining or even improving their synchronisation with peak food availability (Cresswell
492 & McCleery, 2003; Charmantier *et al.*, 2008). The overall impact of change in seasonal
493 phenology at the population level may clearly be dampened if the individual-level effects are
494 variable. Furthermore, the relatively high potential for fine-scale variability in the extent of
495 asynchrony depending on factors such as local warming trends, habitat, and seasonal patterns
496 of prey abundance, could mean that the relatively small reduction in national-scale
497 productivity relative to increasing asynchrony is actually an accurate representation of the
498 population-level effect. The importance of scale is highlighted by recent research on willow

499 warbler *Phylloscopus trochilus*, a declining long-distance migrant in Britain with regionally
500 divergent population trends. Our models suggest this species has a strongly negative
501 productivity-asynchrony sensitivity metric and a declining population, but exhibits no strong
502 long-term productivity trend. However, research has shown that consistently low productivity
503 in southern Britain coupled with poor survival has contributed to population declines in this
504 region, but that these have been offset by recent population recovery in the north fuelled by
505 relatively high productivity (Morrison *et al.*, 2016). As we did not investigate regional
506 relationships between asynchrony and annual productivity in this study, it is plausible that
507 highly spatially variable, potentially opposing, relationships may interfere with our ability to
508 detect the predicted relationships at a national scale.

509 A third explanation is that asynchrony may typically exert only a weak influence on avian
510 breeding success relative to other environmental factors. Reed *et al.* (2013a) suggest that
511 weak population-level effects of strong individual-level asynchrony on productivity are
512 potentially a consequence of high degrees of stochasticity in demographic rates attributable to
513 other environmental factors. Annual productivity estimates in our analysis fluctuated
514 extensively from year to year, to a greater extent than predicted by asynchrony. It is thus
515 possible that unmeasured environmental factors influence productivity directly (e.g. short-
516 lived severe weather events on the breeding grounds; Siikamäki, 1996; Öberg *et al.*, 2015) or
517 indirectly via carry-over effects from wintering or passage sites (e.g. Ockendon *et al.*, 2013;
518 Finch *et al.*, 2014), possibly either counteracting or obscuring any effect of asynchrony on
519 either annual productivity and/or long-term productivity change.

520 **The relationship between sensitivity to asynchrony and long-term population trends**

521 Given the observed relationship between the sensitivity of productivity to asynchrony and
522 population trends, but the lack of evidence that this can be strongly attributed to asynchrony's

523 effects on productivity, this relationship must 1) either be the product of one or more
524 pathways operating via other trait and demographic mechanisms, and/or 2) spurious and
525 result from an unmeasured driver of population trend that also correlates with sensitivity.

526 For example, the costs of asynchrony may be expressed more strongly as reduced adult
527 survival if increased parental effort is necessitated by reduced food availability (Thomas *et*
528 *al.*, 2001; te Marvelde *et al.*, 2011). In short-lived songbirds, which constitute the majority of
529 species included in this study, we might expect parents to prioritise chick-rearing in order to
530 maximise their fitness. Alternatively, juveniles fledging from more asynchronous breeding
531 attempts may have reduced survival and therefore a lower chance of subsequent recruitment
532 into the breeding population (e.g. Sanz *et al.*, 2003). Both of these alternative demographic
533 mechanisms could plausibly explain the observed relationship between sensitivity to
534 asynchrony and population trend, if asynchrony effects are expressed only weakly via
535 productivity but more strongly via one or both of these other pathways. Recent integrated
536 demographic modelling of British-breeding birds, including some of the species in this study,
537 indeed suggests that population change may be most strongly driven by variation in
538 recruitment and adult survival rather than productivity (Robinson *et al.*, 2014).

539 However, we also cannot exclude the possibility that our findings are the consequence of an
540 unmeasured driver of population trend which also correlates with sensitivity of productivity
541 to asynchrony. For example, the observed relationship may be a consequence of habitat
542 and/or diet specialisation being simultaneously correlated with both population change and
543 sensitivity (Miller-Rushing *et al.*, 2010). More specialised species may show greater
544 sensitivity to asynchrony than generalists, and are also likely to be more sensitive to changes
545 in habitat quality, land cover and other pressures; their populations have tended to decline
546 relative to the most widespread generalists in the UK (Sullivan *et al.*, 2016).

547 Ultimately, elucidating the mechanisms by which sensitivity to asynchrony is associated with
548 population change and identifying the underlying causes of interspecific variation identified
549 in this study will require knowledge about the specific 1) functional links between
550 invertebrate prey availability and individual bird species, and 2) demographic drivers of
551 population change at the level of the individual species. Thus far, existing evidence from this
552 and other studies supporting a strong effect of asynchrony on productivity or population
553 trends has been limited (reviewed in Knudsen *et al.*, 2011; Pearce-Higgins & Green, 2014). A
554 possible explanation is that sensitivity to asynchrony is associated with sensitivity to other
555 constraints experienced either during the breeding season or at any point over the annual
556 cycle. This could be directly, if sensitive species are more likely to be affected by other
557 stressors that will alter their ability to exploit temporal peaks in key food resources, or
558 indirectly if sensitive species tend to be more specialised in their diet or habitats, and
559 therefore more susceptible to other pressures. It is therefore plausible, if not likely, that the
560 sensitivity to asynchrony identified in this study may constitute a broader index of
561 environmental stress, which will generally be more pronounced for declining species, rather
562 than asynchrony acting as a driver of population change in and of itself.

563 Trophic asynchrony as a consequence of climate change has been proposed as an important
564 factor contributing to population declines in birds, yet studies have thus far found mixed
565 evidence for a negative impact. British birds have advanced their timing of breeding over the
566 last three decades, and those species which have advanced laying the least have the most
567 negative population trends. However, annual productivity was reduced by only a small
568 amount as asynchrony increased, and species whose productivity was more sensitive to
569 asynchrony did not exhibit greater long-term declines in productivity. While species which
570 were more sensitive to asynchrony exhibited greater long-term population declines, this is
571 unlikely to be causal as our results suggest that population change is not mechanistically

572 driven by the negative impact of asynchrony on productivity. Our findings may be
573 attributable to a range of potential mechanisms: either the effects of asynchrony are more
574 likely to be strongly expressed via demographic pathways other than productivity, the effect
575 of asynchrony is scale-dependent, thus obscuring population-level effects, or perhaps most
576 likely, the effect of asynchrony on population trend is a surrogate for wider sensitivity of that
577 species to other environmental pressures, which are the ultimate cause of decline.

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832 **TABLES**

833 Table 1. Likelihood ratio test results and parameter estimates for the analysis examining the
 834 relationship between annual productivity and relative asynchrony (model (11)). Covariates
 835 were removed using single-term deletion from the linear mixed effects model: *Annual*
 836 *productivity* = $\alpha + \beta_1 \cdot \text{relative asynchrony} + \beta_2 \cdot \text{migration strategy} + \beta_3 \cdot \text{temperature} + \beta_4 \cdot$
 837 *precipitation* + $b_1 + \varepsilon$ where species (b_1) is a random intercept. Variables in bold are
 838 significant at the $p = 0.05$ level. As is convention in R, categorical fixed effect estimates for
 839 the different levels of migratory strategy are given as an absolute value for an assigned
 840 ‘reference’ level (LD) with remaining estimates given as differences from this baseline.

	Estimate	SE	df	χ^2	p
relative asynchrony	-0.003	0.002	1	4.664	0.031
migratory strategy			2	2.881	0.237
LD	1.319	0.204			
SD	-0.113	0.091			
RES	0.022	0.101			
temperature	-0.021	0.012	1	3.092	0.079
precipitation	0.000	0.001	1	0.447	0.504

841

842 Table 2. Test results and parameter estimates for the analysis examining the relationship
 843 between the productivity-asynchrony sensitivity metric (dP/dA) and long-term population
 844 (dN/dT) and productivity (dP/dT) trends. Variables in bold are significant at the $p = 0.05$
 845 level. Categorical fixed effect estimates for the different levels of migratory strategy are
 846 given as an absolute value for the ‘reference’ level (LD) with remaining estimates given as
 847 differences from this baseline.

		Estimate	SE	df	SS	MS	F	p
	migratory strategy			3	0.357	0.119	2.875	0.067
Population change	LD	0.0059	0.0076					
	SD	0.0278	0.0084					
	RES	0.0139	0.0060					
	productivity-asynchrony sensitivity metric	1.6661	0.7339	1	0.213	0.213	5.154	0.036
	residuals			17	0.703	0.041		
	migratory strategy			3	0.634	0.211	7.303	0.002
Productivity change	LD	-0.0145	0.0060					
	SD	-0.0147	0.0067					
	RES	-0.0108	0.0048					
	productivity-asynchrony sensitivity metric	0.1999	0.5855	1	0.003	0.003	0.090	0.768
	residuals			17	0.492	0.029		

848

849

850 **FIGURES**

851 Figure 1. Diagram of the analytical framework showing predictor variables and their
852 derivation. Predictors of interest are highlighted in bold. Grey-shaded boxes show the
853 analyses and their respective response variables. Analysis 4 is described in the text of the
854 Methods only. Detailed descriptions of response and predictor variables are given in Table
855 S3.

856 Figure 2. Population change (dN/dT) for individual species (identified by their 5-letter codes,
857 Table S1) between 1983 and 2010 in relation to the rate of change in lay date (dL/dT) over
858 the same period. The solid black line shows the linear regression relationship, controlling for
859 migratory strategy, while dashed lines show 95% confidence limits. The vertical grey line
860 shows the average advance in the spring phenology of all lower trophic taxa, indicating that
861 the majority of bird species are advancing their lay dates more slowly than spring phenology.

862 Figure 3. The linear regression relationship between relative asynchrony (the mean centred
863 difference between bird phenology and spring phenology) and mean spring (Mar-May)
864 temperature.

865 Figure 4. The population mean relationship \pm 95% confidence limits (solid and dashed lines
866 respectively) between annual productivity and relative asynchrony across all migratory
867 strategies, holding temperature and precipitation constant at their means. More positive
868 asynchrony values equate to birds breeding later than average relative to spring phenology.

869 Figure 5. Population (a) and productivity (b) change between 1983 and 2010 of each species
870 in relation to the productivity-asynchrony sensitivity metric (dP/dA). A value of zero on the
871 y-axis represents no long-term population or productivity change. A negative value on the x-
872 axis equates to a negative association between relative asynchrony and annual productivity.

873 The solid line shows the linear regression relationship, controlling for migratory strategy.

874 Dashed lines show 95% confidence limits.

875 Figure 6. The relationship between observed productivity change (dP/dT) and productivity
876 change as predicted by the asynchrony-productivity pathway ($dA/dT \times dP/dA$). If productivity
877 trends are a product solely of the focal pathway being considered (i.e. the effects of
878 increasing asynchrony on productivity), then we would expect a strong correlation between
879 observed dP/dT and $dA/dT \times dP/dA$ with values lying along the dotted 1:1 line.

880

881 **SUPPORTING INFORMATION**

882 Appendix 1. Detailed methods for calculating phenology metrics.

883 Table S1. Breeding bird species, their migratory strategies and nesting habitats.

884 Table S2. Lower trophic level taxa and phenology metrics.

885 Table S3. Definitions of response and predictor variables in the analyses.

886 Figure S1. Example density curves by year for a resident species showing how the peak lay
887 date metric was calculated.

888 Figure S2. Example density curves by year for a short-distance migrant species showing how
889 the peak lay date metric was calculated.

890 Figure S3. Example density curves by year for a long-distance migrant species showing how
891 the peak lay date metric was calculated.

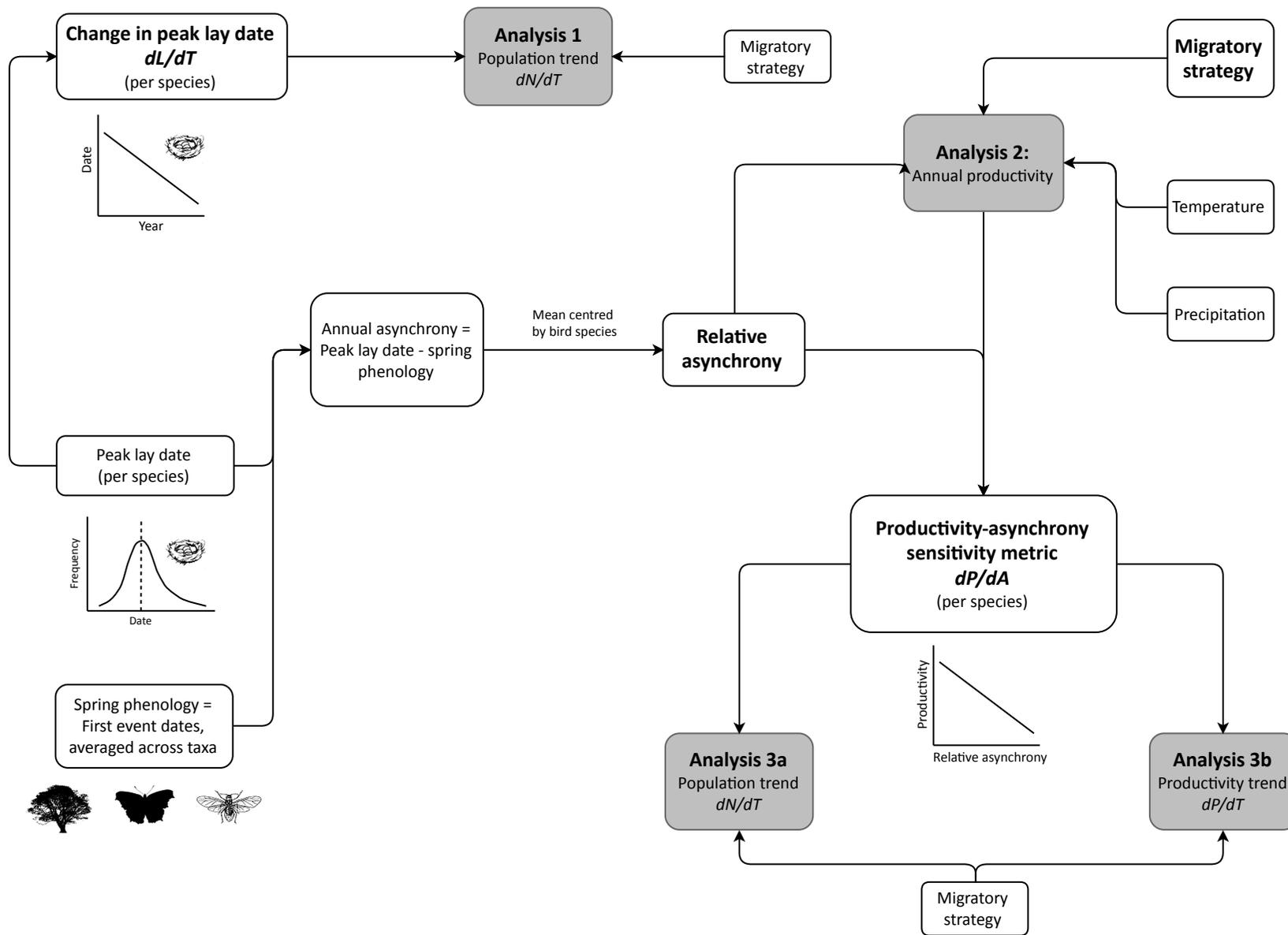
892 Figure S4. Example of bootstrapped density curves used in validation of the bird phenology
893 metric.

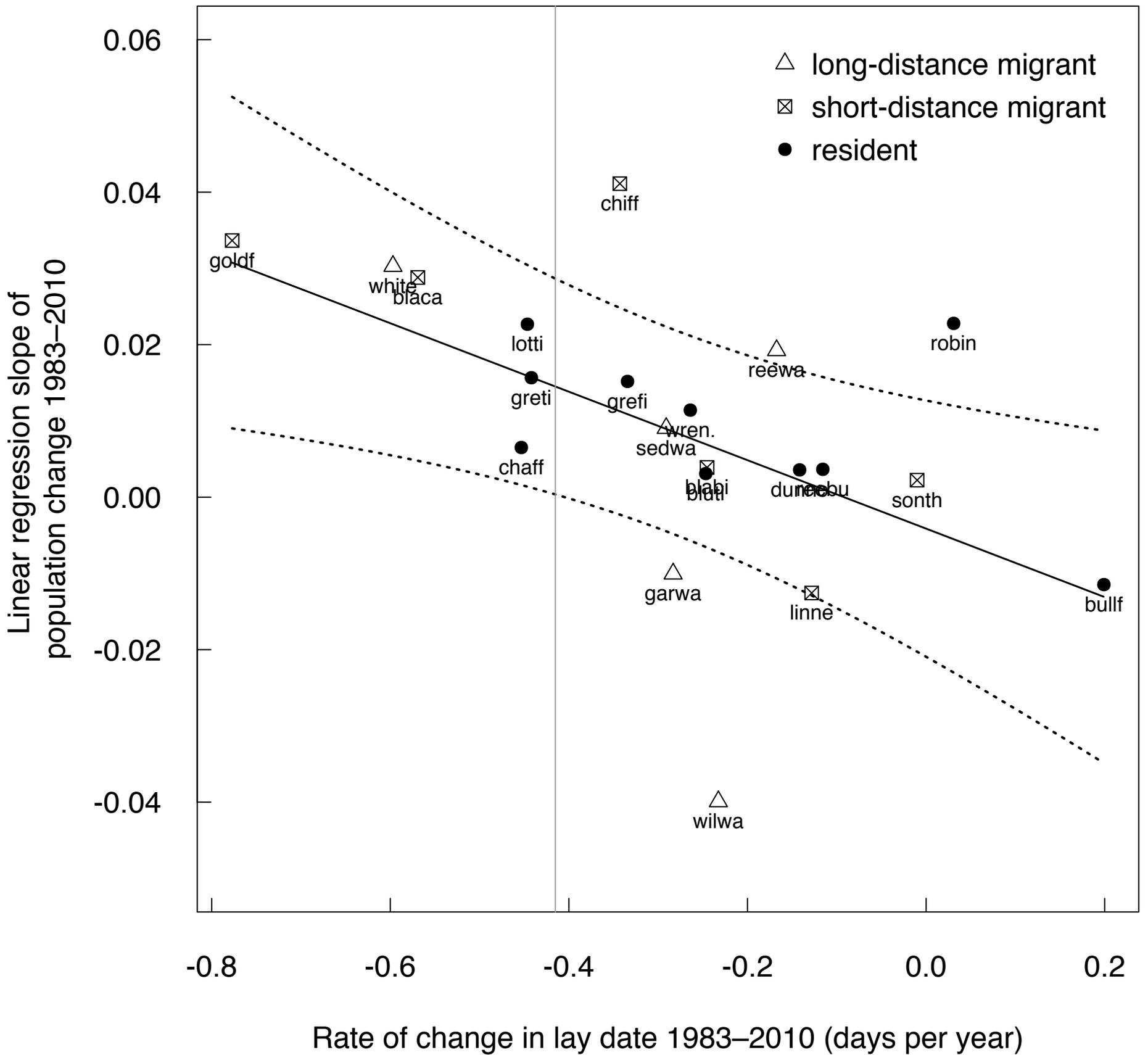
894 Figure S5. Correlation coefficients between the bootstrapped and original bird phenology
895 metrics.

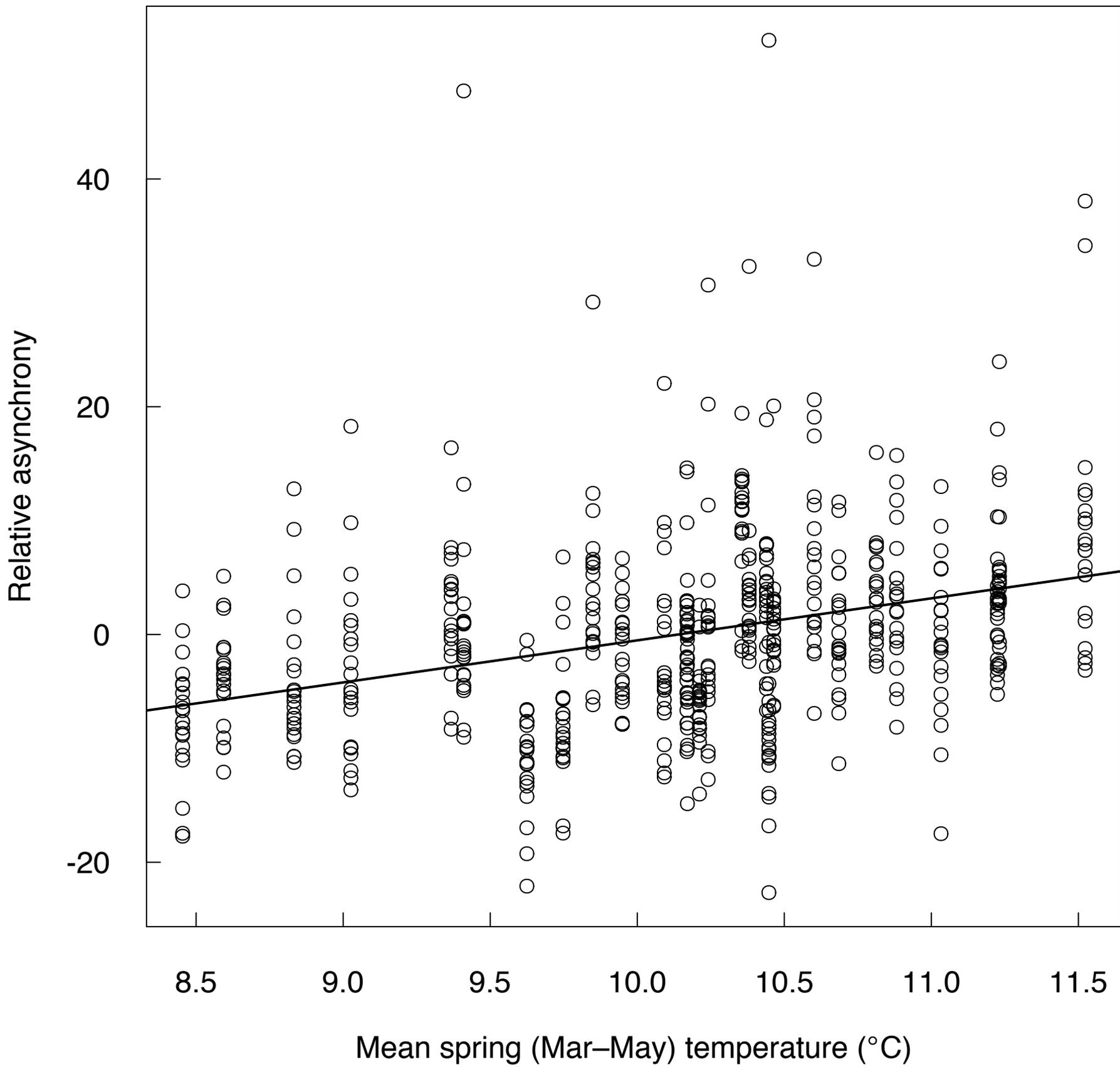
896 Figure S6. The relationship between annual phenology (mean date of first event) and year for
897 plant and invertebrate taxonomic groups.

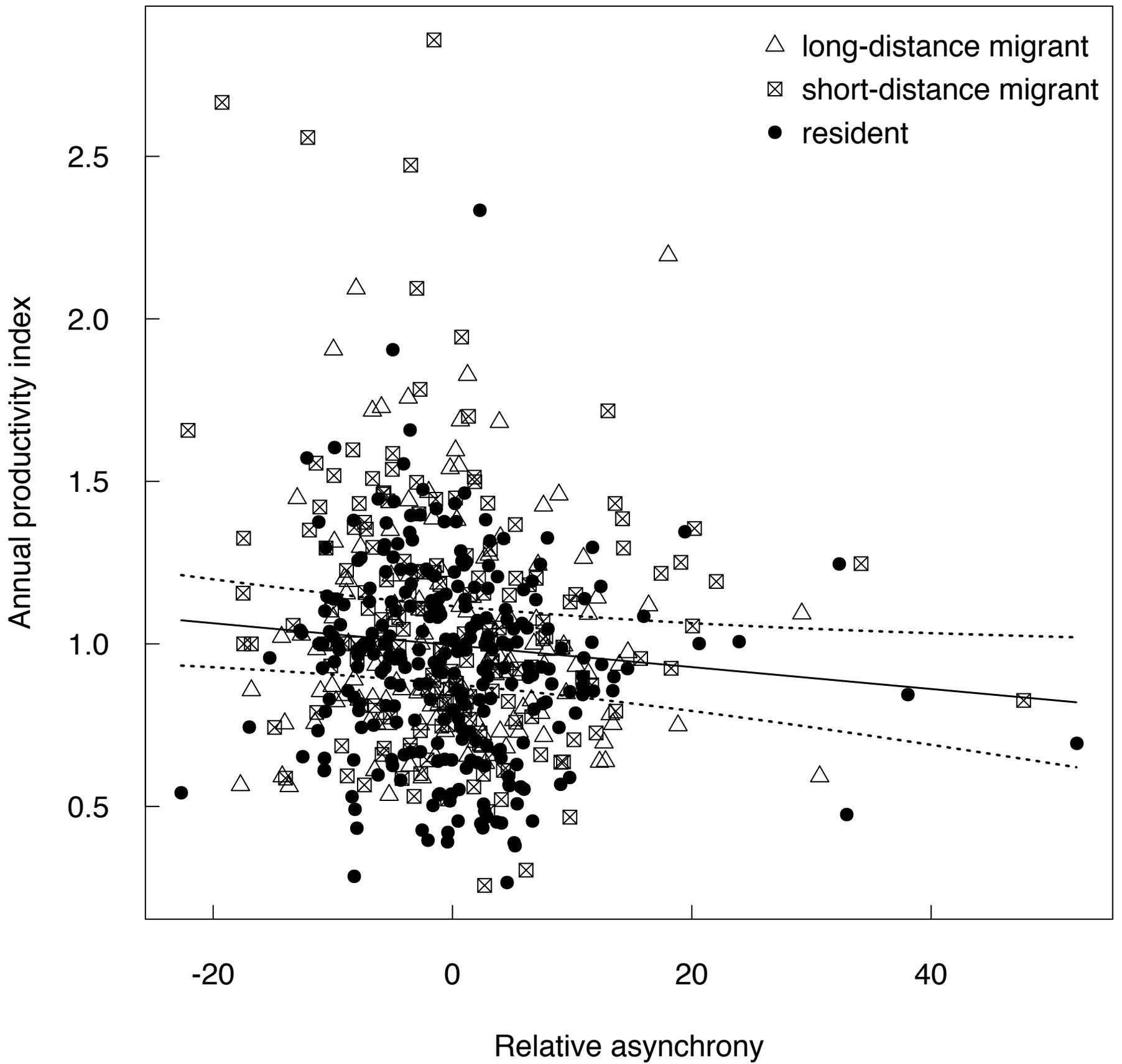
898 Figure S7. Paired plots showing correlation coefficients between plant and invertebrate
899 taxonomic groups.

900 Figure S8. Smoothed kernel density distributions showing the seasonal range of annual first
901 occurrences of birds and lower trophic level taxa.

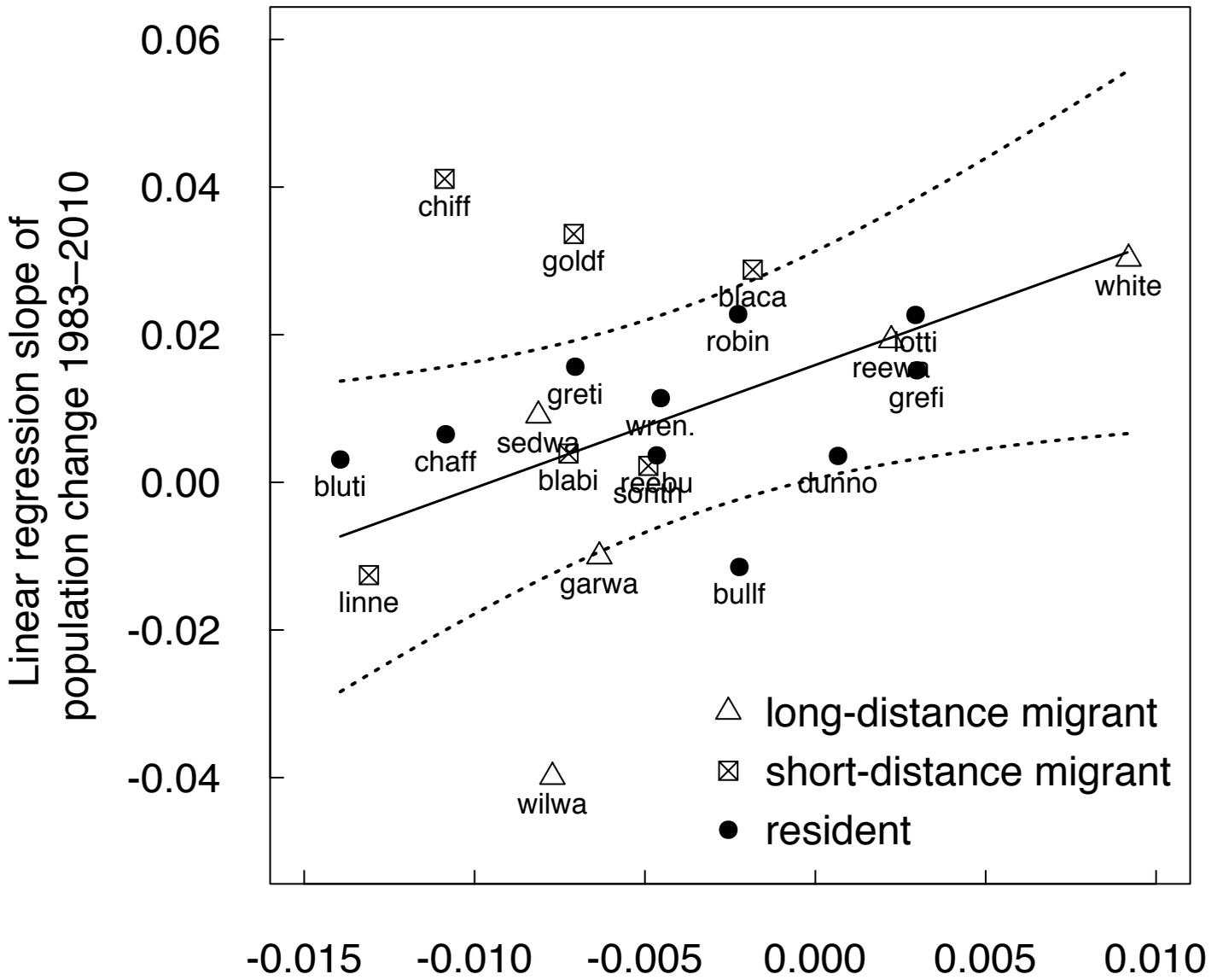








(a)



(b)

