PRIMARY RESEARCH ARTICLE

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

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Abstract

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

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

1 | INTRODUCTION

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

In birds, the ability to advance timing of breeding may be dependent on responsiveness to the seasonal cues that act as a proxy for changes in food abundance (reviewed in Visser et al., 2012). Additionally, selection for advanced breeding may be constrained, either by the costs of breeding too early (e.g. increased risk of cold temperatures and/or insufficient food resources) or by events outside of the breeding season (Finch, Pearce-Higgins, Leech, & Evans, 2014; Jones & Cresswell, 2010; Rubolini, Saino, & Møller, 2010; Visser et al., 2012). Long-distance migratory birds are hypothesized to be at greater risk of seasonal asynchrony in breeding phenology than either short-distance migrants or resident species due to (i) phenology cues experienced at distant wintering sites inadequately reflecting seasonal advancement on breeding grounds (although see Saino & Ambrosini, 2008); and/or (ii) direct constraints imposed on their ability to advance breeding phenology as a result of their migratory behaviour. While migrant laying dates have advanced in response to climate change over recent decades (Crick, Dudley, Glue, & Thomson, 1997; Dunn & Winkler, 2010; Møller, Flensted-Jensen, Klarborg, Mardal, & Nielsen, 2010; Ockendon, Leech, & Pearce-Higgins, 2013), this shift may be insufficient to match advancement of seasonal food peaks (e.g. in the case of Dutch pied flycatcher *Ficedula hypoleuca* populations: Both et al., 2006). Onset of breeding may be constrained by timing of arrival, influenced by environmental conditions away from the breeding grounds (Both, 2010; Both, Bijlsma, & Visser, 2005; Both & Visser, 2001; Finch et al., 2014), and there is evidence that arrival dates of European migrants wintering in sub-Saharan Africa have advanced less rapidly than those of short-distance migrants (Rubolini, Møller, Rainio, & Lehikoinen, 2007; but see Pearce-Higgins & Green, 2014; fig. 2.3). If long-distance migrants are more constrained in their ability to track changes in their breeding environment, the temporal overlap between peak prey availability and offspring demand may be reduced relative to that experienced by short-distance migrants and residents; consequently, long-distance migrants may be more sensitive to further increases in asynchrony. This hypothesis has been suggested as a potential explanation for the more rapid population declines observed in long-distance migratory species (Møller, Rubolini, & Lehikoinen, 2008; Robbins, Sauer, Greenberg, & Droege, 1989; Salido, Purse, Marrs, Chamberlain, & Shultz, 2012; Sanderson, Donald, Pain, Burfield, & van Bommel, 2006; Vickery et al., 2013).

However, there remains uncertainty about the extent to which asynchrony might influence the population dynamics of birds (reviewed in Knudsen et al., 2011; Pearce-Higgins & Green, 2014). To date, much of the evidence relating migrant declines to mismatch has been indirect (e.g. Cormont, Vos, van Turnhout, Foppen, & ter Braak, 2011; Jones & Cresswell, 2010; Saino et al., 2011) and a more recent, comparative study found no evidence of an influence of asynchrony on population trends of a wide range of European and North American bird species (Dunn & Møller, 2014). Furthermore, several recent mechanistic studies identifying relationships between avian phenology and productivity have failed to find any resultant impact on population size (McLean, Lawson, Leech, & van de Pol, 2016; Reed, Jenouvrier, & Visser, 2013). It could therefore be possible that confounding variables related to both laying date and population trends are responsible for the observed relationships; teasing apart such relationships highlights the need for further mechanistic studies.

Only a few studies have directly investigated the relationship between asynchrony and either demography or population change, and these too have demonstrated mixed results (e.g. see table 3 in Dunn, Winkler, Whittingham, Hannon, & Robertson, 2011). While some have identified a negative relationship (e.g. pied flycatcher Both et al., 2006; black grouse *Tetrao tetrix* Ludwig et al., 2006), the strength of the effect has been variable and other studies have found little evidence of impacts (e.g. European golden plover *Pluvialis apricaria* Pearce-Higgins, Dennis, Whittingham, & Yalden, 2010; tree swallow *Tachycineta bicolor* Dunn et al., 2011; great tit Reed, Grøtan, Jenouvrier, Saether, & Visser, 2013). As yet, there is no robust evidence linking changes in asynchrony between birds and their prey to broad-scale variation in productivity or population trends.

It is perhaps unsurprising that studies predicting a general effect of climate change-induced asynchrony on population-level processes have produced conflicting evidence, as there is likely to be considerable variation in the extent of asynchrony between individuals, populations and species. The magnitude of asynchrony observed is likely to depend on many factors, including, but not limited to, spatial variability in spring phenology and peaks in prey abundance; seasonal variation in the rate of warming, should species respond to differently timed cues; habitat seasonality; the strength of seasonality in local prey abundance (sharp versus broad or no peak); the proportion of the population that produces multiple broods; and constraints on the ability of individuals to shift reproductive timing due to events outside of the breeding season (Cresswell & McCleery, 2003; Visser et al., 2003; Both et al., 2006, 2010; Durant, Hjermann, Ottersen, & Stenseth, 2007; Charmantier et al., 2008; Møller, 2008; Burger et al., 2012; Cole, Long, Zelazowski, Szulkin, & Sheldon, 2015; Hinks et al.,

2015; Mayor et al., 2017). While single-population or single-species studies make it difficult to generalize the impacts of seasonal asynchrony, a multi-species, broad-scale approach can produce a more robust assessment of the broad effects of climate change-induced asynchrony on avian population dynamics. Furthermore, any variation between species may help to identify the ecological and demographic mechanisms by which asynchrony may influence abundance.

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

Using this mechanistic approach, we predict that those species which have advanced egg-laying dates the most over time will exhibit more positive population trends (Hypothesis 1). If the mechanism underlying this relationship is indeed attributable to increasing asynchrony with climate warming, we further predict that (a) asynchrony will increase with warmer temperatures; (b) in years of greatest asynchrony, avian productivity will be reduced; and (c) the most negative consequences will be exhibited by long-distance migrants (Hypothesis 2). We expect that those species demonstrating the greatest reductions in productivity as a result of trophic asynchrony are most likely to have experienced the greatest declines in both population size and productivity over the study period (Hypothesis 3). Finally, we expect the associations predicted above to be the result of a causal mechanistic pathway (the asynchrony–productivity pathway; Hypothesis 4).

2 | MATERIALS AND METHODS

2.1 | Bird phenology

The British Trust for Ornithology's (BTO's) Nest Record Scheme (NRS) uses volunteer-collected data to quantify the annual breeding performance of a broad range of bird species across Britain (see Crick, Baillie, & Leech, 2003 for full methods). Observers monitor individual nesting attempts and record location, visit date, and the number and developmental stage of any eggs or chicks present. Very few nests are found during laying, so clutch initiation (first egg) dates are rarely known with certainty. Instead, they are back-

calculated to produce a minimum and maximum lay date estimate (Crick et al., 2003), with the mid-point of this range taken as the nest-specific first egg date estimate, excluding any records where the range is greater than 10 days. In our dataset of 80,495 nests found between 1983 and 2010, the mean value of this range is 5.4 days. Using these nest data, we developed an annual lay date metric for 21 common UK-breeding terrestrial passerines (see Table S1) that represents the peak in initiation of first broods and, consequently, the onset of the breeding season (Figure 1; see Appendix S1 for lay date calculation method and Figs S1–S3 for examples). We only calculated a lay date metric for a species in a given year if at least 10 nests of that species were monitored. The robustness of these estimates was assessed by bootstrapping (Appendix S1; Figs S4 and S5).

2.2 | Spring phenology

We derived a spring phenology metric for primary consumers and producers by modelling first event dates in each year (1983–2010) using survey data from the UK Phenology Network (plants: first flowering and/or leaf dates; www.naturescalendar.org.uk), Rothamsted Research suction traps (aphids: first flight dates; see Bell et al., 2015 for methods) and light traps (moths: fifth percentile of catch date; see Conrad, Warren, Fox, Parsons, & Woiwod, 2006 for methods), and the UK Butterfly Monitoring Scheme (butterflies: first appearance on survey transects; see www.ukbms.org for methods). Annual metrics from all taxonomic groups were correlated with each other (Fig S7), and were averaged to create a single, annual index of spring phenology (Figure 1; see Appendix S1 for a complete description of methods and Figs S6 and S8 for the annual and seasonal variation in phenology across taxonomic groups; Table S2 gives all species included in the spring phenology metric calculations).

2.3 | Relative asynchrony

Direct estimates of the seasonal variation in abundance of avian prey that can be directly matched (i.e. functionally linked) to bird phenology (e.g. as for Visser, van Noordwijk, Tinbergen, & Lessells, 1998; Visser et al., 2015; Burger et al., 2012; Reed, Jenouvrier et al., 2013) were not available at a national scale. We therefore cannot explicitly say whether a species is "matched" or "mismatched" with the peak abundance of its prey. Instead, we derived a measure of *relative asynchrony* for each species by relating our measure of spring phenology to the timing of bird egg laying. Specifically, we subtracted the annual spring phenology metric derived from plants and invertebrates above, from the estimated annual lay date metric for each bird species to derive an annual index of the timing of breeding relative to spring phenology (i.e. an index of annual asynchrony; Figure 1). Because we do not know the actual degree of temporal matching between the bird species featured in this study and the phenology of their prey, the absolute annual asynchrony values are unimportant; for one species, breeding 30 days before the spring phenology metric may be optimal, whilst for another optimal
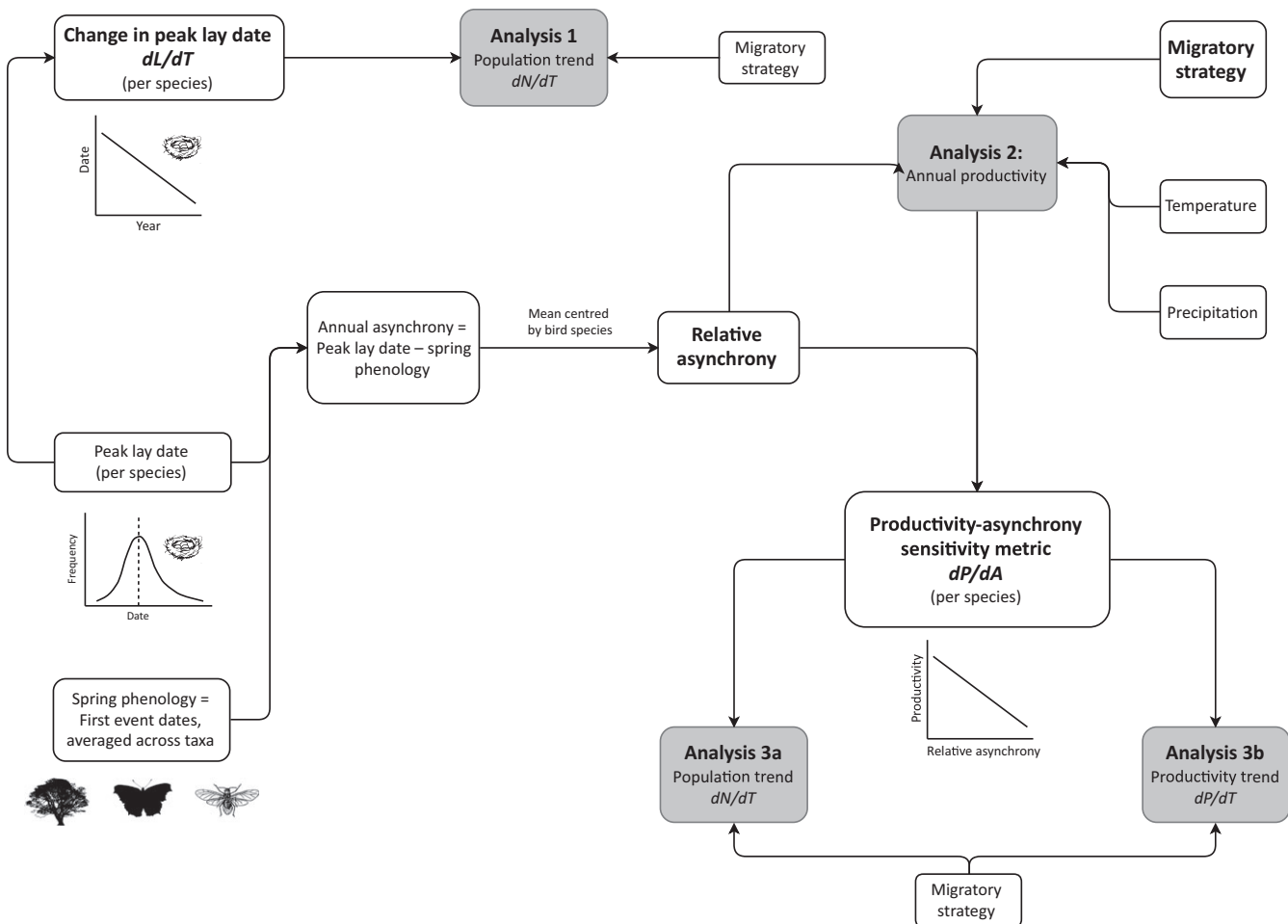
FIGURE 1 Diagram of the analytical framework showing predictor variables and their derivation. Predictors of interest are highlighted in bold. Grey-shaded boxes show the analyses and their respective response variables. Analysis 4 is described in the text of the Methods only. Detailed descriptions of response and predictor variables are given in Table S3

breeding may occur 20 days afterwards. Instead, we focus on comparing species-specific variation in annual asynchrony values *relative to* the species-specific mean over the study period. To permit comparison of this relative change across species, we centred annual asynchrony values by taking the difference between each annual value and the mean value (mean asynchrony) for each species across the study period. The resulting scaled metric (hereafter referred to simply as relative asynchrony; Figure 1) represents apparent asynchrony, or divergence from average levels of asynchrony for that species: positive values occur in years when birds breed relatively later than average for the species with respect to spring phenology; negative values occur in years where birds breed earlier than average.

2.4 | Bird productivity

Annual productivity indices (ratio of juveniles to adults) were generated from capture data collected during standardized mist-netting and ringing activities of volunteers at ~130 sites across Britain operated as part of the BTO's Constant Effort Sites (CES) scheme (Peach,

Buckland, & Baillie, 1996; Robinson, Julliard, & Sarraco, 2009). The CES productivity estimate integrates productivity across the full season (i.e. the number of young raised to independence across all broods), which is likely to be representative of full-season productivity for multi-brooded species, and also incorporates a component of post-fledging mortality. The CES productivity estimate thus provides a better estimate of the annual production of potential recruits (Streby, Refsnider, & Andersen, 2014) than simply using the number of fledglings produced per nesting attempt derived from individual nesting attempts recorded under the Nest Record Scheme. Previous analyses of these data show associations with population trends or temperature (e.g. Eglington et al., 2014; Morrison, Robinson, Butler, Clark, & Gill, 2016; Robinson, Morrison, & Baillie, 2014), so they are likely to be a robust estimate of true productivity.

2.5 | Migratory strategy

To determine whether the effects of variation in relative asynchrony are dependent on migratory strategy, species were classified as long-distance (sub-Saharan) migrants (*n* = 5), short-distance (intra-

European) migrants ($n = 6$) and residents (where over-wintering range in the UK is approximately the same as the breeding range, $n = 10$; see Table S1). Classification followed Wernham et al. (2002) and Thaxter, Joys, Gregory, Baillie, and Noble (2010), but chiffchaff *Phylloscopus collybita* was classified as a predominantly short-distance migrant given the relative paucity of sub-Saharan ringing recoveries for this species (Robinson, Marchant et al., 2015).

2.6 | Weather effects on productivity

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

2.7 | Conceptual framework for testing predictions

We use a conceptual framework analogous to that of McLean et al. (2016) to test our predictions that increasing asynchrony is related to reduced annual productivity, resulting in long-term productivity declines that are likely to in turn drive population declines. We present the linear effects of x on y as dy/dx, with the productivity–asynchrony relationship given as dP/dA, and laying date, asynchrony, long-term productivity and long-term population trends given as dL/dT, dA/dT, dP/dT and dN/dT, respectively.

2.8 | Statistical analyses

2.8.1 | Analysis 1: The relationship between rate of change in laying date and long-term population change

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

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

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

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

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

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

2.8.2 | Analysis 2: The relationship between relative asynchrony and productivity

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

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

We also tested whether differences in the relationship between productivity and relative asynchrony according to migratory strategy were influenced by relatedness between species. Using a likelihood

ratio test, we found that the species effect alone produced a more optimal random effects structure than when species was nested within family (1|family/species; $\chi^2 = 0.050$, $p = .82$) or within genus (1|genus/species; $\chi^2 = 1.18$, $p = .27$). This indicates that responses exhibited by individual species were independent of phylogenetic relatedness.

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

$$\begin{aligned}\text{Annual productivity} = &\; \alpha + \beta_1 \cdot \text{relative asynchrony} \\ &+ \beta_2 \cdot \text{migration strategy} \\ &+ \beta_3 \cdot \text{relative asynchrony} \cdot \text{migration strategy} \\ &+ \beta_4 \cdot \text{temperature} + \beta_5 \cdot \text{precipitation} \\ &+ b_1 + \varepsilon\end{aligned}$$

(4)

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

$$\begin{aligned}\text{Annual productivity} = &\; \alpha + \beta_1 \cdot \text{relative asynchrony} \\ &+ \beta_2 \cdot \text{relative asynchrony}^2 \\ &+ \beta_3 \cdot \text{migration strategy} + \beta_4 \cdot \text{temperature} \\ &+ \beta_5 \cdot \text{precipitation} + b_1 + \varepsilon\end{aligned}$$

(5)

However, the quadratic term was non-significant ($\chi^2 = 0.485$, $df = 1$, $p = .49$). Models testing different fixed effects were fitted using the maximum likelihood method with the *lme* function.

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

2.8.3 | Analysis 3: The relationship between the sensitivity of productivity to asynchrony and long-term population and productivity trends

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

We first derived a species-specific productivity–asynchrony sensitivity metric (hereafter simply "sensitivity" or d*P/*d*A*; Figure 1) by calculating the absolute slope of the productivity–asynchrony relationship for each individual species ($\beta_1 + \beta_3$) in the model:

$$\begin{aligned}\text{Annual productivity} = &\; \alpha + \beta_1 \cdot \text{relative asynchrony} + \beta_2 \cdot \text{species} \\ &+ \beta_3 \cdot \text{relative asynchrony} \cdot \text{species} \\ &+ \beta_4 \cdot \text{temperature} + \beta_5 \cdot \text{precipitation} + \varepsilon\end{aligned}$$

(6)

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

Next, we modelled both long-term population (d*N/*d*T*; model (7); Analysis 3a) and productivity (d*P/*d*T*; model (8); Analysis 3b) trends for each species as a function of their sensitivity, d*P/*d*A*, including migration strategy as a covariate:

$$\text{Analysis 3a}: \mathrm{d}N/\mathrm{d}T = \alpha + \beta_1 \cdot \mathrm{d}P/\mathrm{d}A + \beta_2 \cdot \text{migratory strategy} + \varepsilon$$

(7)

$$\text{Analysis 3b}: \mathrm{d}P/\mathrm{d}T = \alpha + \beta_1 \cdot \mathrm{d}P/\mathrm{d}A + \beta_2 \cdot \text{migratory strategy} + \varepsilon$$

(8)

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

2.8.4 | Analysis 4: Testing for a proposed causal pathway between asynchrony and productivity

Finally, using a similar methodology to that proposed by McLean et al. (2016), we tested predictions arising from the hypothesis that the relationship between asynchrony and productivity is the result of a causal mechanistic pathway (the asynchrony–productivity pathway). We first tested for an association between productivity trend (d*P/*d*T*) and asynchrony trend (d*A/*d*T*), predicting that species which had experienced the greatest rates of increasing asynchrony over time (d*A/*d*T*) would have exhibited the greatest decreases in productivity over time (d*P/*d*T*). We tested for this negative association using the model:

$$\mathrm{d}P/\mathrm{d}T = \alpha + \beta_1 \cdot \mathrm{d}A/\mathrm{d}T + \varepsilon$$

(9)

Secondly, if the relationship between productivity trends over time (d*P/*d*T*) and the sensitivity of productivity to asynchrony (d*P/*d*A*) is the product of a causal pathway, then d*P/*d*T* can be decomposed as:

$$\mathrm{d}P/\mathrm{d}T = \mathrm{d}A/\mathrm{d}T \times \mathrm{d}P/\mathrm{d}A$$

(10)

We therefore calculated predicted d*P/*d*T* as the product of d*A/*d*T* × d*P/*d*A* and examined the correlation of predicted d*P/*d*T* with observed d*P/*d*T*. If productivity trends are a product solely of the focal pathway being considered (i.e. the effects of increasing asynchrony on productivity), then we would expect a strong correlation between these values. If the two are poorly correlated, then other traits and/or demographic pathways which we have not

directly investigated in this study must have a greater effect on long-term productivity trends, and/or may be counteracting or masking any effect of asynchrony on productivity.

3 | RESULTS

3.1 | Analysis 1: The relationship between rate of change in laying date and long-term population change

On average, birds in the UK have advanced their timing of breeding by 0.28 days per year since 1983 ($F_{1,540} = 49.1$, $p < .001$). Population trend (dN/dT) showed a significant negative relationship with rate of change in lay date (dL/dT; $F_{1,17} = 7.26$, $p = .016$). Species that have advanced laying the least, and which are consequently experiencing the greatest increases in asynchrony, exhibit more negative population trends (Figure 2).

3.2 | Analysis 2: The relationship between relative asynchrony and productivity

Relative asynchrony was positively related to mean spring temperature; in warmer springs, bird phenology was later than average relative to the timing of lower trophic level taxa (Figure 3; $F_{1,580} = 71.9$, $p < .001$).
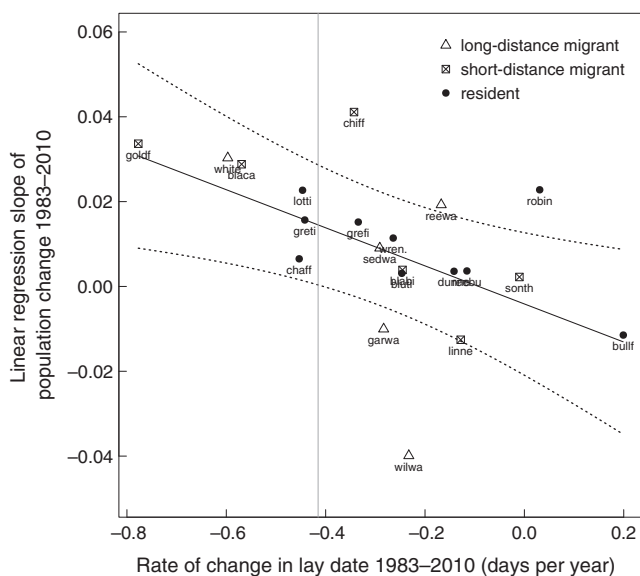

FIGURE 3 The linear regression relationship between relative asynchrony (the mean centred difference between bird phenology and spring phenology) and mean spring (March–May) temperature

We initially tested whether the relationship between productivity and relative asynchrony was dependent on migratory strategy, given as the interaction in the global model (model [4]). This interaction was found to be non-significant ($\chi^2 = 3.03$, $df = 2$, $p = .22$) and was therefore removed, giving the model:

$$
\begin{aligned}
\text{Annual productivity} = \alpha + \beta_1 \cdot \text{relative asynchrony} \\
+ \boldsymbol{\beta_2} \cdot \text{migration strategy} + \beta_3 \cdot \text{temperature} \\
+ \beta_4 \cdot \text{precipitation} + b1 + \varepsilon
\end{aligned}
$$

$$(11)$$

There was a significant negative relationship between productivity and relative asynchrony in this model; none of the other terms were significant (Figure 4; Table 1). Productivity was significantly lower in years where breeding was later than average relative to the phenology of lower trophic level taxa although the marginal R^2 value (calculated after Nakagawa & Schielzeth, 2013) suggests that the model explains a relatively small amount of variation in productivity (marginal $R^2 = .05$).

3.3 | Analysis 3: The relationship between the sensitivity of productivity to asynchrony and long-term population and productivity trends

Population trend (dN/dT) exhibited a significant positive relationship with the species-specific productivity–asynchrony sensitivity metric (dP/dA; Figure 5a; Table 2), when controlling for the effect of migratory strategy. Species displaying greater reductions in their annual productivity as relative asynchrony increased (i.e. more negative dP/dA values) had populations that were either declining or increasing at a slower rate (e.g. linnet *Carduelis cannabina*, blue tit *Cyanistes caeruleus*). In contrast, species which showed a weaker negative

FIGURE 2 Population change (dN/dT) for individual species (identified by their 5-letter codes, Table S1) between 1983 and 2010 in relation to the rate of change in lay date (dL/dT) over the same period. The solid black line shows the linear regression relationship, controlling for migratory strategy, while dashed lines show 95% confidence limits. The vertical grey line shows the average advance in the spring phenology of all lower trophic taxa, indicating that the majority of bird species are advancing their lay dates more slowly than spring phenology
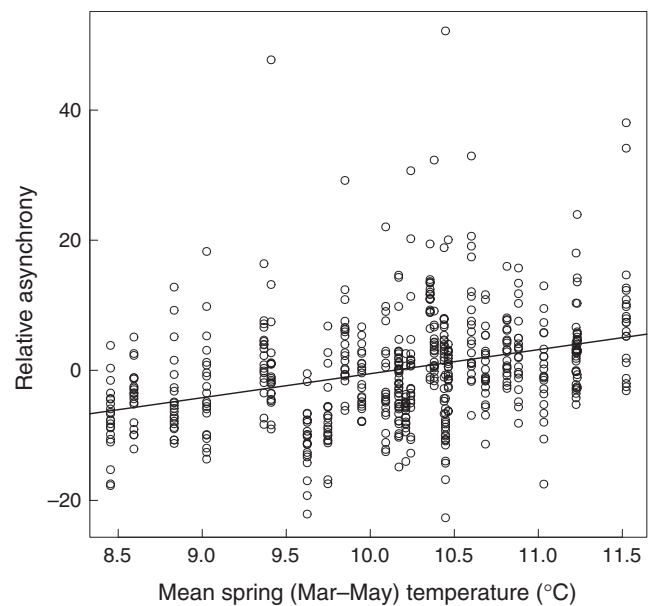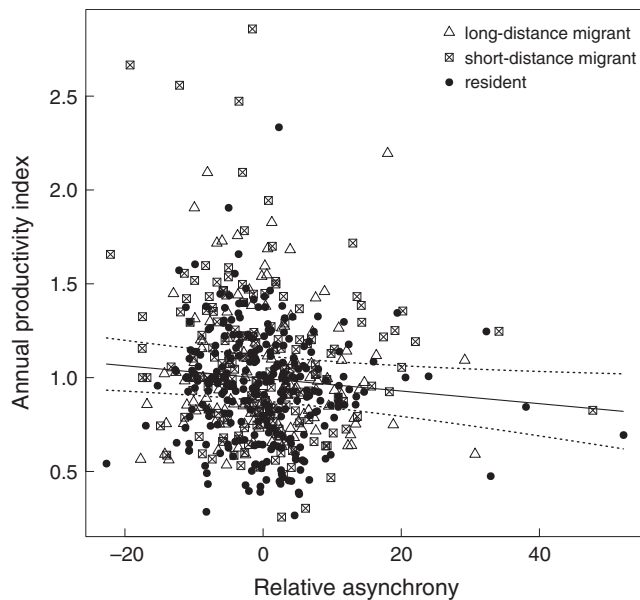
FIGURE 4 The population mean relationship ± 95% confidence limits (solid and dashed lines, respectively) between annual productivity and relative asynchrony across all migratory strategies, holding temperature and precipitation constant at their means. More positive asynchrony values equate to birds breeding later than average relative to spring phenology

TABLE 1 Likelihood ratio test results and parameter estimates for the analysis examining the relationship between annual productivity and relative asynchrony (model [11])

	Estimate	SE	df	χ^2	p
Relative asynchrony	**−0.003**	**0.002**	**1**	**4.664**	**.031**
Migratory strategy			2	2.881	.237
LD	1.319	0.204			
SD	−0.113	0.091			
RES	0.022	0.101			
Temperature	−0.021	0.012	1	3.092	.079
Precipitation	0.000	0.001	1	0.447	.504

Covariates were removed using single-term deletion from the linear mixed effects model: Annual productivity = α + β_1·relative asynchrony + β_2·migration strategy + β_3·temperature + β_4·precipitation + b_1 + ε where species (b_1) is a random intercept. Variables in bold are significant at the p = .05 level. As is convention in R, categorical fixed effect estimates for the different levels of migratory strategy are given as an absolute value for an assigned "reference" level (LD) with remaining estimates given as differences from this baseline.

relationship, or even a positive association between relative asynchrony and productivity, displayed more positive population trends (e.g. long-tailed tit *Aegithalos caudatus*, whitethroat *Sylvia communis*).

While we would predict that long-term productivity declines (d*P*/d*T*) are the demographic mechanism mediating the above association between sensitivity and population trend, when we regressed sensitivity against the long-term productivity trend between 1983 and 2010, controlling for the effect of migratory strategy, we found no significant relationship (Figure 5b; Table 2).
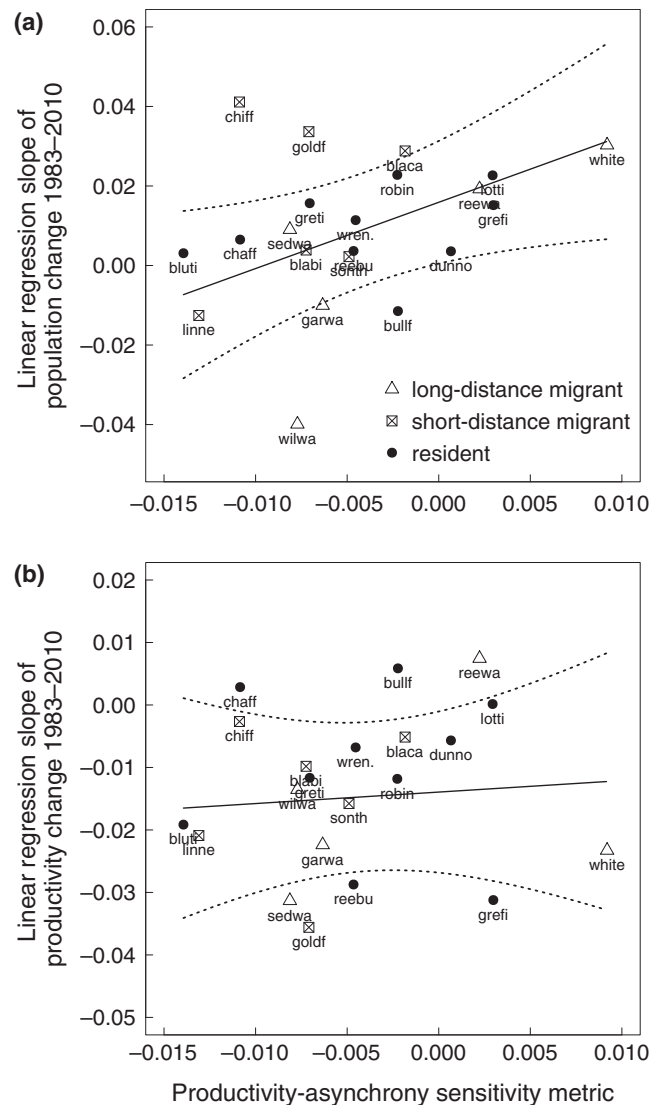

FIGURE 5 Population (a) and productivity (b) change between 1983 and 2010 of each species in relation to the productivity–asynchrony sensitivity metric (d*P*/d*A*). A value of zero on the *y*-axis represents no long-term population or productivity change. A negative value on the *x*-axis equates to a negative association between relative asynchrony and annual productivity. The solid line shows the linear regression relationship, controlling for migratory strategy. Dashed lines show 95% confidence limits

3.4 | Analysis 4: Testing for a proposed causal pathway between asynchrony and productivity

We first tested for an association between productivity trend (d*P*/d*T*) and asynchrony trend (d*A*/d*T*). We found no support for our prediction that species which had experienced increasing asynchrony over time would have more negative productivity trends ($F_{1,17}$ = 0.96, p = .34). We further tested for a proposed causal pathway between productivity and asynchrony by decomposing productivity change (d*P*/d*T*) as the product of asynchrony change and sensitivity to asynchrony (d*A*/d*T* × d*P*/d*A*). Observed productivity change was only weakly correlated with predicted productivity change (d*A*/d*T* × d*P*/d*A*; r = .088; Figure 6), with predicted

TABLE 2 Test results and parameter estimates for the analysis examining the relationship between the productivity–asynchrony sensitivity metric (dP/dA) and long-term population (dN/dT) and productivity (dP/dT) trends

	Estimate	SE	df	SS	MS	F	p
Population change							
Migratory strategy			3	0.357	0.119	2.875	.067
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**	**.036**
Residuals			17	0.703	0.041		
Productivity change							
Migratory strategy			**3**	**0.634**	**0.211**	**7.303**	**.002**
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	.768
Residuals			17	0.492	0.029		

Variables in bold are significant at the p = .05 level. Categorical fixed effect estimates for the different levels of migratory strategy are given as an absolute value for the "reference" level (LD) with remaining estimates given as differences from this baseline.

productivity values indicating that insufficient variation in productivity change is predicted by the proposed pathway.
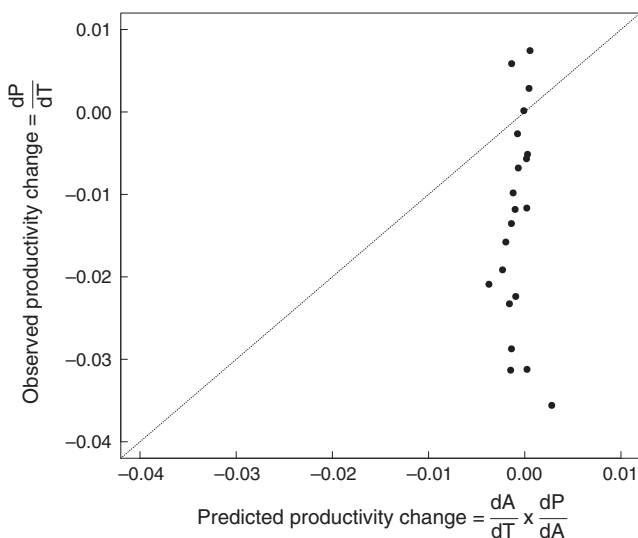
4 | DISCUSSION

Previous studies have identified a significant advance in mean lay dates of British birds since the 1960s in response to increasing spring temperatures (Crick & Sparks, 1999; Crick et al., 1997). This

FIGURE 6 The relationship between observed productivity change (dP/dT) and productivity change as predicted by the asynchrony–productivity pathway (dA/dT × dP/dA). If productivity trends are a product solely of the focal pathway being considered (i.e. the effects of increasing asynchrony on productivity), then we would expect a strong correlation between observed dP/dT and dA/dT × dP/dA with values lying along the dotted 1:1 line

relationship is largely mirrored in this study by advances in peak lay dates between 1983 and 2010. Furthermore, we show that the population trends of common, British-breeding passerines are correlated with their rate of lay date advance. Species which have advanced their lay dates most substantially exhibit more positive population trends over the last three decades. Advances in spring migration arrival dates have similarly been found to correlate with population trends (Møller et al., 2008; Newson et al., 2016).

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

We found that, as predicted by the more marked response of lower trophic levels to temperature change (Thackeray et al., 2016), relative asynchrony between breeding birds and spring phenology increased in warmer springs. This increase in asynchrony was associated with a significant but comparatively small reduction in avian productivity, accounting for only 5% of the observed inter-annual variation in national productivity estimates. The relationship between relative asynchrony and productivity for individual species gives a measure of their sensitivity to asynchrony, which we found to be significantly related to long-term population trend. Those species displaying a more negative productivity response in relation to greater asynchrony exhibited more negative population trends over the study period than species exhibiting less negative, or more positive, responses.

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

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

Also, contrary to the hypothesis that the breeding success of long-distance migrants may be more sensitive to asynchrony than other species and consequently driving their faster population declines (Møller et al., 2008; Robbins et al., 1989; Salido et al., 2012; Sanderson et al., 2006; Vickery et al., 2013), we found no evidence that the relationship between productivity and relative asynchrony varied with migratory distance. This is in keeping with the interpretation of our other results, concluding that the negative effects of asynchrony on productivity are unlikely to be a direct demographic driver of observed population declines in long-distance migrants. The absence of the predicted relationship may be because hypothesized constraints imposed by migratory strategies are not realized, or because the effects of asynchrony on population change operate via other mechanistic pathways, as discussed above. Also, other events on the breeding grounds and at passage and wintering sites, such as hunting, habitat loss and degradation, and climatic variation may be much stronger drivers of population change in long-distance migrants, obscuring any potential impacts of asynchrony (reviewed in Vickery et al., 2013). Ascertaining the primary environmental drivers of population declines in long-distance migrants will first require identification of demographic drivers (e.g. Johnston et al., 2016; Morrison et al., 2016).

4.1 | The relationship between relative asynchrony and productivity

Evidence for a relationship between asynchrony and productivity was much weaker than initially predicted. It is of course possible that our index of spring phenology may be a relatively poor proxy for the temporal patterns of food availability experienced by bird populations. While our study makes use of the best phenological datasets available for primary producers and consumers at extensive spatial scales, there may not be a direct functional link between the taxa we use as a proxy of food availability and the avian consumers

included in the analyses. While avian diets have been studied in detail in several localized systems (e.g. Burger et al., 2012; Naef-Daenzer, Naef-Daenzer, & Nager, 2000; Perrins, 1991), the degree to which these relationships are representative of more extensive spatial scales is currently unclear. Our findings are thus based upon the assumption that the spring phenology index is related to broader patterns of phenology in more functionally relevant taxa. However, evidence from recent studies suggests that indirect measures of spring phenology (e.g. spring green-up) are likely to be indicative of the seasonal availability of functionally relevant invertebrate taxa (e.g. Cole et al., 2015; Hinks et al., 2015; Mayor et al., 2017), and previous analyses of ours and other datasets have identified consistent advances in phenology across a wide range of invertebrate taxa over time and in response to climate warming (e.g. Hassall, Thompson, French, & Harvey, 2007; Pearce-Higgins, Yalden, & Whittingham, 2005; Roy & Sparks, 2000; Thackeray et al., 2010). What we are not able to account for, due to a lack of invertebrate census data, are any confounding impacts of climate change on prey abundance. If warmer springs lead to both greater asynchrony with prey and increased prey numbers, any negative impacts of the former may be offset by the latter. This appears unlikely for many of the bird species considered given the relative importance of moth caterpillars in their diet (Krištín & Patočka, 1997), and the apparent negative effect of warming on moth populations in the UK (Martay et al., 2017).

Scale-dependent effects of asynchrony offer an alternative explanation for the relatively weak association between relative asynchrony and productivity. They may also explain the lack of a relationship between sensitivity to asynchrony and long-term productivity trends. As our aim was to document the broader relationships between asynchrony and productivity across large spatial scales and habitats, we evaluated relationships at the population, not the individual, level. Asynchrony could have a negative impact on breeding success of some individuals within the population, but others may be able to track changes in prey phenology, maintaining or even improving their synchronization with peak food availability (Charmantier et al., 2008; Cresswell & McCleery, 2003). The overall impact of change in seasonal phenology at the population level may clearly be dampened if the individual-level effects are variable. Furthermore, the relatively high potential for fine-scale variability in the extent of asynchrony depending on factors such as local warming trends, habitat and seasonal patterns of prey abundance, could mean that the relatively small reduction in national-scale productivity relative to increasing asynchrony is actually an accurate representation of the population-level effect. The importance of scale is highlighted by recent research on willow warbler *Phylloscopus trochilus*, a declining long-distance migrant in Britain with regionally divergent population trends. Our models suggest this species has a strongly negative productivity–asynchrony sensitivity metric and a declining population, but exhibits no strong long-term productivity trend. However, research has shown that consistently low productivity in southern Britain coupled with poor survival has contributed to population declines in this region, but that these have been offset by recent

population recovery in the north fuelled by relatively high productivity (Morrison et al., 2016). As we did not investigate regional relationships between asynchrony and annual productivity in this study, it is plausible that highly spatially variable, potentially opposing, relationships may interfere with our ability to detect the predicted relationships at a national scale.

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

4.2 | The relationship between sensitivity to asynchrony and long-term population trends

Given the observed relationship between the sensitivity of productivity to asynchrony and population trends, but the lack of evidence that this can be strongly attributed to asynchrony's effects on productivity, this relationship must (i) either be the product of one or more pathways operating via other trait and demographic mechanisms, and/or (ii) spurious and result from an unmeasured driver of population trend that also correlates with sensitivity.

For example, the costs of asynchrony may be expressed more strongly as reduced adult survival if increased parental effort is necessitated by reduced food availability (te Marvelde, Webber, Meijer, & Visser, 2011; Thomas, Blondel, Perret, Lambrechts, & Speakman, 2001). In short-lived songbirds, which constitute the majority of species included in this study, we might expect parents to prioritize chick-rearing to maximize their fitness, at the expense of their own survival. Alternatively, juveniles fledging from more asynchronous breeding attempts may have reduced survival and therefore a lower chance of subsequent recruitment into the breeding population (e.g. Sanz, Potti, Moreno, Merino, & Frías, 2003). Both of these alternative demographic mechanisms could plausibly explain the observed relationship between sensitivity to asynchrony and population trend, if asynchrony effects are expressed only weakly via productivity but more strongly via one or both of these other pathways. Recent integrated demographic modelling of British-breeding birds, including some of the species in this study, indeed suggests that population change may be most strongly driven by variation in recruitment and adult survival rather than productivity (Robinson et al., 2014).

However, we also cannot exclude the possibility that our findings are the consequence of an unmeasured driver of population trend which also correlates with sensitivity of productivity to asynchrony. For example, the observed relationship may be a consequence of habitat and/or diet specialization being simultaneously correlated with both population change and sensitivity (Miller-Rushing, Høye, Inouye, & Post, 2010). More specialized species may show greater sensitivity to asynchrony than generalists, and are also likely to be more sensitive to changes in habitat quality, land cover and other pressures; their populations have tended to decline relative to the most widespread generalists in the UK (Sullivan, Newson, & Pearce-Higgins, 2016).

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

In conclusion, trophic asynchrony as a consequence of climate change has been proposed as an important factor contributing to population declines in birds, yet studies have thus far found mixed evidence for a negative impact. British birds have advanced their timing of breeding over the last three decades, and those species which have advanced laying the least have the most negative population trends. However, annual productivity was reduced by only a small amount as asynchrony increased, and species whose productivity was more sensitive to asynchrony did not exhibit greater long-term declines in productivity. While species which were more sensitive to asynchrony exhibited greater long-term population declines, this is unlikely to be causal as our results suggest that population change is not mechanistically driven by the negative impact of asynchrony on productivity. Our findings may be attributable to a range of potential mechanisms: either the effects of asynchrony are more likely to be strongly expressed via demographic pathways other than productivity, the effect of asynchrony is scale-dependent, thus obscuring population-level effects, or perhaps most likely, the effect of asynchrony on

population trend is a surrogate for wider sensitivity of that species to other environmental pressures, which are the ultimate cause of decline.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

ETHICAL STATEMENT

All applicable national guidelines for the care and use of animals were followed.

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