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Synchrony in adult survival is remarkably strong among common temperate songbirds across France

Manon Ghislain[1,2,3] | **Timothée Bonnet**[4,5] | **Ugoline Godeau**[1,2,6,7] | **Olivier Dehorter**[2] | **Olivier Gimenez**[8] | **Pierre-Yves Henry**[1,2]

[1]Mécanismes adaptatifs et évolution (MECADEV UMR 7179), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Brunoy, France

[2]Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, CP135, Paris, France

[3]PatriNat (OFB-MNHN-CNRS-IRD), Centre d'expertise et de données sur le patrimoine naturel, Muséum national d'Histoire naturelle, Paris, France

[4]Division of Ecology and Evolution, Research School of Biology, ANU College of Science, The Australian National University, Canberra, ACT, Australia

[5]Centre d'Études Biologiques de Chizé (CEBC UMR 7372), Centre National de la Recherche Scientifique, Villiers en Bois, France

[6]Institut national de Recherche en Sciences et Technologies pour l'Environnement et l'Agriculture, Ecosystèmes Forestiers (UR EFNO), Domaine des Barres, Nogent-Sur-Vernisson, France

[7]Institut National de Recherche pour l'Agriculture l'Alimentation et l'Environnement, UR 406 Abeilles et Environnement, Avignon, France

[8]Centre d'Ecologie Fonctionnelle et Evolutive (CEFE UMR 5175), Centre National de la Recherche Scientifique, Université de Montpellier, Université Paul-Valéry Montpellier, Ecole Pratique des Hautes Études, Montpellier Cedex 5, France

Correspondence
Pierre-Yves Henry
Email: pierre-yves.henry@mnhn.fr

Abstract

Synchronous variation in demographic parameters across species increases the risk of simultaneous local extinction, which lowers the probability of subsequent recolonization. Synchrony therefore tends to destabilize meta-populations and meta-communities. Quantifying interspecific synchrony in demographic parameters, like abundance, survival, or reproduction, is thus a way to indirectly assess the stability of meta-populations and meta-communities. Moreover, it is particularly informative to identify environmental drivers of interspecific synchrony because those drivers are important across species. Using a Bayesian hierarchical multisite multispecies mark–recapture model, we investigated temporal interspecific synchrony in annual adult apparent survival for 16 common songbird species across France for the period 2001–2016. Annual adult survival was largely synchronous among species (73%, 95% credible interval [47%–94%] of the variation among years was common to all species), despite species differing in ecological niche and life history. This result was robust to different model formulations, uneven species sample sizes, and removing the long-term trend in

Manon Ghislain and Timothée Bonnet are co-first authors.

survival. Synchrony was also shared across migratory strategies, which suggests that environmental forcing during the 4-month temperate breeding season has a large-scale, interspecific impact on songbird survival. However, the strong interspecific synchrony was not easily explained by a set of candidate weather variables we defined a priori. Spring weather variables explained only 1.4% [0.01%–5.5%] of synchrony, while the contribution of large-scale winter weather indices may have been stronger but uncertain, accounting for 12% [0.3%–37%] of synchrony. Future research could jointly model interspecific variation and covariation in breeding success, age-dependent survival, and age-dependent dispersal to understand when interspecific synchrony in abundance emerges and destabilizes meta-communities.

INTRODUCTION

Synchrony corresponds to the coincident change in individual, population, or species characteristics over extended areas, up to thousands of kilometers (Liebhold et al., 2004). Understanding the causes of synchronous variations in population size is important in ecology and conservation because the greater the synchrony, the higher the risk of population, metapopulation, and metacommunity extinction (Koenig & Liebhold, 2016; Liebhold et al., 2004). When populations go down in numbers simultaneously the risk of synchronous local extinctions increases and the opportunity for subsequent demographic rescue through immigration diminishes (Tavecchia et al., 2016). If extinctions occur simultaneously for multiple co-occurring species, communities and ecosystem functioning can be disrupted (Kahilainen et al., 2018; Loreau & de Mazancourt, 2008). However, differences in life history and niches across species should increase community stability by decreasing interspecific synchrony (Pandit et al., 2013).

A major theoretical and empirical challenge is to disentangle the respective roles of the three processes that can cause synchrony. The first process, termed the Moran effect, corresponds to extrinsic forcing: populations that are affected by the same environmental variables are synchronized due to the spatial correlation in constraints (Liebhold et al., 2004; Olmos et al., 2019). In particular, climate forcing may directly drive variation in survival and reproduction (Black et al., 2018; Cattadori et al., 2005; Hansen et al., 2013; Kahilainen et al., 2018; Koenig & Liebhold, 2016; Post & Forchhammer, 2004; Sheppard et al., 2015, but see Vik et al., 2004). Climate forcing in wintering areas is expected to synchronize survival among species that share the same wintering range (e.g., Telenský

et al., 2020). The second process is synchronization through interactions with another trophic level. This includes synchrony due to variation in the abundance of shared prey, notably mast-seeding for seed-eating species (Klapwijk et al., 2018; Liebhold et al., 2004), predators (Huitu et al., 2004), or parasites (Cattadori et al., 2005). Variation in abundance in the trophic level responsible for synchrony may itself be driven by climate forcing (e.g., Dubos et al., 2018). The third process is dispersal, which may synchronize fluctuations in population size for connected populations (Liebhold et al., 2004; Martin et al., 2017; Paradis et al., 1999; but see Sanz-Aguilar et al., 2016; Tavecchia et al., 2016). More generally, any type of simultaneous movement of individuals, including seasonal migratory movements, can synchronize population sizes across distant sites.

Synchrony has mainly been investigated across populations within species, that is, as the spatial covariance in temporal changes in population sizes or vital rates (Liebhold et al., 2004). However, evidence accumulates that different species can show a strong degree of synchrony over wide areas even when they are ecologically, functionally and phylogenetically divergent (Black et al., 2018; Hansen et al., 2013; Post & Forchhammer, 2004). In vertebrate animals this interspecific synchrony (Liebhold et al., 2004) has mainly been studied using two study systems that are subject to trivial environmental forcing: species thriving in cold-driven environments following cyclic dynamics (Hansen et al., 2013; Huitu et al., 2004; Jones et al., 2003; Koenig & Liebhold, 2016; Liebhold et al., 2004; Post & Forchhammer, 2004) and seabirds that gather at a few colonies close to shared, large foraging areas (Lahoz-Monfort et al., 2011, 2013, 2017; Robinson et al., 2013). Existing evidence of

interspecific synchrony in population sizes across a wide range of species comes mainly from large-scale censuses of common wintering birds: six species from the UK (Swallow et al., 2016) and 49 species from North America (Koenig & Liebhold, 2016).

To our knowledge, until recently interspecific synchrony in vital rates, rather than population sizes, had been studied only for a small number of species at a single site or region: one study on two duck species (Péron & Koons, 2012), two studies on two salmon species (Malick et al., 2017; Malick & Cox, 2016), and all others on two to six seabird species (Lahoz-Monfort et al., 2011, 2013, 2017; Robinson et al., 2013). Recently, Telenský et al. (2020) estimated the synchronizing effect of weather variables on breeding sites and wintering sites for the survival of 16 songbird species across the Czech Republic during 2004–2014, albeit without estimating synchrony explicitly. In addition, Morrison et al. (2022) estimated species-specific synchrony—but not overall interspecific synchrony—in reproduction and survival using 26 songbird species across 336 European sites. The lack of research on interspecific synchrony of vital rates likely results from (1) the lack of theory and methods to root (meta)community dynamics in processes operating at the individual level (but see Lahoz-Monfort et al., 2017), and (2) the complexity of methods required to analyze multispecies, multisite, long-term vital rate data (Grosbois et al., 2009; Lahoz-Monfort et al., 2011, 2013, 2017; Swallow et al., 2016).

In the present study, we take advantage of a Constant Effort Sites (CES) mist-netting scheme to investigate interspecific synchrony in yearly fluctuations of annual adult apparent survival for a set of 16 common songbird species at 242 sites across France (Figure 1) over a 16-year period. We analyzed interspecific synchrony using the variance partitioning method of Lahoz-Monfort et al. (2011), splitting between-year variance into a synchronous component common to all species, and an asynchronous component corresponding to a year-by-species interaction. Because our analyses involved species with distinct ecological niches (Appendix S1: Table S1) and because synchrony is expected to be lower with higher species diversity (Pandit et al., 2013), we expected low interspecific synchrony. Further, our species differ in terms of migratory strategies and wintering range: nine species are resident or short-distance migrants, with year-round exposure to temperate climate, whereas seven species are trans-Saharan migrants that winter under the west-African climate (Appendix S1). Therefore, we expected that synchrony would be stronger within a given migratory strategy and that migratory strategy would explain a significant proportion of year-to-year variation among species. If that was the case it would point

to a synchronizing role of conditions on wintering grounds. Winter harshness is commonly proposed to explain a large proportion of year-round mortality in small organisms like songbirds (Grosbois et al., 2006; Johnston et al., 2016; Robinson et al., 2007; Saether et al., 2016; Salewski et al., 2013), including in migratory species (Robinson et al., 2007; Woodworth, Wheelwright, Newman, Schaub, & Norris, 2017). Factors explaining winter mortality could include water availability in arid wintering areas (Telenský et al., 2020) and the cost of thermoregulation in extreme cold or hot conditions (Boyles et al., 2011). On the other hand, if survival was to covary more synchronously and across migration strategies, it would point toward a synchronizing role of conditions on the breeding grounds, possibly due to climate forcing. In addition to factors that explain mortality during winter, climate forcing during the breeding season could synchronize species through its effect on the cost of reproduction through primary and secondary productivity (see details in *Discussion*).

To assess the role of climate forcing during the breeding season (i.e., common to all species) versus nonbreeding season (i.e., common to species wintering in the same climatic region), we estimated the proportion of synchronous variation in annual survival that could be ascribed to local temperatures and precipitations at the breeding sites during the breeding season, and to global climate indices related to conditions on the wintering grounds during the nonbreeding season (the winter North Atlantic Oscillation and the summer Sahel rainfalls, see *Methods*). We predicted that synchronous variation in survival should be in part explained by spring weather conditions.

METHODS

Study sites and species

Mark–recapture data were collected by volunteer bird banders under the French CES banding survey (Julliard & Jiguet, 2002). The full CES dataset is available on request through https://crbpo.mnhn.fr/. We selected data over the period 2001–2016, with the goal of estimating annual apparent survival and recapture probabilities. We consider "apparent survival," rather than "true survival," as our data cannot distinguish between mortality and permanent emigration. At each CES site the local bird community is sampled 3.17 ± 1.06 SD times per breeding season (first session on 21 May $\pm$ 15 days, last session on 4 July $\pm$ 12 days), with 14 ± 7 mist nets (12 m long, 3-to-4 m high, 16 mm mesh size) spread over an area of ~3 ha (4–5 mist nets per hectare). A capture session typically starts at dawn and lasts until midday. For every site
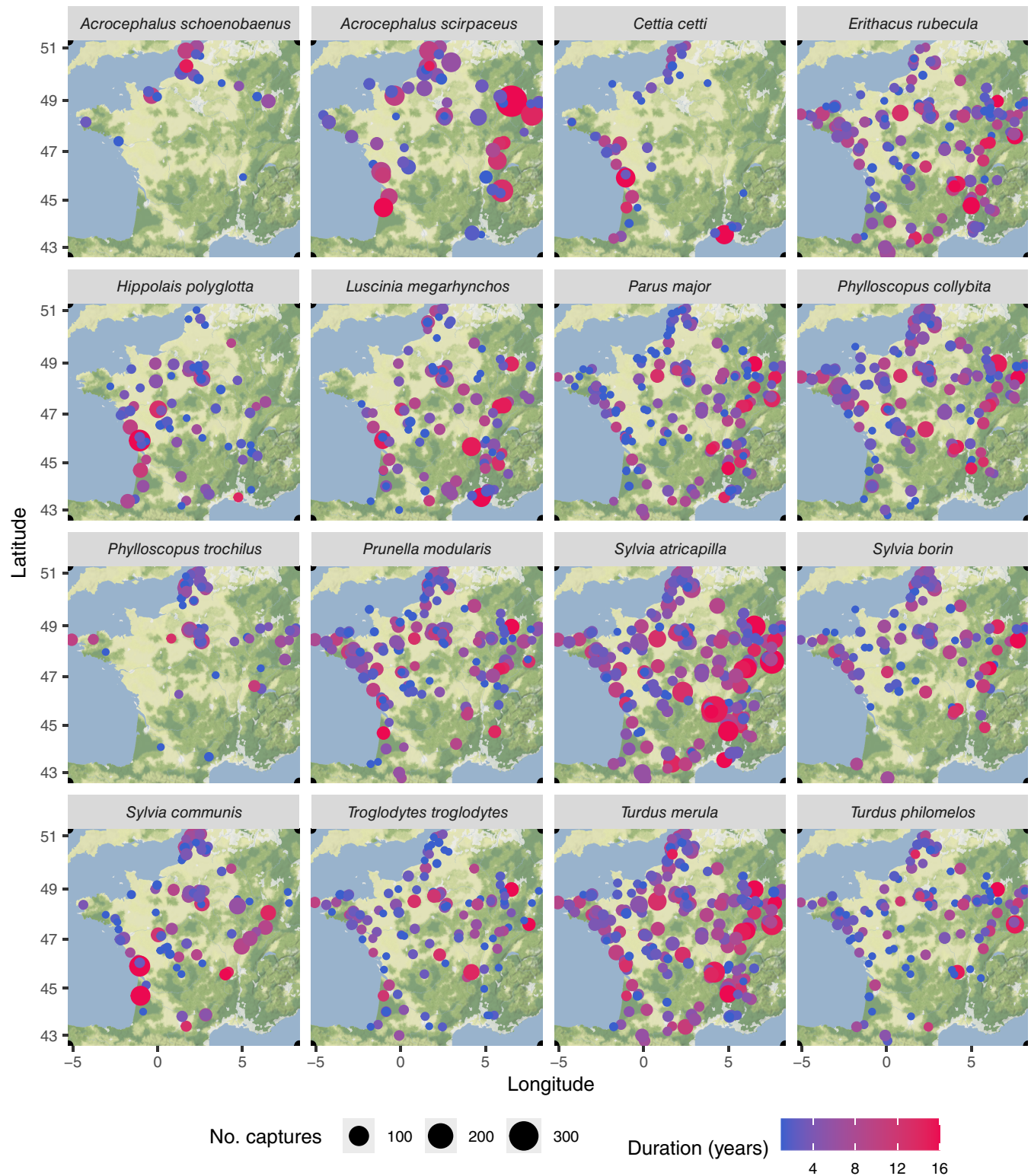
FIGURE 1   For each species, spatiotemporal distribution of the 242 sites across continental France used in this study. Color corresponds to the number of years for which we estimated survival in our models. The true duration of the monitoring at the site is always at least one more year. Point size indicates the total number of captures used in analyses, excluding transient individuals, for a given site.

the number, dates, hours of capture sessions, and mist net locations are held constant across sessions and years. Sites are monitored for an average of 6 ± 4 years. Sites

are typically located in low canopy habitats such as shrublands, open woodlands, and reed beds, where birds are easily captured with 3.5 m high mist nets. Each bird

captured is marked with a metal band bearing a unique identifier, identified at the species level, aged (juvenile or adult), sexed (Svensson, 1992), and released at the point of capture. All recaptures of marked individuals are recorded.

To ensure robustness of site-level parameter estimates we retained only data for species with an average of at least five adult individuals captured per year. Juvenile mortality is highly confounded with dispersal (Johnston et al., 2016) and so we did not consider juvenile data. After excluding the first year of capture for each individual to handle transients (see below), our mark–recapture dataset consists of 20,912 adults from 16 species, including 5198 individuals recaptured at least once across years (see Appendix S1), across 242 sites (Figure 1; Appendix S2: Figure S1) over a period of 16 years (Dehorter & CRBPO, 2017).

Bayesian survival data analysis

We modeled annual apparent survival and recapture probabilities using mark–recapture histories of individual birds with species-dependent and time-dependent Cormack–Jolly–Seber (CJS) models (Lahoz-Monfort et al., 2011). Interannual adult apparent survival probability (ϕ) is the probability that a bird alive in year t is still alive and present at the same CES site in year $t+1$. The recapture probability (p) is the probability that a bird alive and present in the same CES site where it was formerly captured (on year $t-1$ or before) is recaptured in year t. Individuals that were captured only once were considered transient individuals that do not pertain to the local population (Johnston et al., 2016) and were discarded by starting mark–capture histories only at the second year of capture. We also attempted to explicitly model transient rates, but the models were prohibitively long to run. Therefore our estimates are conditional on each bird being alive and present at the same site for at least 2 years. Goodness-of-fit tests for the general group-by-time-dependent CJS model (where the group was site-by-sex) were then run separately for each species using the "*R2ucare*" package (Gimenez et al., 2018; Appendix S3).

We built a Bayesian formulation of the CJS model applying a Markov Chain Monte Carlo (MCMC) sampling procedure (Lahoz-Monfort et al., 2011) implemented in JAGS (Plummer, 2003) called from R version 3.5.1 (R Development Core Team, 2015) using the R package *R2jags* version 4.2.0 (Su & Yajima, 2015). For our base model (Model 1 thereafter), the survival probability ($\phi_{i,t}$) of an individual i at time t was modeled as:

$$\text{logit}(\phi_{i,t}) = \mu_{\text{sp}(i)} + \beta_{\text{sex}}\text{sex}_i + u_{\text{site}(i)} + u_{\text{year}(t)} + u_{\text{year:species}(i,t)},$$

where $\mu_{\text{sp}(i)}$ is a species-specific intercept, β_{sex} is the effect of the bird being female, and $u_{\text{site}(i)}$ is a random deviation for the site i on which the bird breeds; we assume that those deviations follow a normal distribution of mean zero and variance σ_s^2, which we write as $u_{\text{site}} \sim N(0, \sigma_s^2)$. Further, the random deviation for years follows $u_{\text{year}} \sim N(0, \sigma_\delta^2)$, and the random deviations for species within years follow $u_{\text{year:species}} \sim N(0, \sigma_\varepsilon^2)$. Following Grosbois et al. (2009), the year random variance (σ_δ^2) quantifies the amount of between-year variation that is common to all species, across all sites (synchronous, country-level, interannual variation), and the year-by-species random variance (σ_ε^2) quantifies the between-year variation that differs between species (asynchronous, country-level, interannual variation). Note that σ_δ^2 and σ_ε^2 are parameters common to all species.

Therefore, our models accounted for the variation of apparent survival and recapture probabilities between sexes (assuming effects common to all species), species and sites (see Appendix S4 and code shared in Ghislain et al., 2022b on Zenodo). We addressed only synchrony across all sites, ignoring the spatiotemporal variance (i.e., Site:Year random variance) and the within-species spatiotemporal variance (i.e., Species:Site:Year random variance) in apparent adult survival probability. Such a full, hierarchical partitioning of variance was not achievable with the amount of mark–recapture data available within the year by site by species combinations.

We modeled recapture probability for individual i at time t as:

$$\text{logit}(p_{i,t}) = \nu_{\text{sp}(i)} + \gamma_{\text{sex}}\text{sex}_i + \gamma_{\text{het}}\text{het}_i + v_{\text{site}(i)} + v_{\text{year}(t)},$$

where $\nu_{\text{sp}(i)}$ is a species-specific intercept, γ_{sex} is the effect of the bird being female, and γ_{het} is the effect of between-individual heterogeneity in capture probability (detailed in Appendix S4). Finally, v_{site} and v_{year} are both normally distributed with means of zero and variances to be estimated.

We chose weakly informative priors for all parameters. Details on the specification of prior distributions for the parameters and satisfactory convergence criteria are provided in Appendix S4. We report posterior modes as point estimates and 95% highest posterior density credible intervals to show estimation uncertainty. We report posterior probabilities, pMCMC, computed as twice the proportion of MCMC values above 0, for a negative point estimate, or below 0, for a positive point estimate (analog to a two-sided frequentist p-value). All calculations were

done for the full posterior distribution in order to propagate uncertainty.

Interspecific synchrony in survival

From Model 1, we calculated a between-species intraclass correlation (ICC) of temporal variation to quantify country-level, between-year synchrony in adult survival across species, on the logit scale, defined as $ICC = \sigma_\delta^2 / (\sigma_\delta^2 + \sigma_\varepsilon^2)$.

The approach used for Model 1 differs from Lahoz-Monfort et al. (2011) in that we defined σ_ε^2 and ICC common to all species, while Lahoz-Monfort et al. (2011) estimated species-specific parameters, $\sigma_{\varepsilon species}^2$ and $ICC_{species} = \sigma_\delta^2 / (\sigma_\delta^2 + \sigma_{\varepsilon species}^2)$. We also fitted the model corresponding to Lahoz-Monfort et al. (2011) and named it Model 2. In this model, survival follows the same equation as for Model 1, except that $u_{year:species} \sim N(0, \sigma_{\varepsilon species}^2)$, that is, the random deviations for species within years follow different distributions for each species, with one $\sigma_{\varepsilon species}^2$ estimated for each of the 16 species. From Model 2, we calculated the average of the 16 $ICC_{species}$ point estimates and compared it to the global ICC calculated from Model 1. Model 2 allows us to test for effects explaining variation in $ICC_{species}$ among species. Thus, we fitted a general linear model of $ICC_{species}$ as a function of either of two species characteristics: migratory class, a factor with two levels, long-distance versus short-distance or resident species, or species sample size; we integrated the model over each sample of the full posterior distributions of $ICC_{species}$ to propagate estimation uncertainty.

We explain other pros and cons of Model 1 and Model 2 in Appendix S4. Note that we report ICCs on the logit scale, not on the natural scale of survival probability. Arguably, ICC on the logit scale is more biologically relevant because it expresses differences as log odds ratios and does not depend on average survival probability. For the range of parameter values considered (mean survival, variance on the logit scale, and ICC), the difference between ICCs on the two scales is minimal (see Appendix S4).

Migratory strategy (Model 3)

Because of shared conditions among species wintering in the same regions, the migratory strategy could explain part of the overall synchrony in annual survival. To quantify the importance of this effect, we fitted Model 3, a variation of Model 1 with a random effect for the interaction year-by-migratory strategy (long-distance vs. short-distance migrant or resident). The equation for survival thus became:

$$\begin{aligned} logit(\phi_{i,t}) = {} & \mu_{sp(i)} + \beta_{sex} sex_i + u_{site(i)} + u_{year(t)} \\ & + u_{year:species(i,t)} \\ & + u_{year:migration(i,t)}, \text{with } u_{year:species} \\ & \sim N(0, \sigma_{\varepsilon w}^2) \text{ and } u_{year:migration} \sim N(0, \sigma_m^2). \end{aligned}$$

We thus modeled a year-by-migratory strategy variance σ_m^2, while σ_δ^2 remained the year variance common to migratory strategies and species, and $\sigma_{\varepsilon w}^2$ was the within-migratory strategy within-species year variance. The proportion of total annual variance attributed to migratory strategy (i.e., synchrony within-migratory strategy) was estimated as $ICC_m = (\sigma_m^2) / (\sigma_\delta^2 + \sigma_m^2 + \sigma_{\varepsilon w}^2)$. The proportion of total annual variance common to all species was estimated as $ICC = \sigma_\delta^2 / (\sigma_\delta^2 + \sigma_m^2 + \sigma_{\varepsilon w}^2)$. If the migratory strategy explains no synchronous variation, the ICC from Model 3 will approach the ICC calculated from Model 1.

Yearly weather covariates (Models 4 and 5)

Weather conditions during the breeding period (April to July) were characterized for each site and year using daily mean temperature and daily sum precipitation (as in Dubos et al., 2018; Eglington et al., 2015; Gaüzère et al., 2015; Grosbois et al., 2006) from the "E-OBS" meteorological dataset (available at https://www.ecad.eu/), with a 0.25° pixel (approximately 20 km by 28 km) resolution using the R package *climateExtract* (available at https://github.com/RetoSchmucki). Because organisms are expected to be adapted to average local conditions (e.g., Dubos et al., 2019), we tested for an effect of departure from local average weather conditions, that is, local spring weather anomalies. Anomalies were computed for each variable, site and year as the difference between the local value for a given spring and the mean over the 2001–2016 period (as in Dubos et al., 2018). For the effect sizes for temperature and precipitation to be comparable, anomalies were standardized by dividing them by the standard deviation across all sites and years. However, we then used the yearly averages of anomalies across all sites to capture the synchronizing effect of weather variables (Appendix S5: Figure S1).

To explain between-species synchrony in annual survival variations that could be attributed to large-scale fluctuations in spring weather conditions, we fitted Model 4, which added terms to Model 1 including fixed effects for the linear and quadratic effects of spring temperature (θ) and precipitation (π) anomalies, effects known to explain bird survival (Boyles et al., 2011; Pomara & Zuckerberg, 2017), plus the four pairwise interactions between temperature and precipitation:

$$\beta_\theta\theta_{i,t} + \beta_\pi\pi_i + \beta_{\theta 2}\theta_{i,t}^2 + \beta_{\pi 2}\pi_{i,t}^2 + \beta_{\theta:\pi}(\theta_{i,t}\pi_{i,t}) + \beta_{\theta:\pi 2}(\theta_{i,t}\pi_{i,t}^2)$$

$$+ \beta_{\theta 2:\pi}(\theta_{i,t}^2\pi_{i,t}) + \beta_{\theta 2:\pi 2}(\theta_{i,t}^2\pi_{i,t}^2),$$

where, for instance $\beta_{\theta 2:\pi}$ is the coefficient for the interaction between squared standardized temperature deviations and standardized precipitation deviations and $(\theta_{i,t}^2\pi_{i,t})$ is the product of squared standardized temperature deviations and standardized precipitation deviations.

We included quadratic and interactive effects a priori, without performing model selection. This approach should be seen as an attempt to estimate an upper bound to the variance, and thus synchrony, that can be ascribed to the weather variables available, rather than an attempt to test the potential causal effects of weather presented in introduction or to produce a predictive model.

Following Nakagawa and Schielzeth (2013), we estimated the synchronous variance explained by spring weather (σ_{sw}^2) as the variance in partial model predictions (that is, the linear combination of the products of each parameter was estimated by the corresponding weather variable), $\sigma_{sw}^2 = \mathrm{var}(\sum_{h=1}^{8}\beta_h\bar{x}_{ht})$ where h indexes the eight model parameters related to spring weather, β_h is the parameter estimate for the effect of h, and $\bar{x}_{ht}$ is the mean value of the weather variable h in year t (across all sites). By definition σ_{sw}^2 captures only synchronous variation. Therefore we calculated the proportion of synchronous variation related to spring weather as $\sigma_{sw}^2/(\sigma_\delta^2 + \sigma_{sw}^2)$, and the new ICC $= \left(\sigma_{sw}^2 + \sigma_\delta^2\right)/(\sigma_{sw}^2 + \sigma_\delta^2 + \sigma_\varepsilon^2)$.

In Model 5, we added covariates related to winter weather to Model 1. For resident and short-distance migrants, which spend the winter in western Europe or North Africa, we used the North Atlantic Oscillation during winter (wNAO; averaged from December to March, available at http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm). The wNAO captures broad-scale weather variation in Western Europe and North Africa (Forchhammer & Post, 2004), which explains variations in over-winter survival in several European bird species (Robinson et al., 2007; Salewski et al., 2013). For long-distance migrants that winter in Western Africa, we used the Sahel Rainfall during summer (sSR; averaged from July to September, available at http://research.jisao.washington.edu/data_sets/sahel/). The sSR is often used as a proxy of winter Sahel suitability for wintering songbirds, considering that habitat quality in December–February is driven by rainfall during the previous summer (Robinson et al., 2007; Salewski et al., 2013).

As was done for spring weather covariates, we fitted linear and quadratic effects for wNAO and sSR. We estimated the synchronous variance explained by winter weather (σ_{ww}^2) as the variance in partial model predictions from the linear and quadratic effects of wNAO and sSR. The synchronous variance due to winter climate (σ_{ww}^2) is the variance among years in survival, averaged over species, predicted from differences in wNAO and sSR only, which we write as $\sigma_{ww}^2 = \mathrm{var}_t\left(E_{\text{species}}(\phi|\text{winter climate})\right)$. We can decompose the average between the two migratory strategies as:

$$\sigma_{ww}^2 = \mathrm{var}_t(mE_{\text{migratory}}(\phi|\text{sSR}) + (1-m)E_{\text{resident}}(\phi|\text{wNAO})),$$

where m is the proportion of long-distance migratory species. The two conditional averages are the sum of an average survival independent of winter climate and anomalies due to the effects of winter climate:

$$\sigma_{ww}^2 = \mathrm{var}_t(m\alpha_1 + m(\beta_{\text{sSR}}\text{sSR} + \beta_{\text{sSR2}}\text{sSR2})$$
$$+ (1-m)\alpha_2 + (1-m)(\beta_{\text{wNAO}}\text{wNAO} + \beta_{\text{wNAO2}}\text{wNAO2})),$$

where α_1 and α_2 are baseline survival probabilities independent of winter climate and are scalars, hence:

$$\sigma_{ww}^2 = \mathrm{var}_t(m(\beta_{\text{sSR}}\text{sSR} + \beta_{\text{sSR2}}\text{sSR2})$$
$$+ (1-m)(\beta_{\text{wNAO}}\text{wNAO} + \beta_{\text{wNAO2}}\text{wNAO2})).$$

(see Appendix S6 for formula validation).

This variance is a function of the effect of sSR among migratory species, of the effect of wNAO among resident species, and of the small negative covariance between sSR and wNAO (the two indices are expected to be independent, but the empirical Pearson correlation coefficient was -0.12, 95% confidence interval $[-0.58;0.40]$). The proportion of synchronous variance related to winter weather was calculated as $\left(\sigma_{ww}^2\right)/(\sigma_\delta^2 + \sigma_{ww}^2)$, and the ICC $= (\sigma_{ww}^2 + \sigma_\delta^2)/(\sigma_{ww}^2 + \sigma_\delta^2 + \sigma_\varepsilon^2)$. All parameter estimates for all models are provided in Appendix S7.

RESULTS

Interspecific synchrony of annual adult apparent survival

Interannual variation in adult apparent survival probabilities was largely synchronous across the 16 study species (Figure 2). Model 1 ICC of 73%, 95% highest posterior density credible interval $= [47\%$–$94\%]$ indicates that most of the temporal variance in apparent survival probabilities was common to all species (Table 1: Model 1). Conversely, this implies that within-species variation corresponded to only 27% $[6\%$–$53\%]$ of temporal fluctuations of survival probabilities.

Species showed considerable variation in Model 2 $ICC_{species}$ (Figure 3), although estimates came with broad credible intervals. There was no significant association between the value of $ICC_{species}$ and migratory strategy (Figure 3; pMCMC = 0.48) nor with species sample size (pMCMC = 0.31). The mean of the 16 species posterior mode estimates for $ICC_{species}$ was 76% (Table 1: Model 2).
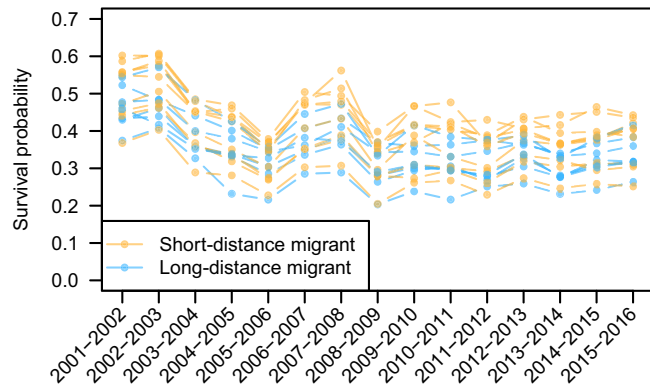
F I G U R E 2 Interannual fluctuation of local survival probabilities by species for adult individuals. Estimates were obtained independently for each species (with resident males as intercept) from a model with fully year-dependent survival and explicitly modeling an interaction between year and migratory behavior (resident/short-distance migrants versus long-distance migrants, i.e., Model 5).

This strong synchrony was robust to (1) the uneven contributions of species to the mark–recapture dataset (ICC = 65% [28%–90%], Appendix S8), (2) the removal of the part of synchrony due to a potential linear trend in survival probabilities (ICC = 56% [23%–86%], Appendix S9; note that this calculation necessarily excludes some true synchrony), (3) the choice of prior distributions (Appendix S10), and (4) the effects of weather and migratory strategy presented below.

Graphically, some years seemed to deviate more from the mean survival probability (Figure 2) and may have contributed more to synchrony: estimates of survival probabilities between the years 2001–2002 and 2002–2003 were larger than average while estimates for the years 2005–2006 and 2008–2009 were particularly low (Appendix S11: Figure S2). However, our ad hoc approach using model estimates failed to identify statistical support for variability in yearly contributions to interspecific synchrony (Appendix S11).

Contributions of migratory strategy to synchrony in survival probabilities

In Model 3 the interaction between year and migratory strategy captured only a small amount of asynchronous variation in survival among species, with $ICC_m = 9\%$ [0%–32%] (Table 1). After removing the synchrony

T A B L E 1 Variance component estimates for survival probability under different models.

Variance component	Model 1 base model	Model 2 species-specific synchrony	Model 3 migration:Year	Model 4 spring weather[a]	Model 5 winter weather[a]
Year (synchrony)	0.098 [0.031–0.234]	0.090 [0.016–0.203]	0.091 [0.009–0.205]	0.091 [0.023–0.216]	0.092 [0.019–0.214]
Model-specific synchrony term	...	-[b]	0.011 [0–0.036]	0.001 [<0.001–0.0029]	0.008 [<0.001–0.020]
Year:Species (asynchrony)	0.034 [0.012–0.068]	0.026[c]	0.032 [0.007–0.065]	0.034 [0.007–0.062]	0.036 [0.010–0.066]
Site	0.155 [0.076–0.232]	0.157 [0.088–0.237]	0.152 [0.085–0.226]	0.156 [0.081–0.232]	0.152 [0.087–0.226]
Variance sum[d]	0.287	...	0.286	0.287	0.286
ICC[e]	73% [47–94]	Mean 76%	65% [30–91]	72% [47–93]	68% [36–95]

Note: Model 1 is the base model and captures all of the synchrony in the year variance parameter. Other models include various effects that may or may not explain some of the synchrony, thus leaving a corrected synchrony as the year variance parameter. Estimates are posterior modes and 95% highest probability density credible intervals.

[a]Weather variables were introduced as fixed effects and the variance they explain was computed post hoc, while all other variance components were directly estimated as random effects.

[b]In Model 2 synchrony is estimated separately for each of the 16 species, see Figure 3.

[c]Mean of the 16 species-specific point estimates.

[d]The sum of the variances is expected to be constant, but may vary slightly due to rounding, and because survival is not directly observed but predicted as a latent variable (i.e., survival does not have a defined variance observable independently of a model).

[e]Intra-class correlations (see *Methods*) are estimates of synchrony across species, that is, the proportion of year variance over "total" temporal variance, which varies across models.
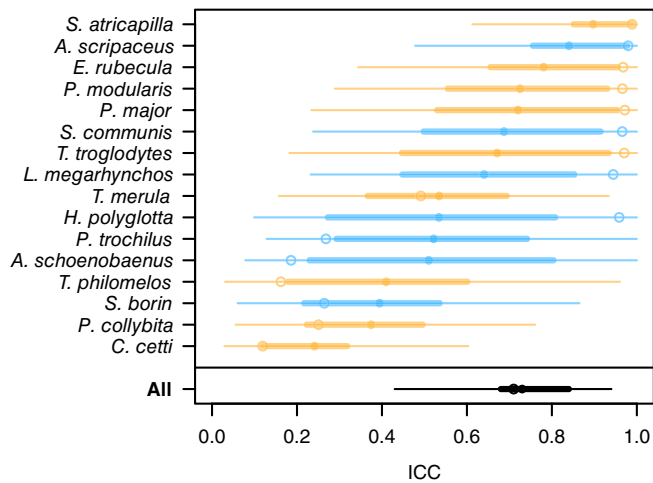
FIGURE 3 Interspecific synchrony for each species and overall. Estimates of intraclass correlations (ICCs) measuring interspecific synchrony in adult survival, for each species separately, and across all species taken together. A lower species-specific synchrony means that mean survival probability is more variable in that species. Species-specific estimates were obtained from Model 2, while the overall estimate was obtained from Model 1. Yellow lines represent short-distance migrants, blue lines represent long-distance migrants. Filled circles represent posterior means, empty circles posterior modes, thick lines 50% quantile CI and thin lines 95% HPD CI.

within-migratory strategy the variance common to all species was ICC = 65% [30%–91%]. This low dependence of synchrony on migratory strategy is apparent in Figures 2 and 3.

Contributions of weather to synchrony in survival probabilities

According to Model 4, spring weather variables taken together explained only 1.4% [0.01%–5.5%] of synchrony, whereas according to Model 5, the winter weather variables explained 12% [0.3%–37%] of the synchrony. Assuming spring and winter weather variables are uncorrelated, together they explain 13% [0.8%–39%] of synchrony and 10% [0.6%–23%] of the total temporal variance (Table 1). There was no clear evidence for an effect of any of the weather-related parameters on survival probability, with all credible intervals overlapping zero (across all species, i.e., additive effects; Appendix S5: Table S1). Higher spring precipitation and more extreme spring temperatures tended to increase survival probability (Appendix S5: Figure S1). Regarding winter weather covariates, survival probability appeared a bit higher for high Sahara rainfall values during summer (sSR), while there was no discernible effect of the North Atlantic

Oscillation during winter (wNAO) across all species (i.e., additive effects; Appendix S5: Figure S2).

DISCUSSION

Unexpectedly, annual fluctuations in adult apparent survival were largely synchronous across the 16 songbird species that dominate bird communities in France: 73% [47%–94%] of between-year variance in survival probabilities was common to all species. This result was robust to differences in migratory strategy among species, uneven species sample sizes, and time de-trending. This strong synchrony is remarkable given that these species differ in various properties linked to apparent survival: they cover the range of songbird migratory strategies, body mass (8–88 g) and number of broods per year, and they partly differ in habitat and ecological specialization (Appendix S1). Moreover, our estimates represent minimal synchrony because they are not controlled for potentially desynchronizing factors like intraspecific and interspecific negative density dependence. Estimated synchrony should be higher if we could control for those factors (Péron & Koons, 2012; Swallow et al., 2016). Our estimates of interspecific synchrony are as high as estimates of spatial synchrony in apparent survival probabilities across some populations of the same species, with for instance values of 67% and 71% in two long-lived birds (Grosbois et al., 2009; Jenouvrier et al., 2009), and higher than the interspecific synchrony in survival (49%) estimated for two closely related duck species (Péron & Koons, 2012). Short-lived vertebrate animals, such as our study species, are under stronger environment dependence than long-lived species (Saether et al., 2016), which may contribute to the high interspecific synchrony observed.

The species-specific synchronies (ICC$_{species}$) varied from very high to low (Figure 3). This means that within some species, such as the Cetti's Warbler, *Cettia cetti* (with ICC = 0.12, 95%CI [0.03; 0.60]), there was considerable temporal variability in adult survival, probably due to the species' high sensitivity to winter harshness (Moussus, 2010). Conversely, in other species such as the widespread Eurasian Blackcap, *Sylvia atricapilla* (with ICC = 0.99, 95% CI [0.61; 1]), the temporal variability in adult survival corresponded almost entirely to the average variability across the 16 species. Morrison et al. (2022) also reported a wide range of species-specific synchronies, although our estimates were generally a bit higher: Our point estimates were never below 0.10 (vs. a minimum of 0.03) and were above 0.80 for nine out of 16 species (vs. 2 out of 26 species). The broader geographic range covered by Morrison et al. (2022), spanning

eight European countries, may contribute to the lower $ICC_{species}$. Differences in $ICC_{species}$ may be influenced by heterogeneity in the spatiotemporal distribution of captures among species (see Figure 1), but we did not find a clear pattern explaining differences in synchrony among species (i.e., range, migration class, sample size, habitat), and species-specific synchronies were estimated with broad confidence intervals. Therefore, the determinants of interspecific synchrony remain to be identified with a larger dataset, if possible involving more species, more diverse life-history traits, and more years. Drivers that differ between species and determine local survival dynamics must occur and operate at the level of sites or regions (Cayuela et al., 2019; Gaüzère et al., 2015; Giraud et al., 2013; Morrison et al., 2013, 2021). In any case, our moderate and high estimates of $ICC_{species}$ indicate that the drivers of annual variations in adult apparent survival at the country level are largely common to many species.

Climate forcing could be responsible for synchronous events of high mortality among species, either through direct or indirect effects. A few studies have shown that climate forcing was responsible for at least a part of the observed interspecific synchrony in abundances or vital rates in common songbirds (Grosbois et al., 2006; Jones et al., 2003; Koenig & Liebhold, 2016; Swallow et al., 2016; Telenský et al., 2020). However, within species, neither broad-scale climatic variables nor local weather variables explained synchronous survival variation in blue tit populations (Bastianelli et al., 2021), and synchronous survival in little auk populations was better explained by trophic interactions than climate (Reiertsen et al., 2021). In the present study we failed to identify a statistically significant role for any climatic variables, and altogether those variables explained only 13% [0.8%–39%] of the interspecific synchrony. Nevertheless, we likely underestimated the importance of climate. First, the variables we used did not explicitly consider weather properties such as extreme temperature or precipitation events (e.g., Gardner et al., 2022), or species-specific periods of sensitivity to weather (van de Pol et al., 2016). Second, we used variables averaged either over spring or winter, which is unlikely to represent the cumulative effect of climatic variations experienced throughout the year. Finally, our modeling investigated the direct effects of weather whereas indirect or delayed effects may be more influential, particularly weather-driven primary and secondary productivity and their effects on the cost of reproduction (see below).

Apart from direct climate forcing other mechanisms could synchronize adult annual local survival across species (Reiertsen et al., 2021). First, synchronous variation in prey abundance could generate interspecific synchrony. Because all songbirds feed their chicks exclusively with invertebrates, a high invertebrate abundance could lower the foraging effort of breeding adults during chick rearing, decrease exposure to predators, and ultimately increase adult survival (Eglington et al., 2015). Therefore, the survival of songbird species could be synchronized by spatial synchrony in invertebrate abundance, itself possibly caused by high precipitation and hot temperatures (Dubos et al., 2018, 2019; Eglington et al., 2015; Jones et al., 2003; Kahilainen et al., 2018; Sheppard et al., 2015). A remarkable food-supplementation experiment even demonstrated that food availability during breeding has a direct effect on annual adult survival in a long-distance migratory species: simply increasing food availability during reproduction (i.e., more than 4–5 months) increased annual survival by 5% (Seward et al., 2013). Moreover, in highly productive years, a higher proportion of adults engage in rearing a second brood (Visser et al., 2003), potentially at a supplementary cost in terms of survival (Woodworth, Wheelwright, Newman, & Norris, 2017). If facultative multibrooding species (62% of studied species; Appendix S1) are synchronous in their choice to lay a second brood, their adult survival could be synchronized by the cost of reproduction. Schaub et al. (2015) demonstrated that the probability of double brooding was actually the most synchronous vital rate across the nine populations of an aerial insectivorous songbird, the Barn Swallow, *Hirundo rustica*.

Second, intraspecific and interspecific competition for shared resources likely operates at the level of the local songbird community, potentially resulting in large-scale, weather-driven density-dependent regulations of adult survival. Nevertheless, intraspecific density dependence can also be a source of asynchrony across species (Martin et al., 2017; Péron & Koons, 2012). The net role of community-level density dependence in synchronizing adult survival probabilities across species remains to be properly investigated (Swallow et al., 2016).

Third, breeding dispersal could contribute to interspecific synchrony in adult apparent survival. Apparent survival results from survival and residency (i.e., absence of dispersal, Saracco et al., 2010) at the scale of study sites. Interspecific synchrony in apparent survival could occur if individuals of different species tend to disperse more synchronously in some years than in others. Following a bad reproductive experience at one location (e.g., weather-driven early reproductive failure) a higher proportion of adults settles away in the following year (e.g., Arlt & Part, 2008). However, only a small proportion of adults typically emigrates between breeding events, even in long-distance migrants (Greenwood & Harvey, 1982), and males, the most resident sex in birds (Amrhein et al., 2012), represent a majority (64%) of individuals in our dataset. Therefore, synchronous breeding dispersal alone

seems unlikely to have caused the estimated high interspecific synchrony in adult apparent survival.

Could conditions during the nonbreeding season explain the high synchrony in adult survival across songbirds in France? Across long-distance migrants, short-distance migrants, and residents, we found that winter conditions explained 12% [0.3%–37%] of the interspecific synchrony. This proportion is low, but potentially significant biologically, and, as already explained, we likely underestimate the synchronizing importance of weather. Winter harshness is commonly proposed to explain variation in year-round mortality in small organisms like songbirds (Grosbois et al., 2006; Johnston et al., 2016; Robinson et al., 2007; Saether et al., 2016; Salewski et al., 2013), including in migratory songbirds (Robinson et al., 2007; Woodworth, Wheelwright, Newman, Schaub, & Norris, 2017). Recent studies on multispecies population synchrony have also emphasized a major role of winter climate forcing, but these few studies were biased toward cold-driven ecosystems, like high-latitude populations that are subject to extreme winter events such as rain-on-snow icing events (Hansen et al., 2013; Jones et al., 2003; Pomara & Zuckerberg, 2017; Post & Forchhammer, 2004). Restricting the analysis to long-distance migrant species only, Telenský et al. (2020) found that water availability on the wintering grounds explained 15% of the temporal variation in survival, but the result was not statistically significant. Overall, it seems likely that conditions on the nonbreeding grounds, especially climate, contribute somewhat to the interspecific synchrony in adult survival, even though the 16 studied species spread from France to Central Africa during the winter.

Differences in migratory strategy explained little temporal variation in survival probability. Synchrony across all species, calculated after removing the synchrony within migration classes, was similar to synchrony calculated without accounting for migratory strategy (Table 1: Model 3). This high synchrony in adult survival across resident and long-distance migrant species, wintering on two different continents (at a distance of 2000–3000 km and 35–45° in latitude) has profound implications for our understanding of the regulation of migratory bird populations. Breeding habitat degradation appears as the major cause of ongoing massive, synchronous population declines (Eglington & Pearce-Higgins, 2012), including in migratory species (Morrison et al., 2013). Our results and these studies suggest that habitat quality or productivity over breeding areas is critical for year-round songbird population dynamics, even for migratory species that spend only 3–4 months per year on their breeding grounds (Morrison et al., 2013).

At least graphically (Figure 2), some years appear to increase synchrony, with large interspecific deviations in survival probabilities. Synchrony is expected to be heterogeneous across years, or even transitory (Klapwijk et al., 2018), and to be largely attributable to the occurrence of environmental disturbances in some years (Cattadori et al., 2005; Keitt, 2008). For instance, Jenouvrier et al. (2009) showed that the high spatial synchrony (71%) in Scopoli's shearwater adult apparent survival was attributed to only two "low" years out of eight. In "normal" years, species specificities (e.g., ecological niche differentiation) would dominate and drive variation in survival probabilities (Liebhold et al., 2004; Robinson et al., 2013). As climate warms and increasingly fluctuates through time with stronger and more frequent extreme weather events, spatial synchrony and interspecific synchrony are likely to increase in strength (Hansen et al., 2013, 2020; Koenig & Liebhold, 2016; Post & Forchhammer, 2004) over wider spatial scales (Black et al., 2018). A longer timer series would be necessary to properly assess the yearly contributions to synchrony and to quantify differences in synchrony over different time periods. Analytical methods are also not yet readily implementable to such multiyear, multisite, multispecies mark–recapture datasets (Cattadori et al., 2005; Lahoz-Monfort et al., 2017).

The accumulation of data over several decades should also allow the fitting of more complex models. In the present work we ignored interactions between site and species or time. However, modeling fine-scale time by space by species variation in survival across sites would provide a more nuanced view of the dynamics of survival. By exploiting the heterogeneity among sites in environmental conditions and species community compositions, such modeling could be used to investigate the causes for differences in interspecific synchrony among sites. It would also allow disentangling the effects of global cross-site weather effects that generate broad-scale synchrony in average survival, from local site-level weather events that necessarily de-synchronize survival among sites (Morrison et al., 2021; fig. 4 in Wan et al., 2022).

Models could also be improved by explicitly accounting for spatial autocorrelation in survival across sites. In the present study we ignored spatial autocorrelation, primarily because of the necessity of limiting model complexity. One might therefore expect our models to underestimate uncertainty in parameter estimates. However, in the present dataset, results should be robust to this simplification: a post hoc analysis exploring the potential spatial autocorrelation of survival estimates across sites, using the random site-level effect estimates (BLUPs), revealed a weak and negative spatial autocorrelation (Moran's $I = -0.05$, null expected $I = -0.004$, null expected I standard deviation $= 0.028$, p-value $= 0.10$): survival tends to be more dissimilar among closer sites than among distant sites. Nonetheless, future models investigating

simultaneous intraspecific and interspecific synchrony could benefit from accounting for spatial autocorrelation to ensure estimation robustness and gain more biological insight.

The present study focused on synchrony in adult apparent survival, but population size fluctuations can be asynchronous despite synchrony in some vital rates. Indeed, vital rates taken separately are expected to be more commonly synchronized than population sizes, due to "compensatory mechanisms" such as life-history trade-offs, demographic buffering (Saether et al., 2016; Schaub et al., 2015), and intraspecific and interspecific density dependence regulations (Lahoz-Monfort et al., 2017; Péron & Koons, 2012; Tavecchia et al., 2016). Ultimately, it is synchrony in population sizes that can cause extinction. Nevertheless, studying synchrony only in population sizes does not allow inference about the mechanisms driving synchrony, and impedes predicting their respective role in future extinction risk. Future research should aim to jointly model synchronous variation and covariation in breeding success, age-dependent survival, and age-dependent dispersal for several co-occurring species. Such modeling would not only allow the study of synchrony of population growth rate and population size, but would also help identify (a)synchronizing mechanisms at complementary organizational levels (individuals, populations, communities).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ghislain et al., 2022a) are available in Dryad at https://doi.org/10.5061/dryad.vx0k6djv3. Code (Ghislain et al., 2022b) is provided in Zenodo at https://doi.org/10.5281/zenodo.8172390.

ORCID

Timothée Bonnet https://orcid.org/0000-0001-7186-5288
Ugoline Godeau https://orcid.org/0000-0003-2104-7046
Pierre-Yves Henry https://orcid.org/0000-0003-2255-7347

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.