Regional spatial synchrony in density-dependent survival of a woodland passerine

Sanjana Ravindran[1*], Alexander Eyo[1], Albert B. Phillimore[1], Hannah Froy[1]

[1]Institute of Ecology and Evolution, University of Edinburgh, Edinburgh EH9 3FL, Scotland

*Corresponding author email: sravindr@ed.ac.uk

Abstract

Spatial population synchrony, the tendency of geographically separated populations to fluctuate in concert, reduces opportunities for demographic rescue and increases extinction risk, yet the demographic processes underlying it remain poorly understood. Adult survival is a key driver of population dynamics but few studies have quantified its spatial synchrony or identified the mechanisms that generate it. Spatially correlated environmental drivers such as winter weather are predicted to synchronize survival via the Moran effect, whereas density-dependent regulation is typically expected to desynchronize local dynamics. However, where population density itself varies synchronously across space, density-dependent effects on survival may instead act as a synchronizing force. Here we use a 12-year mark-recapture study of blue tits (*Cyanistes caeruleus*) breeding across 44 woodland sites along a 220 km latitudinal transect in Scotland to quantify synchrony in adult apparent survival and identify its drivers. Using hierarchical Cormack-Jolly-Seber models, we partitioned variance in annual apparent survival into spatial, temporal and spatiotemporal components, and quantified synchrony as the intra-class correlation (ICC) of shared temporal variance. Adult survival was highly spatially synchronous (ICC = 0.81, 95% CrI: 0.19–1.00), though the wide credible interval reflects considerable uncertainty in the precise magnitude of this synchrony. Survival was negatively associated with annual fluctuations in local breeding density, consistent with density-dependent regulation. Since local density was itself strongly spatially synchronous (ICC = 0.96), these density-dependent effects contributed to synchrony in survival. Annual fluctuations in local winter minimum temperature were also highly synchronous across sites (ICC = 0.89) and were associated with further reductions in shared temporal variance in survival, although we detected no statistically significant direct effect of temperature on survival. Our results are consistent with adult survival in this short-lived resident passerine being spatially synchronous over hundreds of kilometres, potentially driven by local weather conditions and density-dependent processes that are themselves regionally synchronous. Such synchrony in a key demographic rate heightens the collective vulnerability of spatially distinct populations to concurrent decline, underscoring the potential value of landscape-wide monitoring and management of woodland bird populations under ongoing environmental change.

Introduction

Spatial population synchrony – the tendency of geographically separated populations to exhibit positively correlated temporal fluctuations in population size – is a widespread ecological phenomenon with profound implications for metapopulation stability and extinction risk (Leibold et al., 2004). When populations fluctuate synchronously, the capacity for demographic rescue through dispersal is reduced, increasing the risk of regional collapse (Heino et al., 1997). The magnitude of spatial synchrony has direct consequences for conservation: strong synchrony implies simultaneous declines across populations and demands landscape-wide interventions, whereas weak synchrony may allow more targeted, site-specific actions (Morrison et al., 2022). Understanding both the extent of synchrony among populations and disentangling the relative contributions of large-scale environmental drivers from more local processes is therefore central to determining the appropriate scale of management response and predicting population responses to climate change (Hansen et al., 2020).

Three main mechanisms are typically proposed to generate spatial synchrony in population dynamics. First, synchrony can arise through climate forcing, or the Moran Effect, whereby geographically separated populations respond similarly to spatially correlated environmental fluctuations (Moran, 1953; Koenig, 2002). Second, dispersal of individuals between local populations can directly couple their dynamics (Paradis et al., 2000). Third, synchrony may emerge through trophic interactions, for example where fluctuations in predators, prey or food resources are themselves spatially correlated (Elton & Nicholson, 1942; Koenig & Knops, 2001). Several empirical studies in wild bird and mammal populations have identified a key role for spatially correlated weather (i.e. the Moran effect) as a driver of spatial population synchrony (Koenig & Liebhold, 2016; reviewed in Hansen et al., 2020). However, distinguishing between these mechanisms remains a major empirical challenge, particularly since multiple processes may act concurrently and interact with one another (Kendall et al., 2000; Reuman et al., 2023).

Most theoretical and empirical research on spatial synchrony has focused on fluctuations in population abundance (Liebhold et al., 2004). Yet this is an integrated outcome of multiple demographic processes, including survival, reproduction and dispersal, which may differ in their responses to environmental variation. Examining synchrony in these underlying vital rates may therefore reveal the mechanisms generating correlated population fluctuations. Adult survival is one such vital rate. Although classically expected to have the strongest influence on population growth in long-lived species (Gaillard et al., 1998; Saether & Bakke, 2000), it can also drive dynamics in shorter-lived taxa (Crone, 2001; Lebreton & Clobert, 1991). A recent study of 33 passerine species over 21 years across Europe reported adult survival as a more important driver of annual changes in population size than breeding productivity (Nousiainen et al., 2025). Despite this, intraspecific synchrony in adult survival and the mechanisms underpinning it have been most extensively studied in seabirds (Grosbois et al., 2009; Jenouvrier et al., 2009; Tavecchia et al., 2008; Reynolds et al., 2011; Reiertsen et al., 2021; Horswill et al., 2023). However, the unusual biology of migratory, colonially breeding and exceptionally long-lived seabirds is likely to shape the processes generating spatial synchrony and limiting

the generalisability of these mechanistic insights to other species, including songbirds with faster life histories (Martin et al., 2023).

Several extrinsic factors are likely to shape adult survival synchrony in temperate passerines. Low winter temperatures represent a major source of mortality through food scarcity and elevated thermoregulatory costs (Lack, 1954; Newton, 1998; Marsh & Dawson, 1989). Several studies of hole-nesting Paridae inhabiting the northern part of the species range have shown that adult survival declines markedly during severe winters (reviewed in Grosbois et al., 2006). Previous studies have highlighted winter climate forcing as a key driver of population synchrony in high-latitude, cold-limited ecosystems (Jones et al., 2003; Post & Forchhammer, 2004; Pomara & Zuckerberg, 2017). Trophic interactions such as regionally synchronous beech masting events represent an additional large-scale synchronizing force, with heavy crops buffering overwinter survival in great and blue tits across continental Europe (Sæther et al., 2007; Koenig & Knops, 2001). Spatially correlated raptor predation pressure may further reinforce synchrony in prey survival (Dhondt et al., 1998).

In contrast, intrinsic density-dependent processes are classically predicted to desynchronize populations through two non-mutually exclusive mechanisms. First, density-dependent feedbacks introduce site-specific temporal structure into population dynamics. When local density is high, increased intraspecific resource competition, reduced territory availability and greater predation or disease are expected to lower survival and fecundity (Sinclair & Pech, 1996). As density falls, conditions improve, generating negative feedback that is thought to be driven primarily by each population's own prior density rather than by a shared environmental driver (Ranta et al., 1997). Since these temporal dynamics are specific to each site, spatially separated populations may exhibit different survival trajectories, reducing spatial synchrony. Second, the strength or form of density dependence may vary among sites depending on spatial heterogeneity in habitat quality, resource availability or predator pressure (Engen & Sæther, 2005; Walter et al., 2017). Populations may then respond differently to identical environmental fluctuations, reducing synchrony below what environmental forcing alone would predict (Liebhold et al., 2006). Together, these mechanisms mean that density regulation may generate both independent local dynamics and reduce the synchronizing influence of shared environmental forcing. However, where fluctuations in population density are itself spatially synchronous, density dependence also has the potential to transfer synchrony to demographic rates, a process that has been largely overlooked and could act to maintain synchrony in a system. Finally, although dispersal can couple population dynamics, the high site fidelity of adult passerine breeders likely limits its contribution to survival synchrony relative to natal dispersal (Greenwood & Harvey, 1982).

Understanding the drivers of synchrony in adult survival is particularly important in short-lived passerines, which are expected to be more sensitive to environmental variation than species with slower life histories (Morris et al., 2008). Using data on 26 songbird species across 334 sites across Europe over ten years, Morrison et al. (2022) established that spatial synchrony in adult survival is widespread but varies considerably in magnitude, though they did not identify the mechanisms responsible. Grosbois et al. (2006) found climate forcing to explain part of the synchrony in adult

survival of Mediterranean blue tit populations however, a subsequent study by Bastianelli et al. (2021) found no support for climatic or local weather conditions on this synchrony. A study of interspecific synchrony in adult survival of French songbirds also failed to find support for the Moran effect, suggesting that large-scale shared environmental forcing may play a more limited role than expected (Ghislain et al. 2024). The processes generating spatial synchrony in survival thus remain poorly resolved. In particular, the synchronizing role of the Moran effect and the contribution of local density dependence – which may either synchronize or desynchronize survival depending on the spatial structure of population density – have rarely been disentangled and quantified empirically.

In this study, we used a 12-year dataset of 44 nestbox populations of blue tits *Cyanistes caeruleus* distributed along a 220km latitudinal transect in Scotland to quantify synchrony in apparent survival of adult breeders. These populations span ~2° in latitude and ~400m in elevation, with considerable variation in woodland habitat type and quality across sites (Shutt et al., 2018; Macphie et al., 2025; Figure 1), offering an unusual opportunity to identify drivers of spatial synchrony across a heterogeneous landscape. Using mark–recapture data from breeding adults (aged 1+), we aimed to:

1. Estimate spatial, temporal and spatiotemporal variance in annual apparent survival of breeding adult blue tits using a Cormack-Jolly-Seber (CJS) model, and use these components to quantify the magnitude of average synchrony across populations.
2. Quantify the contribution of a direct Moran effect, by testing whether fluctuations in local winter weather drive correlated interannual variation in survival across sites.
3. Quantify the contribution of density-dependent processes, by testing whether fluctuations in local breeding density are associated with shared temporal variation in survival across sites.

We predicted that fluctuations in winter weather will synchronize adult survival, consistent with a Moran effect. The influence of local density fluctuations on survival synchrony should depend on the spatial structure of density itself: it will act as a desynchronizing force if local density fluctuates independently among sites, but may transfer and maintain synchrony if local density is itself spatially correlated.

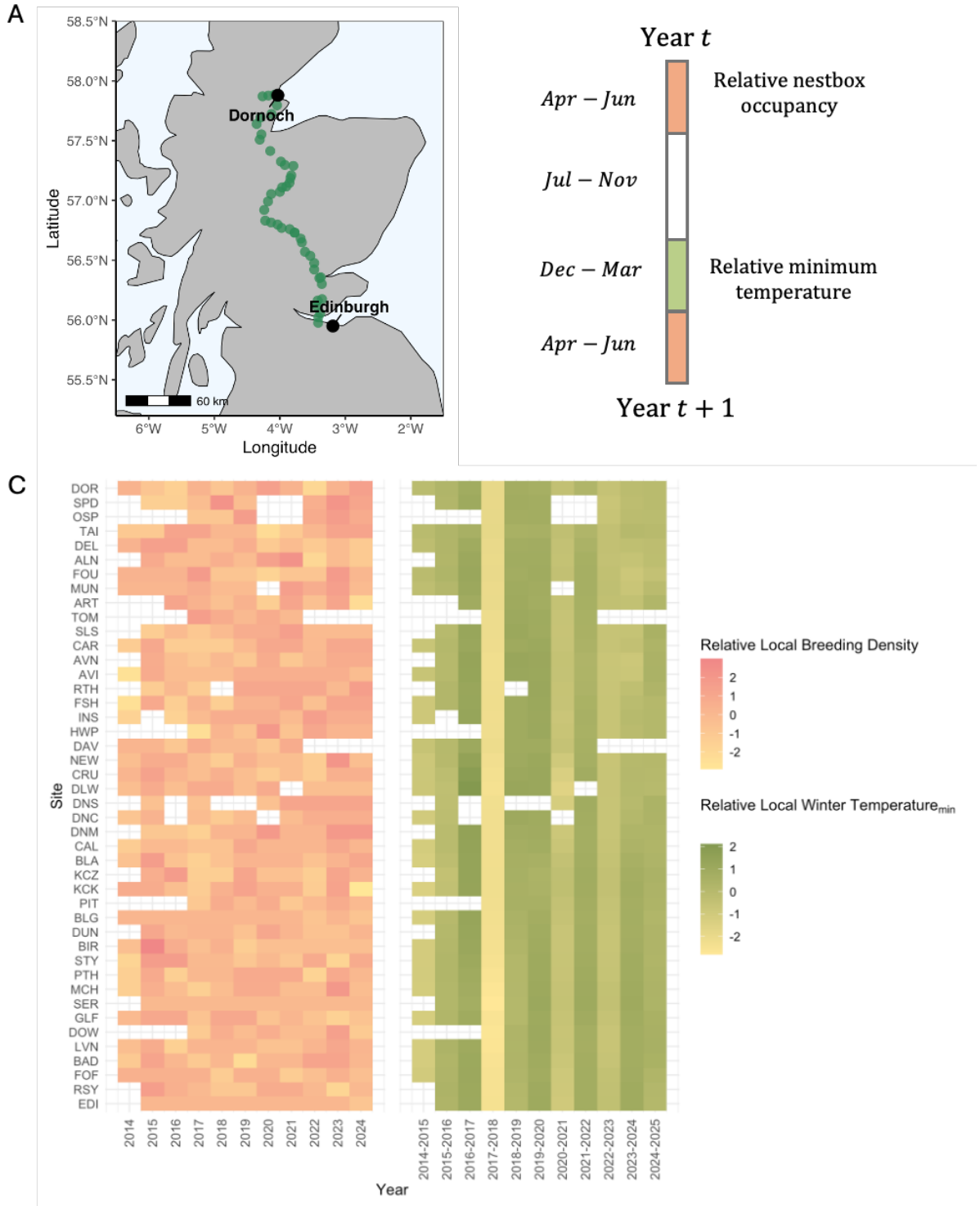

Figure 1: A) Map showing the 44 study sites along the transect from Edinburgh to Dornoch in Scotland; B) Annual survival was estimated from breeding season of year t to year t+1 with ecological variables (local breeding anomaly and local minimum temperature anomaly) measured during spring (April to June of year t) and during winter (December of year t to March of year t+1) respectively; C) Spatiotemporal variation in the two ecological variables considered in this study: local breeding anomaly during spring and local minimum temperature anomaly during winter (values are z-standardized). Here, sites are ordered by increasing latitude from bottom to top. Uncoloured cells indicate missing site:year combinations, arising either because a site had not yet been incorporated into the transect study at that time point or because no breeding adults were captured at that site in that year.

Methods

Study system

We established nestboxes at 44 woodland sites along a 220 km latitudinal transect from Edinburgh (55°98 N, 3°40 W) to Dornoch (57°89 N, 4°08 W) in Scotland. Each site has 6-8 small-hole nestboxes preferred by blue tits, with the exception of one site that has four nestboxes. Monitoring began in 2014 across 30 sites, expanding to 40 in 2015 and 44 in 2017. Sites vary in elevation (10 – 433 m) and woodland habitat composition, with the dominant tree species being one of birch, oak, sycamore or willow at most sites (Shutt et al., 2018; Macphie et al., 2025). Pairwise inter-site distances range from 0.162 to 217 km, with a mean distance between adjacent sites of 5.277 km (Figure 1A). During each breeding season (April–June), fieldworkers visited each site every 2 days. We captured adult breeders when nestlings were 10–14 days old, primarily inside the nestbox or sometimes using a short mist-net positioned immediately adjacent to it. Our approach means that we do not capture adults that fail early during the breeding season and do not go on to relay, reducing recapture rates. On first capture, we fit unmarked adult birds with British Trust for Ornithology – numbered metal rings under licence which allows for unique identification. We sexed adults based on the presence or absence of a brood patch or cloacal protuberance and assigned age class (age 1 year or age 2+ years) from plumage and extent of moult (Jenni & Winkler, 2020).

We estimated apparent survival from one breeding season to the next (spring year *t* to year *t+1*) for 2107 adult blue tits captured across the 44 sites between 2014 and 2025, representing 436 unique site-years. Of the 2107 adults, 1150 were female and 957 were male. We first ringed most individuals (n = 1289; 61%) as one-year-olds, with the remainder (n = 818; 39%) first ringed aged two years or older (treated as minimum age in this study). We recaptured a third of individuals (n = 741; 35%) at least once in subsequent breeding seasons. Although natal dispersal is observed in this species with juveniles typically dispersing within 1 – 20km of their natal territory, breeding dispersal among adults is less frequent and over shorter distances (Paradis et al., 1998). We excluded five individuals recaptured at a different site from their initial breeding site. These rare instances of inter-site breeding dispersal occurred between three pairs of neighbouring sites that were either 0.2 km (n=2), 4.9 km (n=1) or 5.6 km (n=2) apart. We report the number of individuals captured across all sites and years of the study in Supplementary Table S1.

Ecological predictors

We considered two categories of ecological predictors: an exogenous environmental driver (local winter temperature) and an endogenous measure of local population density (spring nestbox occupancy).

We characterized local winter weather conditions (i.e. the local realisation of climate at each site) using daily minimum temperatures which we interpolated to each site's centroid coordinates, following the same approach as used to generate the 1 km x 1 km Met Office gridded climate data (Hollis et al., 2019). We focussed on minimum temperatures during winter since low winter temperatures are expected to increase

the energetic costs of thermoregulation in small passerines like blue tits, impacting their overwinter survival (Scholer et al., 2020; Salewski et al., 2013; Robinson et al., 2007). We defined winter as December (year *t*) through March (year *t+1*) and calculated the mean daily minimum temperature across this period for each site-year combination (range: -2.375 – 2.999 °C; mean = 0.400; median = 0.418; sd=1.088; n=484).

To capture information on local density of the breeding population, we quantified spring nestbox occupancy as the proportion of available nestboxes occupied by blue tits at each site in year *t*. Occupancy required field confirmation of blue tit nesting with at least one breeding metric recorded (clutch size, date of nestling ringing or fledging success). Thus, we obtained nestbox occupancy values for each site-year combination (range: 0 – 1; mean=0.618; median=0.625; sd=0.261; n=456). Because occupancy is bounded at 1, the density metric is censored at high densities, reducing our power to detect density effects. In this study, 15% of site-years had occupancy values of 1 while 2% of site-years had occupancy values of 0. There were 3 sites whose occupancy values were 1 for >75% of years.

To examine how annual fluctuations in these ecological predictors influence apparent annual survival and its synchrony, we isolated the temporal variation in each predictor using a within-subject centering approach (van de Pol & Wright, 2009). Specifically, for every site, we subtracted the long-term site mean from each yearly observation, yielding annual deviations that represent year-to-year departures from local averages. By removing between-site differences in our ecological predictors, the within-subject centering approach allows us to focus on the temporal variation that can synchronise or desynchronise demographic responses across populations. Site means for winter temperature were estimated from all available site-years (n = 484) while site means for nestbox occupancy were from observed site-years only (n = 456).

Mark-recapture modelling to estimate apparent survival

We estimated inter-annual apparent survival of adults at all sites using a capture-mark-recapture modelling framework to account for imperfect detection. Individual capture-recapture histories for 2107 breeding adults were used to estimate apparent survival (ϕ) and recapture (p) probabilities using a hierarchical Cormack-Jolly-Seber (CJS) model conditional on first capture (Lebreton et al., 1992). Apparent survival was defined as the probability that an individual alive during the breeding season in year t was also alive during the next breeding season in year $t + 1$. Although a contribution of emigration cannot be fully excluded in a CJS model, the short breeding dispersal distances and high inter-year site fidelity of adult blue tits suggest apparent survival largely reflects true survival (Valcu & Kempenaers, 2008). Recapture probability (p) was the probability that provided an individual is alive, it was recaptured in year *t+1* having previously been caught (in year *t* or earlier).

We accounted for spatial, temporal and spatiotemporal variation in both apparent survival and recapture probabilities by fitting site, year and their interaction (i.e. site-by-year) as random effects. Only site-years when individuals were (re)captured received their own site-by-year interaction random effect (n=436 site-years for

survival sub-model). Since annual survival could differ between sexes and with age, we included individual sex as a fixed factor (male = 0, female = 1), and age in years (linear and quadratic terms) as a time-varying continuous fixed effect in our survival sub-models. Age was z-standardized to mean=0 and sd=1, prior to inclusion in the model.

The survival probability (ϕ) of an individual *i* at site *s* and year *t* was modelled as:

$$logit\left(\phi_{i,s,t}\right) = \mu_{survival} + \beta_s sex_i + \beta_{a1} age_{i,t} + \beta_{a2} age_{i,t}^2 + u_{s_i} + u_t + u_{s_i:t}$$

The recapture probability (p) of an individual *i* at site *s* at year *t* was modelled as:

$$logit\left(\mathrm{p}_{i,s,t}\right) = \mu_{recapture} + u_{s_i} + u_t + u_{s_i:t}$$

Here, $\mu_{survival}$ and $\mu_{recapture}$ are intercepts for the survival and recapture sub-models. β_s, β_{a1} and β_{a2} are the slope estimates for sex and age (linear and quadratic terms), respectively. u_{s_i}, u_{year_t} and $u_{s_i:year_t}$ are the random effects of site, year and site-by-year interaction respectively, each assumed to follow a normal distribution with mean=0 and variances σ_s^2, σ_t^2 and $\sigma_{s,t}^2$.

To examine the contributions of our ecological predictors to temporal variation and spatial synchrony in survival, we fitted three additional models by modifying the base survival sub-model, while the recapture sub-model remained unchanged. The following fixed effects were sequentially added to the base survival sub-model: i) relative local winter temperature, ii) relative local breeding density, and iii) both predictors simultaneously. The full survival sub-model was:

$$\begin{aligned} logit\left(\phi_{i,s,t}\right) = {} & \mu_{survival} + \beta_s sex_i + \beta_{a1} age_{i,t} + \beta_{a2} age_{i,t}^2 \\ & + \beta_w relative\ winter\ temperature_{s,t} + \beta_d relative\ breeding\ density_{s,t} \\ & + u_{s_i} + u_t + u_{s_i:t} \end{aligned}$$

where β_w and β_d are slope estimates for relative local winter temperature and relative local breeding density, respectively. Both covariates were divided by their standard deviation prior to inclusion to allow direct comparison of effect sizes. The random effects structure remained unchanged across all models. CJS models were fitted in a Bayesian framework using Stan with Markov Chain Monte Carlo (MCMC) sampling (Carpenter et al., 2017). Details of priors used, CJS model validation and goodness-of-fit tests are provided in Supplementary Methods & Results.

In a separate analysis, we controlled for the effects of a clutch swap experiment conducted between 2017 – 2019 across 37 sites on annual. We found that accounting for this experimental treatment did not influence our main biological conclusions and hence, we present the model excluding this treatment effect in our main results (further details in Supplementary Methods & Results).

<u>Estimating spatial synchrony in adult apparent survival</u>

We estimated spatial synchrony in adult apparent survival as the intraclass correlation coefficient (ICC), defined as the proportion of total temporal variance attributable to shared year effects rather than site-specific year effects (following Grosbois et al., 2009; Reiertsen et al., 2021; Horswill et al., 2023; Lahoz-Montfort et al., 2011; Schaub et al., 2015);

$$ICC = \frac{\sigma^2_{year}}{\sigma^2_{year} + \sigma^2_{site:year}}$$

This metric ranges from 0 (complete asynchrony, where all temporal variation is site-specific) to 1 (complete synchrony, where all sites fluctuate identically across years). ICCs were calculated from posterior distributions of the CJS models and are reported on the logit scale (Ghislain et al. 2024).

Ecological drivers of spatial synchrony in adult apparent survival

To quantify the contribution of annual fluctuations in our ecological predictors to spatial synchrony in adult survival, we examined how the intraclass correlation coefficient (ICC) and random effect variance components, particularly the shared temporal variance (σ^2_{year}) changed as these predictors were sequentially added to the base survival sub-model (Lahoz-Montfort et al., 2011). A spatially synchronous predictor to which populations respond similarly should reduce σ^2_{year} and ICC when included. On the other hand, an asynchronous predictor would reduce spatiotemporal variance, potentially increasing ICC. Since spatial synchrony in each predictor is a necessary condition for it to contribute to survival synchrony, we additionally estimated spatial synchrony (ICCs) in both local winter temperature and breeding density using (generalized) linear mixed models (further details in Supplementary Methods & Results; Tables S4A and S4B). Following Grosbois et al. (2009) and Horswill et al. (2023), we also quantified the contributions of our ecological predictors to shared and site-specific temporal variation in survival (further details in Supplementary Methods & Results).

Results

Spatial, temporal and spatiotemporal variance and synchrony in adult apparent survival

The average annual apparent survival probability of adult blue tits was 0.443 (95% CrI: 0.395 – 0.488), with some variation across time and across space (Table 1; Figure 2A, 2B). There was more spatial variation in survival compared to overall temporal variation.

Spatiotemporal variation in survival across all 44 sites showed patterns consistent with spatial synchrony (Figure 4A). The baseline model revealed that most temporal variance in annual survival was shared across sites rather than being site-specific (ICC: 0.808; 95% CrI: 0.188–0.999; Table 2A; Figure 4A). However, the 95% CrIs were wide, indicating high uncertainty in this estimate.

Survival differed between sexes with males having higher annual survival compared to females (Figure 3A; Table 1). There was support for a quadratic association of age on annual survival, with survival increasing to around three years old before declining to the oldest recorded age of eight years (Figure 3B; Table 1).

The average recapture probability was 0.761 (95% CrI: 0.721–0.798; Table 1), with the spatial, temporal and spatiotemporal variation in recapture probabilities exceeding that of survival probabilities (Figure S1, Table 1).

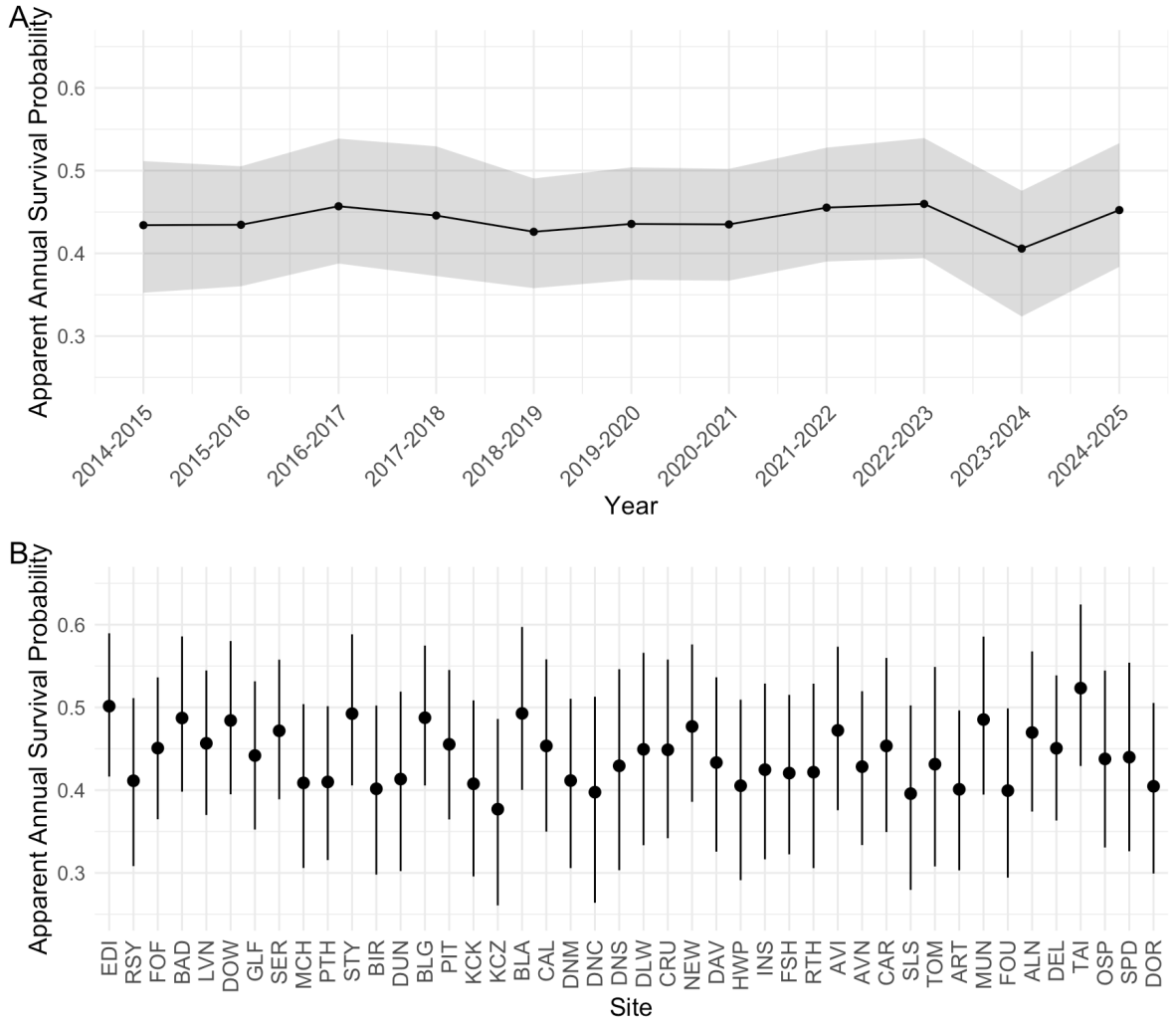

Figure 2: Temporal and spatial variation in apparent annual survival probability of adult blue tits. A) represents variation in apparent survival of adults across years while B) represents variation in apparent adult survival across sites. Posterior medians and 95% CrIs displayed (Table 1).

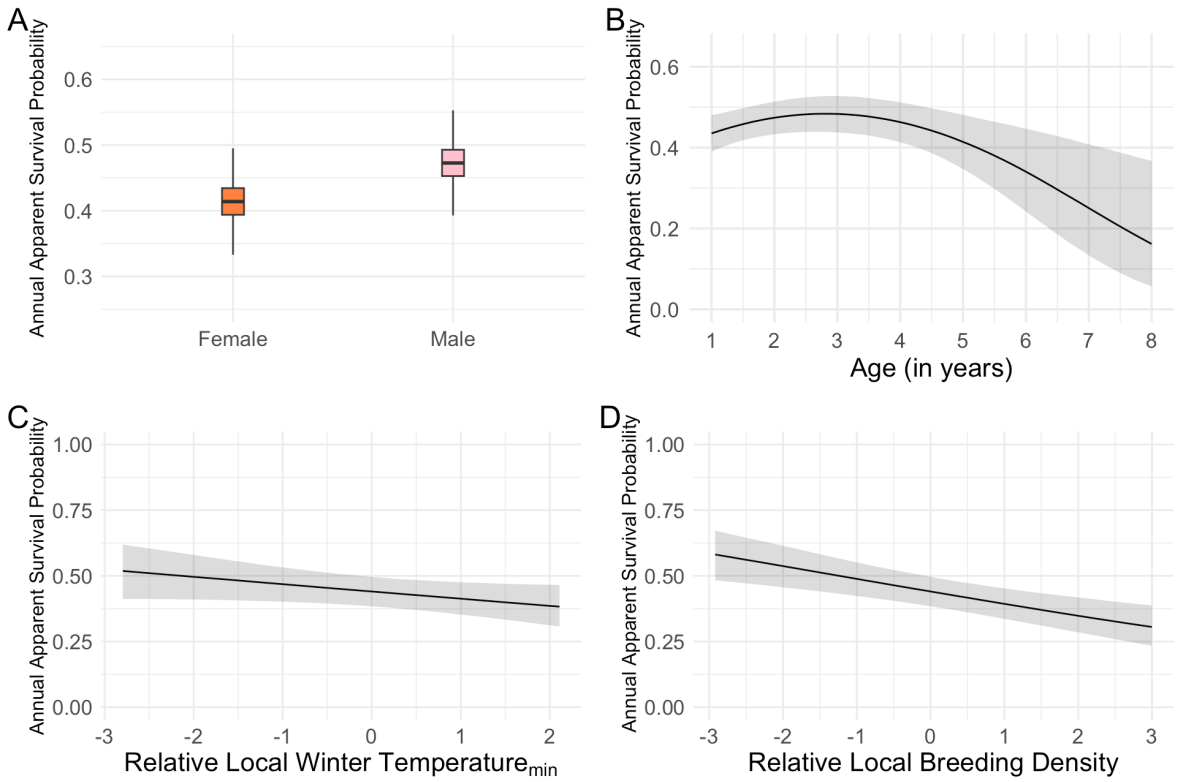

Figure 3: Adult annual apparent survival probabilities according to A) Sex, B) Age, C) Relative local winter minimum temperatures and D) Relative local breeding density. Posterior median and 95% CrIs displayed (Table 1). For each fixed effect, the slopes are predicted setting other fixed effects at their mean values and sex at 0.5.

Table 1: Results from Cormack-Jolly-Seber model investigating effects of sex, age, relative winter temperature and relative local breeding density on annual apparent survival probability. Estimates of recapture probability and random effects of site, year and interaction between site and year for both sub-models also reported. Posterior median, 95% CrI shown along with effective sample size and Rhat. All parameter values are on logit scale. Results in bold indicate estimates where the 95% CrIs don't overlap zero.

Parameter	*median*	*2.50%*	*97.50%*	*n_eff*	*Rhat*
Survival Probability					
Intercept	-0.109	-0.347	0.122	9797	1.000
Sex (female)	**-0.238**	**-0.383**	**-0.096**	18022	1.000
Age (linear)	**-0.531**	**-0.961**	**-0.127**	9454	1.000
Age (quadratic)	**-0.409**	**-0.701**	**-0.121**	10450	1.000
Relative local winter temperature	-0.112	-0.231	0.012	11118	1.000
Relative local breeding density	**-0.194**	**-0.297**	**-0.092**	17242	1.000
Year variance	0.015	0.000	0.104	6085	1.000
Site variance	0.055	0.008	0.136	5135	1.000
Site:Year variance	0.011	0.000	0.09	3146	1.001
Recapture Probability					
Intercept	1.352	0.913	1.821	5881	1.000
Year variance	0.091	0.001	0.602	5258	1.000

Site variance	0.693	0.250	1.594	5860	1.000
Site:Year variance	0.185	0.001	0.786	2195	1.001

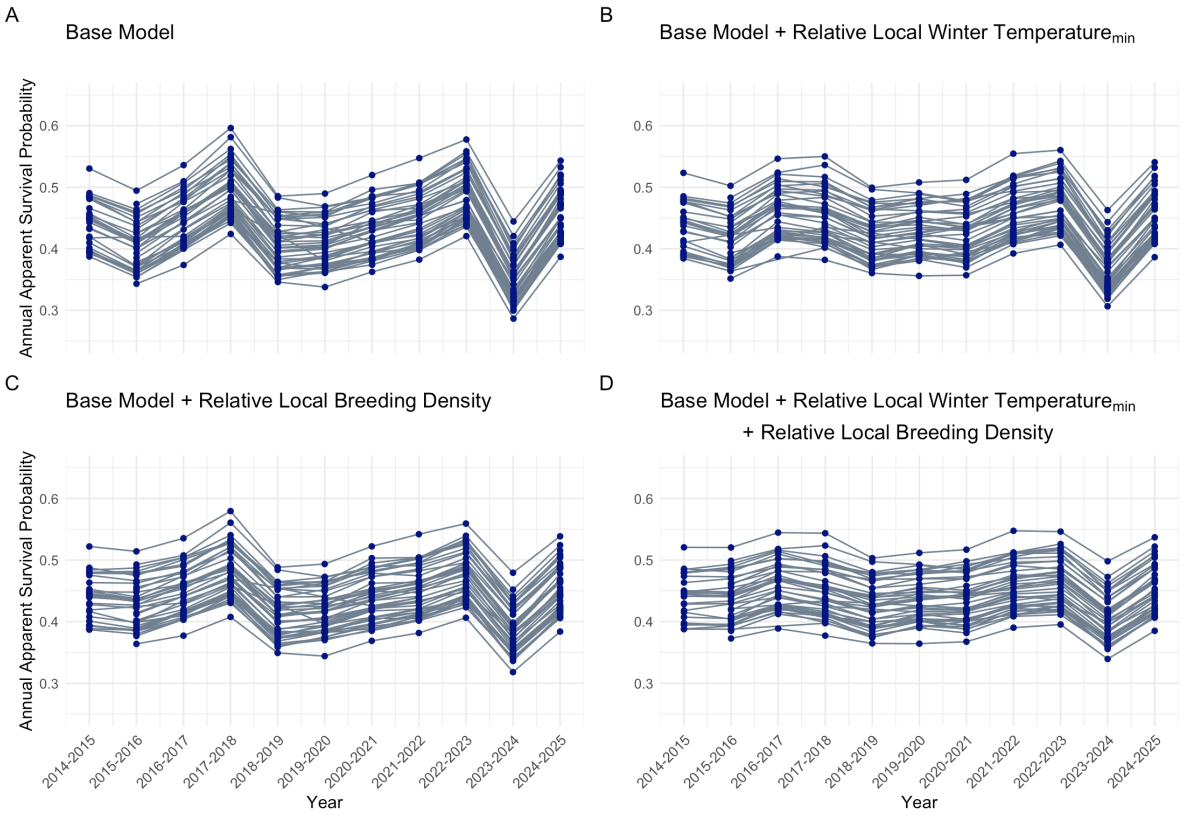

*Figure 4: Spatiotemporal patterns in apparent survival probability of adult blue tits obtained from random effect estimates. Coloured lines show the temporal trajectories of mean survival across each of the 44 sites over the 12-year study period. Results presented are from a) base model with fixed effects of sex and age and random effects of site, year and site:year fitted; b) base model plus relative winter temperature; c) base model plus relative local breeding density; d) base model plus relative winter temperature and relative local breeding density. The predictions based on the global intercept plus 0.5*sex (producing a sex-averaged estimate, as males and females were coded 0 and 1 respectively) plus random effect deviations are displayed and they exhibit shrinkage towards the grand mean.*

Contribution of fluctuations in local winter temperature to spatial synchrony in adult survival

There was a weak negative association between annual apparent adult survival and relative local winter minimum temperature, with the 95% credible intervals overlapping zero (−0.112; 95% CrI: −0.231–0.012; Figure 3C; Table 1). Yearly fluctuations in mean daily minimum temperature in winter were strongly correlated among sites, with strong spatial synchrony observed in absolute winter minimum temperature (ICC_{Temp}= 0.894, 95% CrI: 0.806 – 0.952; Table S4A).

There was a 37.7% reduction in shared temporal variance in survival, when comparing the posterior median values for models excluding and including this predictor (Table 2, Figure 5). However, the 95% credible intervals of both these variances overlapped. In contrast, the site-specific variance was largely unchanged

between the two models with highly overlapping credible intervals (Table 2, Figure 5). This pattern was reflected in the median ICC estimate, which decreased by 9.2% to 0.733 (95% CrI: 0.038–0.999; Table 2) upon inclusion of this predictor, however there was considerable uncertainty here too. Our results lend support to spatially synchronous fluctuations in local winter minimum temperature contributing to shared temporal variation in adult survival (Figure 4B).

Contribution of fluctuations in local breeding density to spatial synchrony in adult survival

We found annual survival was negatively associated with relative local breeding density (−0.194; 95% CrI: −0.297 – −0.092; Figure 3D; Table 1). Strong spatial synchrony was observed in local breeding density ($ICC_{Density}$= 0.955, 95% CrI: 0.499–0.999; Table S4B).

Comparing σ^2_{year} between models without and with relative local breeding density indicated a 43.3% reduction in shared among-year variance, with overlapping credible intervals (Table 2, Figure 5). $\sigma^2_{site:year}$ remained largely unchanged with highly overlapping credible intervals (Table 2, Figure 5). The median ICC decreased by 11.7% to 0.713 (95% CrI: 0.041–0.999, Table 2), upon inclusion of this predictor. Similar to winter temperature, these results also suggest annual deviations in local density contribute to survival synchrony (Figure 4C).

Contribution of fluctuations in both ecological predictors to spatial synchrony in adult survival

Comparing σ^2_{year} between the model excluding both covariates and the model including both indicated a 71.7% reduction in shared among-year variance although the 95% CrIs for both overlapped (Table 2, Figure 5). The site-specific variance $\sigma^2_{site:year}$ remained highly similar between the two models (Table 2, Figure 5). Upon including both our ecological predictors in the model, the median ICC decreased by 29.5% to 0.570 (95% CrI: 0.006 –0.999; Table 2; Figure 5). Our findings therefore suggest that relative local winter minimum temperature and local breeding density show evidence of each contributing to spatial synchrony in adult blue tit survival (Figure 4D).

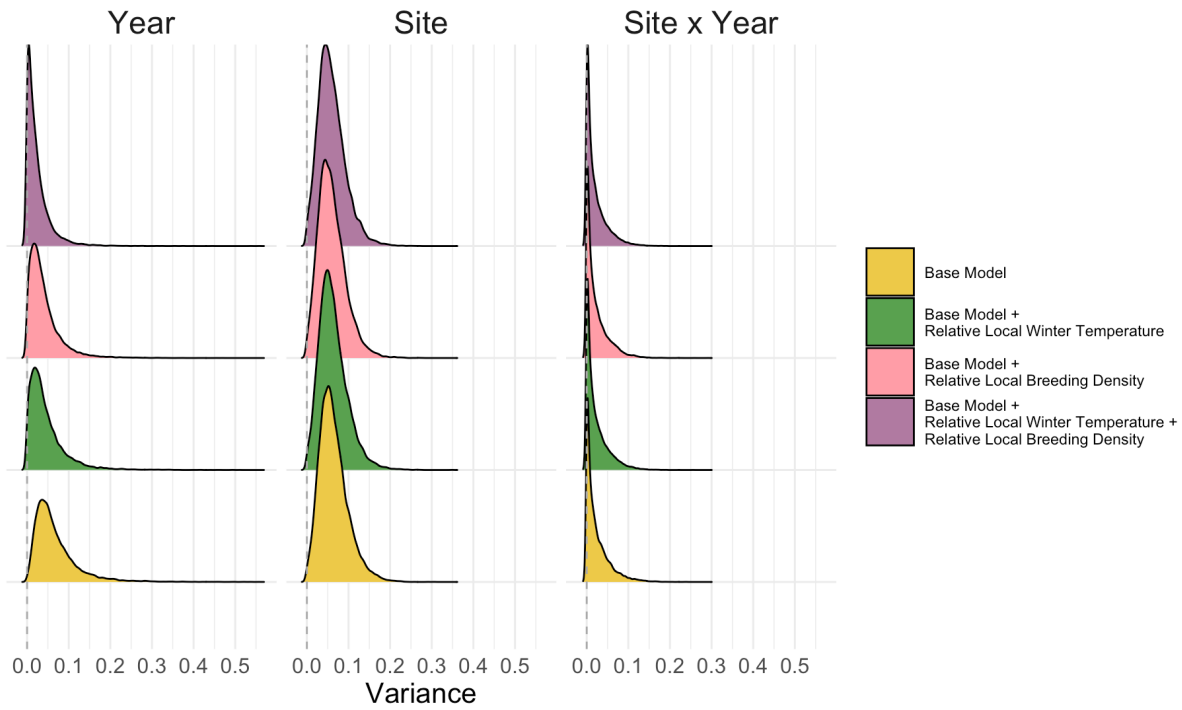

Figure 5: Posterior distributions of random effect variance components across different adult annual apparent survival sub-models: a) base model (sex and age fitted as fixed effects); b) base model including relative local winter minimum temperature as an additional fixed effect; c) base model including relative local breeding density as an additional fixed effect; d) base model including both relative local winter minimum temperature and relative local breeding density as additional fixed effects. All models included random effects of site, year and the interaction of site and year fitted for both the apparent survival and recapture sub-models.

Table 2: Spatial synchrony (ICC) measures alongside among-site, among-year and site-by-year variance components estimated from a) base model (sex and age fitted as fixed effects); b) base model including relative local winter minimum temperature as an additional fixed effect; c) base model including relative local breeding density as an additional fixed effect; d) base model including both relative local winter minimum temperature and relative local breeding density as additional fixed effects. All models included random effects of site, year and the interaction of site and year fitted for both the apparent survival and recapture sub-models. All variances and ratios of variances (ICC) reported are on logit scale.

Parameter	*median*	*2.50%*	*97.50%*	*n_eff*	*Rhat*
A) Base Model					
Year Variance	**0.053**	0.010	0.211	6666	1.000
Site Variance	0.059	0.011	0.146	4019	1.001
Site:Year Variance	0.014	0.000	0.104	2833	1.002
Spatial synchrony (ICC)	0.808	0.188	0.999	2852	1.002
B) Base Model + Relative Local Winter Temperature$_{min}$					
Year Variance	**0.033**	0.001	0.165	5171	1.000
Site Variance	0.058	0.011	0.144	4294	1.001

Site:Year Variance	0.013	0.000	0.096	2619	1.002
Spatial synchrony (ICC)	0.733	0.038	0.999	2587	1.001
C) Base Model + Relative Local Breeding Density					
Year Variance	**0.030**	0.001	0.143	5733	1.000
Site Variance	0.055	0.009	0.137	4999	1.001
Site:Year Variance	0.012	0.000	0.094	2603	1.000
Spatial synchrony (ICC)	0.713	0.041	0.999	2549	1.001
D) Base Model + Relative Local Winter Temperature$_{min}$ + Relative Local Breeding Density					
Year Variance	**0.015**	0.000	0.104	6085	1.000
Site Variance	0.055	0.008	0.136	5135	1.000
Site:Year Variance	0.011	0.000	0.09	3146	1.001
Spatial synchrony (ICC)	0.570	0.006	0.999	3367	1.001

Discussion

Using mark-recapture data from nestbox breeding populations of blue tits across 44 sites spanning a 220km transect in Scotland over 12 years, we found evidence for spatial synchrony in adult apparent survival with most of the temporal variance shared across sites. Annual fluctuations in local winter minimum temperature and local breeding density contributed to shared temporal variance in survival, with both predictors themselves being strongly spatially synchronous. Adult apparent survival was additionally found to be density-dependent. On average, males survived better than females and annual survival also varied quadratically with age. Together, our findings are consistent with regional winter weather and density-dependent processes as potential synchronizing mechanisms underpinning survival synchrony in a short-lived sedentary, temperate passerine.

Our median ICC estimate aligned with the high spatial synchrony in adult survival reported in great tits in France (ICC = ~0.72; Ghislain et al., 2024) studied at a larger spatial scale, and with highly similar survival dynamics reported across Mediterranean blue tit populations (Grosbois et al., 2006; Bastianelli et al., 2021). Despite differences in life history, our estimates were also consistent with the high spatial synchrony in survival reported in European seabirds (ICC: 0.67–0.87; Grosbois et al., 2009; Horswill et al., 2023; Reiertsen et al., 2021). In contrast, Morrison et al. (2022) examined intraspecific survival synchrony in 26 passerine species across eight European countries and reported relatively lower ICC estimates for most. This is unsurprising given that spatial synchrony is known to decay with distance and they investigated populations separated by thousands of kilometres, whereas our sites lie within a 220 km transect and are therefore exposed to broadly similar weather conditions (Liebhold et al., 2004). The wide 95% credible interval around our ICC estimate reflects uncertainty in the precise magnitude of synchrony, and we recognise that detecting site-by-year interactions from mark-recapture data

requires sufficient within-site annual captures to reliably distinguish the spatiotemporal variance component from zero (Figure 4). Nonetheless, our results suggest that adult survival in blue tits across the study region is highly spatially synchronous and governed primarily by shared rather than site-specific local processes. This has potentially important consequences for both population dynamics and management. High synchrony in adult survival could influence synchrony in population abundance, the magnitude of which depends on the elasticity of population growth rate to adult survival in this relatively short-lived passerine and also, the contribution of temporal variance in survival to realised variation in population growth rate (Schaub et al., 2015). Our study also suggests that woodland generalist species like blue tits may act as a potentially useful ecological indicator, since temporal patterns in adult survival estimated at a few well-monitored sites may be representative of survival trajectories across the wider region.

Annual deviations in local winter minimum temperature explained some shared temporal variance in annual survival with a median contribution of 39.2%, while only contributing 3.5% to site-specific temporal variation in survival, though the 95% CrIs were wide throughout (Table S6). The high spatial synchrony in winter minimum temperature is consistent with a classic Moran effect whereby regional weather conditions simultaneously impose favourable or adverse conditions across sites, likely synchronising thermoregulatory and foraging challenges experienced by individuals during the non-breeding season (Moran, 1953). However, including the within-site annual deviation in winter minimum temperature as a covariate reduced among-year variance in survival without producing a statistically significant direct effect (Table 2). This suggests that when an environmental variable is highly spatially synchronous, even an imprecisely estimated effect on survival may explain shared temporal variance across populations, consistent with a Moran effect whose magnitude is uncertain rather than absent. The contribution of spatially synchronous winter minimum temperature to survival synchrony should therefore be interpreted cautiously.

For density to act as a synchronizing mechanism, it must itself fluctuate synchronously across sites and we found support for this, detecting high spatial synchrony in local breeding density at the nestbox level (Table S4B). Two plausible mechanisms may transfer synchrony in density fluctuations to observed synchrony in survival. First, if conditions during the preceding spring (e.g. weather-mediated variation in food availability or nestbox competition) are simultaneously favourable or harsh across all sites, density variation will be regionally correlated through a Moran effect on the breeding population. Second, there could be carry-over effects of density via survival: if overwinter survival and recruitment are regionally high in year *t*, spring breeding densities in year *t+1* will be high synchronously across sites, and – given the density-dependence we detected – this elevated density will in turn suppress survival in winter *t+1* across sites (Norris, 2005; Fay et al., 2022). In this way, both exogenous forcing (via shared environmental drivers) and endogenous feedback (via density-dependent carry-over effects) could transfer synchrony in density to survival. Such feedback between survival synchrony and density synchrony represents an important yet underexplored mechanism capable of maintaining synchrony in demographic rates across space. The joint contribution of fluctuations in local winter temperature and breeding density to shared temporal

variance is not well identified with our dataset, as evidenced by the very wide credible intervals on the posterior distributions of ICC and contribution estimates (Tables 2 & S6). Cautious interpretation is therefore warranted, though our ecological predictors were more likely to positively contribute to global, compared to local, temporal variance in survival (probability = 0.83 vs. 0.53 respectively; Table S6).

Beyond the Moran effect and density-dependent processes, other unmeasured but regionally synchronous drivers could additionally underpin spatially synchronous survival dynamics e.g. fluctuations in food availability and predator abundance. Regionally synchronous fluctuations in caterpillar abundance have been identified as a primary driver of population synchrony in forest songbirds (Jones et al., 2003). Substantial interannual variation in caterpillar abundance has been reported for our focal study system, suggesting that fluctuations in this key prey resource has the potential to contribute to spatially synchronous interannual variation in blue tit survival (Macphie et al., 2026). Mast seeding by European beech is known to be highly synchronous over distances of up to 1500 km, with mast years elevating winter seed abundance available to consumers including small passerines (Bogdziewicz et al., 2025), with the over-wintering survival of some tit populations very sensitive to this (Perrins, 1965; Reed et al., 2013). While beech masting constitutes an important winter food resource for passerines in Sweden and continental Europe, it is not expected to directly determine survival of small passerines like blue tits in the UK (Dhondt et al., 2012 but see Saether et al., 2007). Spatial synchrony in abundance of avian and mammalian predators such as sparrowhawks and pine martens could also underlie spatially synchronous blue tit survival dynamics (Jarillo et al., 2020; Liebhold et al., 2004).

We found a negative association between annual survival and annual deviations in local breeding density, consistent with density-dependent regulation operating temporally within sites. This may reflect increased mortality driven by intraspecific competition for limited resources or breeding territories in years of relatively high local density (Newton, 1998; Rodenhouse et al., 1997). Other unmeasured density-dependent factors, such as fluctuations in predators or inter-specific competitors may also contribute (McKellar et al., 2014). In addition, we found a positive association between absolute local breeding density and survival, suggesting that permanent among-site differences in density reflect habitat quality with high-quality sites supporting both higher densities and better survival on average (Table S5). Our local density metric was based on only 6–8 nest-boxes in each site-year and measurement error will attenuate the estimated density effect toward zero. In addition, some individuals may have bred in unmonitored natural cavities in high-density years, inflating the apparent negative relationship between survival and relative local breeding density. Nevertheless, the observed negative effect of yearly density fluctuations on survival suggests that conditions in the monitored nestboxes broadly reflect fluctuations in site-level densities relevant to survival.

There are several potential explanations for why the effects of winter minimum temperature on annual survival were imprecisely estimated (Table 1, Table S5). Firstly, averaging across the entire winter (December – March) period may mask critical shorter time windows and we did not employ a data-driven approach such as sliding-window analysis here to identify precise temporal windows important for

survival. Second, since adults are captured on the nest every spring, the exact timing of mortality is unknown. Weather conditions in autumn could potentially be more influential for adult survival, especially if winters are not extremely harsh, as was observed in long-tailed tits in the UK (Gullett et al., 2014). Third, mean local minimum temperature during December–March captures only one aspect of winter severity. Precipitation, snow cover, frequency or duration of cold and wet spells, extreme weather events during winter may be more limiting but not well-represented in a seasonal average of daily minimum temperatures used here (Trenberth & Shea, 2005). Together, these factors likely contribute to the imprecise effect estimate, given the limited temporal replication (n=12 years) and the coarse characterisation of winter severity.

In conclusion, our study suggests that adult blue tit survival is highly synchronous at a regional scale, with most temporal variation in survival shared across 44 sites spanning a 220 km transect. Annual fluctuations in local winter minimum temperature and local breeding density each contributed to this shared temporal variance, consistent with a Moran effect and spatially correlated density-dependent processes acting as potential synchronising mechanisms. Spatial synchrony in survival and breeding density may additionally interact through carry-over effects whereby synchronised survival propagates into synchronised breeding density, which in turn reinforces survival synchrony via density dependence. Such feedback represents an important yet underexplored mechanism capable of sustaining synchronised demographic dynamics across space. With global warming leading to increasingly frequent and extreme climatic events, spatial synchrony in demographic rates is likely to strengthen across broad spatial scales, heightening the collective vulnerability of geographically separated breeding populations (Black et al., 2018). Long-term monitoring of a woodland generalist species such as the blue tit with relatively high abundance, well-known biology and ease of monitoring, will be essential for uncovering the processes that contribute to spatiotemporal dynamics of demographic rates under ongoing environmental change.

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Author Contributions

Sanjana Ravindran: Conceptualization, data curation, investigation, formal analysis, methodology, visualization, writing – original draft, and writing – review and editing. Alexander Eyo: Data curation, formal analysis, and writing – review and editing. Albert B. Phillimore: Data curation, project administration, funding acquisition, and writing – review and editing; Hannah Froy: Conceptualization, data curation, investigation, funding acquisition, and writing – review and editing.

Data & Code Availability

Data and code will be made available in an open repository upon acceptance.

Conflict of Interest Statement

The authors declare no competing interests.

References

Liebhold, A., Koenig, W. D., & Bjørnstad, O. N. (2004). Spatial synchrony in population dynamics. Annu. Rev. Ecol. Evol. Syst., 35(1), 467-490.

Heino, M., Kaitala, V., Ranta, E., & Lindström, J. (1997). Synchronous dynamics and rates of extinction in spatially structured populations. Proceedings of the Royal Society of London. Series B: biological sciences, 264(1381), 481-486.

Morrison, C. A., Butler, S. J., Clark, J. A., Arizaga, J., Baltà, O., Cepák, J., ... & Gill, J. A. (2022). Demographic variation in space and time: implications for conservation targeting. Royal Society Open Science, 9(3), 211671.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., ... & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. science, 344(6187), 1246752.

Hansen, B. B., Grøtan, V., Herfindal, I., & Lee, A. M. (2020). The Moran effect revisited: spatial population synchrony under global warming. Ecography, 43(11), 1591-1602.

Bjørnstad, Ottar N., Rolf A. Ims, and Xavier Lambin. "Spatial population dynamics: analyzing patterns and processes of population synchrony." Trends in Ecology & Evolution 14.11 (1999): 427-432.

Moran, Patrick AP. "The statistical analysis of the Canadian lynx cycle." Australian Journal of Zoology 1.3 (1953): 291-298.

Koenig, Walter D. "Global patterns of environmental synchrony and the Moran effect." Ecography 25.3 (2002): 283-288.

Paradis, E., Baillie, S. R., Sutherland, W. J., & Gregory, R. D. (2000). Spatial synchrony in populations of birds: effects of habitat, population trend, and spatial scale. Ecology, 81(8), 2112-2125.

Elton, C., & Nicholson, M. (1942). The ten-year cycle in numbers of the lynx in Canada. The Journal of Animal Ecology, 215-244.

Koenig, W. D., & Knops, J. M. (2001). Seed-crop size and eruptions of North American boreal seed-eating birds. Journal of Animal Ecology, 70(4), 609-620.

Koenig, W. D., & Liebhold, A. M. (2016). Temporally increasing spatial synchrony of North American temperature and bird populations. Nature Climate Change, 6(6), 614-617.

Jones, J., P. J. Doran, and R. T. Holmes. 2003. “Climate and Food Synchronize Regional Forest Bird Abundances.” Ecology 84: 3024–3032.

Kendall, B. E., Bjørnstad, O. N., Bascompte, J., Keitt, T. H., & Fagan, W. F. (2000). Dispersal, environmental correlation, and spatial synchrony in population dynamics. The American Naturalist, 155(5), 628-636.

Reuman, D. C., Castorani, M. C., Cavanaugh, K. C., Sheppard, L. W., Walter, J. A., & Bell, T. W. (2023). How environmental drivers of spatial synchrony interact. Ecography, 2023(10), e06795.

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in ecology & evolution*, *13*(2), 58-63.

Sæther, B. E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. Ecology, 81(3), 642-653.

Crone, E. E. (2001). Is survivorship a better fitness surrogate than fecundity?. Evolution, 55(12), 2611-2614.

Lebreton, J. D., & Clobert, J. (1991). Bird population dynamics, management, and conservation: the role of mathematical modelling. Bird population studies, 105-125.

Nousiainen, I., Bosco, L., Lehikoinen, P., Robinson, R., Arizaga, J., Cepák, J., ... & Lehikoinen, A. (2025). Adult survival has a stronger role than productivity in the annual population change of European songbirds. Oecologia, 207(11), 173.

Grosbois, V., Henry, P. Y., Blondel, J., Perret, P., Lebreton, J. D., Thomas, D. W., & Lambrechts, M. M. (2006). Climate impacts on Mediterranean blue tit survival: an investigation across seasons and spatial scales. *Global Change Biology*, *12*(12), 2235-2249.

Tavecchia, G., Minguez, E., De León, A., Louzao, M., & Oro, D. (2008). Living close, doing differently: small-scale asynchrony in demography of two species of seabirds. Ecology, 89(1), 77-85.

Grosbois, V., Harris, M. P., Anker-Nilssen, T., McCleery, R. H., Shaw, D. N., Morgan, B. J., & Gimenez, O. (2009). Modeling survival at multi-population scales using mark–recapture data. Ecology, 90(10), 2922-2932.

Jenouvrier, S., Thibault, J. C., Viallefont, A., Vidal, P., Ristow, D., Mougin, J. L., ... & Bretagnolle, V. (2009). Global climate patterns explain range-wide synchronicity in survival of a migratory seabird. Global Change Biology, 15(1), 268-279.

Reynolds, T. J., Harris, M. P., King, R., Swann, R. L., Jardine, D. C., Frederiksen, M., & Wanless, S. (2011). Among-colony synchrony in the survival of common guillemots Uria aalge reflects shared wintering areas. Ibis, 153(4), 818-831.

Reiertsen, T. K., Layton-Matthews, K., Erikstad, K. E., Hodges, K., Ballesteros, M., Anker-Nilssen, T., ... & Wanless, S. (2021). Inter-population synchrony in adult survival and effects of climate and extreme weather in non-breeding areas of Atlantic puffins. Marine Ecology Progress Series, 676, 219-231.

Horswill, C., Warwick-Evans, V., Esmonde, N. P., Reid, N., Kirk, H., Siddiqi-Davies, K. R., ... & Wood, M. J. (2023). Interpopulation differences and temporal synchrony in rates of adult survival between two seabird colonies that differ in population size and distance to foraging grounds. Ecology and Evolution, 13(10), e10455.

Martin, E. C., Hansen, B. B., Lee, A. M., & Herfindal, I. (2023). Generation time and seasonal migration explain variation in spatial population synchrony across European bird species. *Journal of Animal Ecology*, *92*(9), 1904-1918.

Lack, D. (1954). Cyclic mortality. The Journal of Wildlife Management, 18(1), 25-37.

Newton, I. (1998). Population limitation in birds. Academic press.

Marsh, R. L., & Dawson, W. R. (1989). Avian adjustments to cold. In Animal adaptation to cold (pp. 205-253). Berlin, Heidelberg: Springer Berlin Heidelberg.

Post, E., and M. C. Forchhammer. 2004. “Spatial Synchrony of Local Populations Has Increased in Association with the Recent Northern Hemisphere Climate Trend.” Proceedings of the National Academy of Sciences of the United States of America 101: 9286–9290.

Pomara, L. Y., and B. Zuckerberg. 2017. “Climate Variability Drives Population Cycling and Synchrony.” Diversity and Distributions 23: 421–434.

Dhondt, A. A., Kempenaers, B., & Clobert, J. (1998). Sparrowhawk Accipiter nisus predation and Blue Tit Parus caeruleus adult annual survival rate. *Ibis*, *140*(4), 580-584.

Sinclair, A. R. E., & Pech, R. P. (1996). Density dependence, stochasticity, compensation and predator regulation. Oikos, 164-173.

Ranta, E., Kaitala, V., Lindström, J., & Helle, E. (1997). The Moran effect and synchrony in population dynamics. *Oikos*, 136-142.

Bjørnstad, O. N., Ims, R. A., & Lambin, X. (1999). Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in ecology & evolution*, *14*(11), 427-432.

Engen, S., & Sæther, B. E. (2005). Generalizations of the Moran effect explaining spatial synchrony in population fluctuations. The American Naturalist, 166(5), 603-612.

Walter, J. A., Sheppard, L. W., Anderson, T. L., Kastens, J. H., Bjørnstad, O. N., Liebhold, A. M., & Reuman, D. C. (2017). The geography of spatial synchrony. Ecology Letters, 20(7), 801-814.

Greenwood, P. J., & Harvey, P. H. (1982). The natal and breeding dispersal of birds. *Annual review of ecology and systematics*, *13*, 1-21.

Morris, W. F., Pfister, C. A., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. S., ... & Menges, E. S. (2008). Longevity can buffer plant and animal populations against changing climatic variability. *Ecology*, *89*(1), 19-25.

Bastianelli, O., Robert, A., Doutrelant, C., de Franceschi, C., Giovannini, P., & Charmantier, A. (2021). Identifying drivers of spatio-temporal variation in survival in four blue tit populations. Peer Community Journal, 1.

Ghislain, M., Bonnet, T., Godeau, U., Dehorter, O., Gimenez, O., & Henry, P. Y. (2024). Synchrony in adult survival is remarkably strong among common temperate songbirds across F rance. *Ecology*, *105*(6), e4305.

Shutt, J. D., Bolton, M., Cabello, I. B., Burgess, M. D., & Phillimore, A. B. (2018). The effects of woodland habitat and biogeography on blue tit Cyanistes caeruleus territory occupancy and productivity along a 220 km transect. Ecography, 41(12), 1967-1978.

Macphie, K. H., Samplonius, J. M., Hadfield, J. D., Pearce Higgins, J. W., & Phillimore, A. B. (2025). Tree taxon effects on the phenology of caterpillar abundance and biomass. *Oikos*, *2025*(4), e10972.

Jenni, L., & Winkler, R. (2020). *Moult and ageing of European passerines*. Bloomsbury Publishing.

Paradis, E., Baillie, S. R., Sutherland, W. J., & Gregory, R. D. (1998). Patterns of natal and breeding dispersal in birds. *Journal of Animal ecology*, *67*(4), 518-536.

Hollis, D., McCarthy, M., Kendon, M., Legg, T., & Simpson, I. (2019). HadUK-Grid—A new UK dataset of gridded climate observations. *Geoscience data journal*, *6*(2), 151-159.

Scholer, M. N., Strimas-Mackey, M., & Jankowski, J. E. (2020). A meta-analysis of global avian survival across species and latitude. *Ecology Letters*, *23*(10), 1537-1549.

Salewski, V., Hochachka, W. M., & Fiedler, W. (2013). Multiple weather factors affect apparent survival of European passerine birds. *PLoS One*, *8*(4), e59110.

Robinson, R. A., Baillie, S. R., & Crick, H. Q. (2007). Weather-dependent survival: implications of climate change for passerine population processes. *Ibis*, *149*(2), 357-364.

Van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within-versus between-subject effects using mixed models. Animal behaviour, 77(3), 753.

Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological monographs, 62(1), 67-118.

Valcu, M., & Kempenaers, B. (2008). Causes and consequences of breeding dispersal and divorce in a blue tit, Cyanistes caeruleus, population. *Animal Behaviour*, *75*(6), 1949-1963.

Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., ... & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of statistical software*, *76*, 1-32.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical science*, *7*(4), 457-472.

Oro, D., & Doak, D. F. (2020). Breeding transients in capture–recapture modeling and their consequences for local population dynamics. Scientific Reports, 10(1), 15815.

Genovart, M., & Pradel, R. (2019). Transience effect in capture-recapture studies: The importance of its biological meaning. PLoS one, 14(9), e0222241.

Brown, W. S., Kéry, M., & Hines, J. E. (2007). Survival of timber rattlesnakes (Crotalus horridus) estimated by capture–recapture models in relation to age, sex, color morph, time, and birthplace. Copeia, 2007(3), 656-671.

Lahoz-Monfort, J. J., Morgan, B. J., Harris, M. P., Wanless, S., & Freeman, S. N. (2011). A capture–recapture model for exploring multi-species synchrony in survival. Methods in Ecology and Evolution, 2(1), 116-124.

Schaub, M., von Hirschheydt, J., & Grüebler, M. U. (2015). Differential contribution of demographic rate synchrony to population synchrony in barn swallows. Journal of Animal Ecology, 84(6), 1530-1541.

Norris, D. R. (2005). Carry-over effects and habitat quality in migratory populations. *Oikos*, *109*(1), 178-186.

Fay, R., Hamel, S., Van de Pol, M., Gaillard, J. M., Yoccoz, N. G., Acker, P., ... & Sæther, B. E. (2022). Temporal correlations among demographic parameters are ubiquitous but highly variable across species. *Ecology Letters*, *25*(7), 1640-1654.

Macphie, K. H., Pick, J., Pearce-Higgins, J., Hadfield, J. D., & Phillimore, A. B. (2026). Timing isn't everything: impacts of maximum abundance and duration of a seasonal resource on consumer fitness.

Bogdziewicz, M., Kelly, D., Zwolak, R., Szymkowiak, J., & Hacket-Pain, A. (2025). Dynamics, mechanisms, and consequences of mast seeding. *Annual Review of Ecology, Evolution, and Systematics*, *56*.

Perrins, C. M. (1965). Population fluctuations and clutch-size in the Great Tit, Parus major L. *The Journal of Animal Ecology*, 601-647.

Reed, T.E., Grøtan, V., Jenouvrier, S., Sæther, B.E. and Visser, M.E., 2013. Population growth in a wild bird is buffered against phenological mismatch. *Science*, *340*(6131), pp.488-491.

Dhondt, A. A. (2012). *Interspecific competition in birds* (Vol. 2). Oxford University Press.

SÆther, B. E., Engen, S., Grøtan, V., Fiedler, W., Matthysen, E., Visser, M. E., ... & Winkel, W. (2007). The extended Moran effect and large-scale synchronous fluctuations in the size of great tit and blue tit populations. Journal of Animal Ecology, 76(2), 315-325.

Jarillo, J., Sæther, B. E., Engen, S., & Cao-García, F. J. (2020). Spatial scales of population synchrony in predator-prey systems. *The American Naturalist*, *195*(2), 216-230.

Rodenhouse, N. L., Sherry, T. W., & Holmes, R. T. (1997). Site-dependent regulation of population size: a new synthesis. Ecology, 78(7), 2025-2042.

McKellar, A. E., Marra, P. P., Boag, P. T., & Ratcliffe, L. M. (2014). Form, function and consequences of density dependence in a long-distance migratory bird. Oikos, 123(3), 356-364.

Gullett, P., Evans, K. L., Robinson, R. A., & Hatchwell, B. J. (2014). Climate change and annual survival in a temperate passerine: partitioning seasonal effects and predicting future patterns. Oikos, 123(4), 389-400.

Trenberth, K. E., & Shea, D. J. (2005). Relationships between precipitation and surface temperature. Geophysical Research Letters, 32(14).

Black, B. A., van der Sleen, P., Di Lorenzo, E., Griffin, D., Sydeman, W. J., Dunham, J. B., ... & Bograd, S. J. (2018). Rising synchrony controls western North American ecosystems. *Global change biology*, *24*(6), 2305-2314.

Supplementary Methods and Results

For all our CJS models, we specified weakly informative priors for all parameters: normally-distributed N(0, 1) priors for fixed effect slopes and half-Cauchy(0, 2.5) priors for random effect standard deviations. For the logit-scale intercepts of survival and recapture probability, we specified normally-distributed N(0, 1.5) priors which are weakly informative on the logit scale. Four MCMC chains were run in parallel, each with 8000 iterations (4000 warm-up and 4000 sampling). Convergence was confirmed by Rhat < 1.01 and effective sample sizes > 1000 for all parameters (Gelman & Rubin, 1992). All reported parameter estimates are posterior medians with 95% credible intervals. We used rstan v.2.32.6 to run the models in R version 4.4.1 (2024-06-14) using RStudio Version 2024.09.0+375.

Goodness-of-fit testing using R2ucare v1.0.2 (Gimenez et al., 2018) revealed a significant overall violation of CJS assumptions ($\chi^2 = 59.433, df = 35, p < 0.01$), attributable to a transience effect (test3sr): newly marked individuals had lower subsequent recapture probability than previously marked individuals (Genovart & Pradel., 2019). This violation of the *test3sr* assumption is fairly common (reported in ~40% of mark-recapture studies in a review by Oro & Doak, 2020). Such a lack of fit is typically attributed to unmodelled age-related heterogeneity in survival, conventionally addressed by accounting for age effects in survival, which all models presented here include (Genovart & Pradel., 2019; Brown et al., 2007). After removing the contribution of *test3sr*, the adjusted goodness-of-fit test indicated satisfactory model fit (overall goodness-of-fit test: ($\chi^2 = 25.864, df = 25, p = 0.41$)).

Table S1: Number of breeding adults caught A) across the 12 years and B) across the 44 sites (ordered from south to north) of this study.

A)

Year	Number of adult captures
2014	115
2015	220
2016	213

2017	315
2018	349
2019	351
2020	334
2021	325
2022	329
2023	359
2024	300
2025	123

B)

Site	Number of adult captures	Site	Number of adult captures
EDI	131	DLW	21
RSY	86	CRU	42
FOF	140	NEW	83
BAD	97	DAV	49
LVN	119	HWP	42
DOW	95	INS	56
GLF	115	FSH	93
SER	140	RTH	43
MCH	72	AVI	76
PTH	115	AVN	101
STY	106	CAR	50
BIR	70	SLS	54
DUN	44	TOM	16
BLG	135	ART	92
PIT	110	MUN	82
KCK	63	FOU	74
KCZ	66	ALN	71
BLA	78	DEL	112
CAL	48	TAI	90
DNM	61	OSP	53
DNC	25	SPD	43
DNS	17	DOR	57

Validation of our CJS model using a simulation study

To evaluate the behaviour of our CJS model over a broad range of parameter values, we simulated nine data sets that crossed high (0.8), medium (0.5) and low (0.2) mean survival and recapture probabilities. Each data set contained capture histories for 2,000 individuals observed at 40 sites over 10 years, mirroring the structure of our empirical study. Random effects for site, year and site-by-year interaction were fitted for both the survival and recapture sub-models, with no fixed

effects specified. Prior specification was identical to that specified in our empirical study (see Methods). Four MCMC chains were run in parallel, each with 4000 iterations (2000 warm-up and 2000 sampling). Convergence was assessed using Rhat values which were <1.01 and effective sample sizes >1000 for all parameters across all models, indicating satisfactory convergence.

In every scenario, the point estimate was close to the true value and the true value lay inside the corresponding 95% credible interval (Table S2). Although only one replicate was analysed per scenario due to computational costs associated with running many replicates, these results suggest that the CJS model is approximately unbiased over a broad range of survival and recapture probabilities that could potentially occur in a short-lived passerine system.

Table S2: True and estimated mean survival and recapture probabilities from CJS models run on simulated datasets. Posterior mean and 95% CrIs reported.

True mean survival probability	*True mean recapture probability*	*Estimated mean survival probability*	*Estimated mean recapture probability*
High survival (0.8)	High recapture (0.8)	0.811 (0.786 – 0.835)	0.790 (0.771 – 0.809)
High survival (0.8)	Medium recapture (0.5)	0.811 (0.787 – 836)	0.502 (0.477 – 527)
High survival (0.8)	Low recapture (0.2)	0.817 (0.781 – 0.853)	0.205 (0.185 – 0.226)
Medium survival (0.5)	High recapture (0.8)	0.477 (0.457 – 0.497)	0.813 (0.772 – 0.853)
Medium survival (0.5)	Medium recapture (0.5)	0.473 (0.440 – 0.506)	0.514 (0.465 – 0.564)
Medium survival (0.5)	Low recapture (0.2)	0.463 (0.395 – 0.531)	0.212 (0.169 – 0.263)
Low survival (0.2)	High recapture (0.8)	0.189 (0.153 – 0.227)	0.832 (0.707 – 0.941)
Low survival (0.2)	Medium recapture (0.5)	0.176 (0.136 – 0.222)	0.540 (0.389 – 0.729)
Low survival (0.2)	Low recapture (0.2)	0.219 (0.127 – 0.335)	0.125 (0.063 – 0.219)

<u>Effect of 2017-2019 clutch swap experiment on annual apparent survival of adults</u>

Between 2017 and 2019, clutch swap experiments were conducted across 37 sites involving 269 nestboxes. Because of this experiment, breeding adults captured at these nestboxes (n=459 observations of 380 individuals) may experience differential costs of reproduction on survival, compared to unmanipulated individuals. We

investigated whether being a part of the clutch-swap experiment in year *t* influenced survival from year *t* to *t+1* by including a time-varying fixed effect of experiment (a factor with two levels: 0=unmanipulated and 1=experimentally manipulated) alongside all other fixed and random effects as in the CJS model reported in the main text. We found no difference in average apparent annual survival between the two treatment groups, with the temporal variance in survival remaining unchanged (Supplementary Table S3).

Table S3: Results from Cormack-Jolly-Seber model investigating effects of sex, age, clutch swap experiment, relative winter temperature and relative local breeding density on annual apparent survival probability. Estimates of recapture probability and random effects of site, year and interaction between site and year for both sub-models also reported. Posterior median, 95% CrI shown along with effective sample size and Rhat. All parameter values are on logit scale. Results in bold indicate estimates where the 95% CrIs don't overlap zero.

Parameter	*median*	*2.50%*	*97.50%*	*n_eff*	*Rhat*
Survival Probability					
Intercept	-0.115	-0.363	0.115	10007	1.001
Sex (female)	**-0.238**	**-0.383**	**-0.093**	22147	1.000
Age (linear)	**-0.529**	**-0.961**	**-0.112**	9958	1.000
Age (quadratic)	**-0.406**	**-0.705**	**-0.115**	10665	1.000
Clutch Swap Experiment (1)	0.071	-0.191	0.339	16440	1.000
Relative local winter temperature	-0.110	-0.231	0.022	10236	1.000
Relative local breeding density	**-0.193**	**-0.295**	**-0.091**	16049	1.000
Year variance	0.018	0.000	0.117	5604	1.001
Site variance	0.055	0.008	0.138	3815	1.001
Site:Year variance	0.012	0.000	0.093	3132	1.001
Recapture Probability					
Intercept	1.341	0.910	1.813	6075	1.001
Year variance	0.088	0.000	0.624	5494	1.002
Site variance	0.687	0.256	1.592	5374	1.000
Site:Year variance	0.184	0.001	0.782	2045	1.002

<u>Spatial synchrony in absolute local winter minimum temperature and local breeding density at the nestbox level</u>

Since we expect spatial synchrony in local winter temperature and local breeding density to be driving any observed spatial synchrony in adult survival, we also estimated ICCs in both these ecological variables. We fitted absolute local winter minimum temperature with normally-distributed errors where year and site were fitted as random effects in this model (n=436). The residual variance in this model captured spatiotemporal (site-by-year) variation. For local breeding density, we fit a binomial model for occupancy (0=unoccupied; 1=occupied) at the nestbox level where year, site and the interaction between them were fitted as random effects (n=3141). This was done since sampling variance could be substantial with only 6-8 nestboxes monitored at each site, increasing variance in the realized occupancies

(measured as absolute local breeding density) (Santin-Janin et al., 2014). By fitting a binomial model at the nestbox level, we can separate this sampling variance from the spatiotemporal variance we are interested in. Then, we estimated spatial synchrony (ICCs) for both absolute local winter temperature and local breeding density (at the nestbox level) as:

$$ICC_{temp} = \frac{\sigma^2{}_{year}}{\sigma^2{}_{year}+\sigma^2{}_{residual}} \quad ; \quad ICC_{density} = \frac{\sigma^2{}_{year}}{\sigma^2{}_{year}+\sigma^2{}_{site:year}}$$

Models were run using '*rstanarm'* setting default weakly informative priors and running 4 chains of 8000 iterations. Convergence was confirmed based on Rhat < 1.01 and effective sample size > 1000 for all parameters.

We found high spatial synchrony in both absolute local winter temperature (ICC: 0.894, 95% CrI: 0.806 – 0.952; Table S4A) and local breeding density at the nestbox level (ICC: 0.955, 95% CrI: 0.499 – 0.999; Table S4B). This indicates that spatial synchrony in both these ecological variables contributes in part to the observed spatial synchrony in adult survival.

Table S4A: Results from a Gaussian model of absolute local winter where year and site were fitted as random effects. All parameter estimates and spatial synchrony (ICC) reported alongside their posterior medians and 95% CrIs.

Parameter	*Median*	*2.5%*	*97.5%*	*p-value*
Fixed Effect				
Intercept	0.409	-0.035	0.804	0.071
Random Effect	*Variance*			
Year variance	0.296	0.120	0.609	
Site variance	0.796	0.518	1.131	
Residual variance	0.035	0.031	0.041	
Spatial Synchrony (ICC)	0.894	0.806	0.952	

Table S4B: Results from a binomial model of local breeding density where year, site and site:year interaction term were fitted as random effects. All parameter estimates and spatial synchrony (ICC) reported alongside their posterior medians and 95% CrIs.

Parameter	*Median*	*2.5%*	*97.5%*	*p-value*
Fixed Effect				
Intercept	0.715	0.340	1.114	< 0.001
Random Effect	*Variance*			
Year variance	0.049	0.009	0.197	
Site variance	1.319	0.823	2.211	
Site:Year variance	0.002	0.000	0.027	
Spatial Synchrony (ICC)	0.955	0.499	0.999	

Effect of absolute local winter minimum temperature and absolute local breeding density on apparent annual survival of adults

To understand whether site-level variation in our environmental predictors predicted annual apparent survival of adult blue tits, we re-ran our full CJS model fitting additional fixed effects of absolute local winter minimum temperature and absolute local breeding density. We found site-mean local breeding density to positively predict survival to the next breeding season. There was no association between site-mean local winter minimum temperature and survival to the subsequent spring (Table S5).

Table S5: Results from Cormack-Jolly-Seber model investigating effects of sex, age, mean local winter minimum temperature, mean local breeding density, relative winter temperature and relative local breeding density on annual apparent survival probability. Estimates of recapture probability and random effects of site, year and interaction between site and year for both sub-models also reported. Posterior mean, 95% CrI shown along with effective sample size and Rhat. All parameter values are on logit scale. Results in bold indicate estimates where the 95% CrIs don't overlap zero.

Parameter	*median*	*2.50%*	*97.50%*	*n_eff*	*Rhat*
Survival Probability					
Intercept	-0.109	-0.347	0.121	10484	1.000
Sex (female)	**-0.235**	**-0.384**	**-0.089**	20563	1.000
Age (linear)	**-0.532**	**-0.957**	**-0.127**	9063	1.000
Age (quadratic)	**-0.404**	**-0.706**	**-0.121**	10574	1.000
Absolute local winter temperature	-0.027	-0.165	0.108	8526	1.000
Relative local winter temperature	-0.111	-0.230	0.015	10362	1.000
Absolute local breeding density	**0.151**	**0.020**	**0.281**	8683	1.000
Relative local breeding density	**-0.180**	**-0.284**	**-0.078**	17653	1.000
Year variance	0.017	0.000	0.109	5683	1.000
Site variance	0.043	0.003	0.121	4553	1.001
Site:Year variance	0.012	0.000	0.093	2979	1.002
Recapture Probability					
Intercept	1.381	0.945	1.845	5652	1.000
Year variance	0.087	0.000	0.609	5188	1.000
Site variance	0.634	0.217	1.514	5224	1.002
Site:Year variance	0.195	0.001	0.813	2081	1.001

Contributions of ecological predictors to shared and site-specific temporal variation in survival

We estimated the proportion of shared and site-specific temporal variation in survival explained by each ecological predictor using the full posterior distribution of σ^2_{year} and $\sigma^2_{site:year}$ variance components to predictors (Grosbois et al., 2009; Horswill et al., 2023). For each MCMC draw, we calculated:

$$\text{Contribution}_{year} = \frac{{\sigma^2}_{year,excl} - {\sigma^2}_{year,incl}}{{\sigma^2}_{year,excl}}$$

$$\text{Contribution}_{site:year} = \frac{{\sigma^2}_{site:year,excl} - {\sigma^2}_{site:year,incl}}{{\sigma^2}_{site:year,excl}}$$

where ${\sigma^2}_{year,excl}$, ${\sigma^2}_{year,incl}$ are posterior draws of the random year-effect variance and ${\sigma^2}_{site:year,excl}$, ${\sigma^2}_{site:year,incl}$ are posterior draws of the site-by-year random effect variance from the models excluding and including the ecological predictor, respectively. We report the median and 95% credible interval of the resulting posterior distribution of $\text{Contribution}_{year}$ and $\text{Contribution}_{site:year}$. We also computed the posterior probability that the contribution of our ecological predictors to shared and site-specific temporal variance in survival was positive, estimated as the proportion of posterior samples for which the contribution exceeded zero.

The posterior median contribution of relative local winter minimum temperature to synchronous variation in survival was 39.2% (95 % CrI: -5.561 – 0.983), however its contribution to site-specific variance was small at 3.5% (95% CrI: -442.835 – 0.998). The site:year variance contribution exhibited very wide 95% credible intervals, driven by some posterior draws in which ${\sigma^2}_{site:year,excl}$ approached zero (Table S6).

For relative local breeding density, the posterior median contribution to shared (${\sigma^2}_{year}$) and site-specific (${\sigma^2}_{site:year}$) variation in survival was 45.5% and 6.1% respectively, although the 95% CrIs were very wide (Table S6).

The posterior median contribution of both ecological predictors to shared temporal variation in survival was 72.9% however, the 95% credible interval was very wide. Since the probability that the contribution of both predictors to shared and site-specific temporal variance was positive was 0.83 and 0.53 respectively, this suggests that our ecological predictors were more likely to explain shared (rather than site-specific) temporal variance in survival (Table S6).

Table S6: Contributions of i) relative local winter minimum temperature, ii) relative local breeding density and iii) both ecological predictors to shared and site-specific temporal variance in adult annual survival. Median and 95% CrIs of the posterior distributions reported. The posterior probability that the contribution is positive is also displayed.

	Median contribution	*2.50%*	*97.50%*	*P (contribution > 0)*
Relative Local Winter Temperature$_{min}$				
Year Variance	0.392	-5.561	0.983	0.663
Site:Year Variance	0.035	-442.835	0.998	0.508
Relative Local Breeding Density				
Year Variance	0.455	-4.588	0.983	0.700
Site:Year Variance	0.061	-384.796	0.998	0.511

Relative Local Winter Temperature$_{min}$ and Relative Local Breeding Density				
Year Variance	0.729	-2.723	0.998	0.830
Site:Year Variance	0.139	-337.974	0.998	0.526

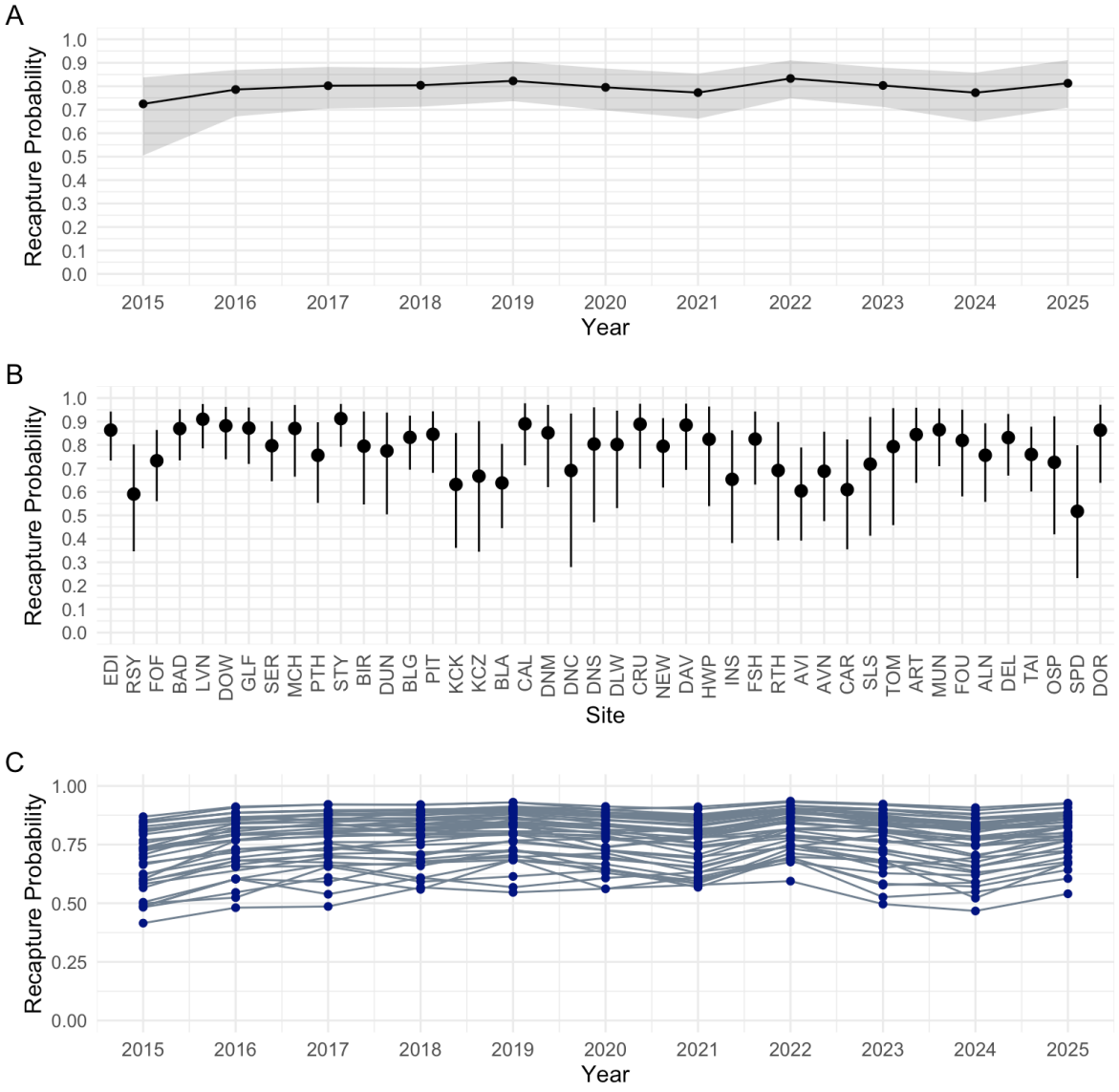

Figure S1: (A) Temporal, (B) spatial and (C) spatiotemporal variation in recapture probability. Posterior median (for A,B, C) and 95% CrIs (for A, B) displayed (Table 1).