Multi-population analysis reveals spatial consistency in drivers of population dynamics of a declining migratory bird

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ABSTRACT

1. Many migratory species are in decline across their geographical ranges. Single-population studies can provide important insights into drivers at a local scale, but effective conservation requires multi-population perspectives. This is challenging because relevant data are often hard to consolidate, and state-of-the-art analytical tools are typically tailored to specific datasets.
2. We capitalized on a recent data harmonization initiative (SPI-Birds) and linked it to a generalized modeling framework to identify the demographic and environmental drivers of large-scale population decline in migratory pied flycatchers (*Ficedula hypoleuca*) breeding across Britain.
3. We implemented a generalized integrated population model (IPM) to estimate age-specific vital rates, including their dependency on environmental conditions, and total and breeding population size of pied flycatchers using long-term (34-64 years) monitoring data from seven locations representative of the British breeding range. We then quantified the relative contributions of different vital rates and population structure to changes in short- and long-term population growth rate using transient life table response experiments (LTREs).
4. Substantial covariation in population sizes across breeding locations suggested that change was the result of large-scale drivers. This was supported by LTRE analyses, which attributed past changes in short-term population growth rates and long-term population trends primarily to variation in annual survival and dispersal dynamics, which largely act during migration and/or non-breeding season. Contributions of variation in local reproductive parameters were small in comparison, despite sensitivity to local temperature and rainfall within the breeding period.

5. We show that both short- and longer-term population changes of British-breeding pied flycatchers are likely linked to factors acting during migration and in non-breeding areas, where future research should be prioritized. We illustrate the potential of multi-population analyses for informing management at (inter)national scales and highlight the importance of data standardization, generalized and accessible analytical tools, and reproducible workflows to achieve them.

Keywords: annual survival, comparative analysis, environmental effects, integrated population model, full annual cycle, LTRE, multi-population, pied flycatcher

1 INTRODUCTION

Globally, many migratory species have been in decline over recent decades due to climate and land-use changes (Kubelka *et al.* 2022), but implementing effective conservation actions remains challenging. A central reason is that effective management of animal populations requires in-depth knowledge about demographic processes under different environmental conditions (Williams, Nichols & Conroy 2002), and such knowledge is hard to obtain for migratory species as they experience a range of environments throughout their annual cycle and along migration routes (Hostetler, Sillett & Marra 2015; Kubelka *et al.* 2022). Additionally, different populations may overlap and mix in either breeding or wintering areas, necessitating conservation effort at large spatial scales (Webster & Marra 2005). Integrated population models (IPMs) have become key tools for studying links between environment, demographic rates, and population dynamics (Plard *et al.* 2019; Schaub & Kery 2021). Through joint analysis of multiple types of individual- and population-level data, IPMs provide in-depth insights into demographic processes, even when data are scarce, and frequently increase precision of estimates (Schaub & Kery 2021). While the flexibility of Bayesian modelling frameworks allows tailoring IPMs to any combination of available data from any given study population, there have been few efforts to generalize such models to allow consistent applications across multiple populations.

A major hurdle to implementing multi-population studies is limited sharing of data across species ranges and challenges with harmonizing data collected and curated by different people and institutions (Culina *et al.* 2021). To begin addressing these issues, researchers working with long-term individual-based monitoring data on hole-nesting bird species set up the SPI-Birds Network and Database (www.spibirds.org, Culina *et al.* 2021). Among the over 30 species currently contained in the database is one of the best-studied Afro-Palearctic migrants: the European pied flycatcher (*Ficedula hypoleuca*).

Like many other bird species breeding in Europe and spending the boreal winter in sub-Saharan Africa, breeding populations of pied flycatchers (hereafter “flycatchers”) have decreased over recent decades (29% decrease since 1980 across Europe, PECBMS 2020). Population declines have been linked to climatic factors and weather effects in both breeding and non-breeding areas (e.g. Goodenough, Elliot & Hart 2009; Selonen *et al.* 2021), as well as breeding season trophic mismatch as a consequence of warming springs (Both *et al.* 2006). Most relevant studies focus, however, on single breeding populations or relatively small regions, and to what degree breeding vs. non-breeding site conditions influence population dynamics remains an unanswered but crucial question for practitioners aiming to implement conservation measures at regional, national, and international scales.

In this study we aim to identify environmental and demographic drivers of the large-scale decline of flycatchers across Britain (43% since 1995, Woodward *et al.* 2020). We capitalize on SPI-Birds’ data harmonization to develop and fit a generalized IPM to long-term mark-recapture and nest box survey data from seven flycatcher populations representative of the British breeding range. We then use state-of-the-art transient life table response experiments (Koons *et al.* 2016; Koons, Arnold & Schaub 2017) to assess the relative importance of breeding season drivers (via reproduction) and non-breeding season drivers (via survival and immigration) for both short-term fluctuations in population growth rates and longer-term population trends.

2 METHODS

2.1 Study species

Pied flycatchers are short-lived (<9 years) woodland songbirds that migrate annually between boreal/temperate breeding grounds in Europe and non-breeding areas in western Africa. In Britain, the species breeds primarily in oak- (*Quercus spp.)* dominated woodlands across western England, Wales and Scotland (Balmer *et al.* 2013). Flycatchers are hole-nesting and readily take to human-provided nest boxes. Within a breeding season, British flycatchers typically lay a single clutch of 6-7 eggs although replacement clutches may be laid if the first clutch is lost early in the season (Lundberg & Alatalo 1992). Average laying date in British populations has advanced by 10 days over the last 50 years (Woodward *et al.* 2020) and is later at higher latitudes (Burgess *et al.* 2018). The incubation period is 13-15 days, and young typically fledge 16-17 days after hatching. Fledglings and adults then remain close to natal areas for around 45 days, and adults at least begin southward migration between mid July and mid-August (Bell *et al.* 2022). Among flycatcher populations breeding in Britain, first breeding is often delayed until two years old, but both breeding and non-breeding birds migrate to the breeding areas each spring (Harvey, Stenning & Campbell 1985; Both *et al.* 2017). Despite a high degree of philopatry, some individuals disperse, with breeding dispersal up to 8 km, and natal dispersal as far as 660 km but more typically <3 km (Lundberg & Alatalo 1992; Both, Robinson & van der Jeugd 2012).

2.2 Study areas and durations

We collected individual- and population-level data from seven populations of flycatchers representative of the British breeding distribution. Study populations (encompassing on average 89-550 nestboxes monitored for 34-64 years) covered a latitudinal gradient encompassing Scotland, Wales, and England and were located in oak-dominated woodlands (Figure 1). Most of the breeding populations initially established after the first nestboxes had been provided (e.g. Campbell 1965) and nestboxes were provided in excess in all subsequent years (excess calculated to average 40-44% in populations TEI and EDM).

2.3 Data collection and preparation

Individual- and population-level data on flycatchers were largely collected by volunteers, many organized through PiedFly.Net. Datasets were obtained in a harmonized standard format via the SPI-Birds database (www.spibirds.org, Culina *et al.* 2021) and reformatted for female-based analysis in R (v4.0.3, R Core Team 2020) as detailed in the following sections (code available via GitHub).

2.3.1 Breeding survey data

Flycatchers display a strong preference for breeding in nestboxes as opposed to natural cavities (Slagsvold 1987), which allows for comprehensive monitoring (nearly all nesting attempts recorded) when nestboxes are provided in excess, as in our study populations. For all study locations, nestboxes were surveyed at least weekly throughout the breeding season (April-July). For each nest, we recorded the total number of incubated eggs and fledglings, defined as the number of young alive at the last survey pre-fledging and, where necessary, estimated first egg laying date through back-calculations from observations of incomplete clutches (assuming one egg is laid daily). Additionally, we identified the social parents of each nest from uniquely numbered leg rings whenever possible (see section 2.3.2).

For our IPM analysis, we extracted five structurally different types of data from the entire breeding survey data of each population. At the population level, these were the annual number of females laying clutches (approximated as the number of first clutches laid, n = 18,893), and the annual sums of eggs and fledglings produced by all surveyed nests. At the individual level, we extracted data on clutch sizes (n = 6670) and fledgling numbers (n = 4836) observed in nests laid by females of known age in each year.

2.3.2 Mark-recapture data

Most (>95%) nestlings hatched in nestboxes in our study sites were marked with a uniquely numbered leg ring when 8-12 days old. Breeding adults were captured in nestboxes using one-way traps inside entrances and assumed to be immigrants into the focal breeding population if not ringed at first capture. Immigrant status was also assigned to the small subset (n = 148) of birds ringed as nestlings or adults in any of the other six studied before capture in the focal population.

We re-arranged the mark-recapture data for each population into two different types of input data for the IPM. First, we formatted the individual-level data for all birds marked as nestlings (n = 83,263) and adult females (n = 6123) into unique capture histories. Initial captures and recaptures of adult males were omitted since the present analyses focused on females. Second, we extracted the annual number of newly immigrated breeding females, approximated as the annual number of females newly ringed as adults.

2.3.3 Environmental data

Environmental factors are known to affect reproductive output of flycatchers, resulting in less reproduction and recruitment in years with more rainfall and lower temperatures during the nestling stage (Siikamaki 1996; Veistola, Lehikoinen & Eeva 1997). Accounting for effects of rainfall and temperature can therefore improve estimation of vital rates. To capture the relevant time periods for environmental covariates affecting nestlings we estimated relevant time windows for each year and population (to account for spatial and temporal variation in breeding phenology) as 8 days either side of the 0.25 quartile mean annual hatch date. Hatch date was typically not observed directly but approximated as the observed date of first egg + number of days spent laying + incubation period (14 days).

Little is known about environmental or other impacts on flycatchers after fledging and before southward migration, although it is likely that weather – and rainfall in particular –affects juvenile survival during this period (Cox *et al.* 2014; Naef-Daenzer & Grüebler 2016). We thus defined a second set of time windows for environmental impacts corresponding to this post-fledging period as 30 days from the assumed date of fledging (= hatch date + 16-day nestling period + 1).

For three of our seven study populations, information on date of first egg was sparse or missing so we used the estimated windows for the closest population in which windows could be estimated. Year-specific time windows estimated for East Dartmoor were thus used for the Teign Valley and Okehampton populations (distance 11 and 27 km, respectively), and windows for Denbigh were used for the Dinas population (distance 195 km).

We downloaded data on daily interpolated minimum temperature and total precipitation for 5x5 km squares encompassing each study location for May-August each year 1955-2019 (2020 was not yet available) from CEDA (Met Office 2019) using the R packages “raster” and “ncdf4” (Hijmans *et al.* 2015; Pierce & Pierce 2019). We then averaged the daily temperature and rainfall values over each population- and year-specific time-interval and used the resulting aggregated values as environmental covariates. All covariates were z-standardised prior to analysis.

2.4 IPM construction and implementation

We developed a workflow for fitting a generalized IPM (“SPI-IPM”) to any dataset on hole-nesting birds contained in the SPI-Birds database. It is immediately applicable to any species with a life-history similar to that of flycatchers, and straightforward to extend to others (e.g. multiple clutches per year commonly found in tit species). Data formatting, model specification, and model implementation are documented in detail in a code manual that accompanies the code on the SPI-IPM GitHub repository. We therefore keep the following description of model specification and implementation to a minimum, and refer the reader to

Chapters 2-4 in the code manual for more details (static version: supplementary file "SPI-IPM_CodeManual_Ch2-4.pdf"). All parameters in the model are defined in Table S1.1.

2.4.1 Age-structured population model and data likelihoods

We describe population dynamics using a female-based age-structured population model with a pre-breeding census. We focus on females only because female availability likely limits reproduction in systems with high numbers of non-breeders (Both *et al.* 2017). Females were divided into two age classes: "yearling" (1-year old birds hatched in the preceding breeding season) and "adult" (birds older than one year), as reproductive output is expected to differ between them (Fay *et al.* 2021). The dynamics of the female segment of the population over the time interval from spring in year t to spring in year $t+1$ can be described as:

$$N_{tot,t+1} = \begin{bmatrix} N_{Y,t+1} \\ N_{A,t+1} \end{bmatrix} = \begin{bmatrix} 0.5\ F_{Y,t}\ sJ_t & 0.5\ F_{A,t}\ sJ_t \\ sA_t & sA_t \end{bmatrix} \begin{bmatrix} N_{Y,t} \\ N_{A,t} \end{bmatrix} + \begin{bmatrix} Imm_{Y,t+1} \\ Imm_{A,t+1} \end{bmatrix}$$

$N_{tot,t+1}$ represents the total number of yearling and adult females in the population upon arrival in the breeding areas in year $t+1$. We refer to N_{tot} as "total population size" as it includes all females, irrespective of whether they breed in a nestbox or not. The number of yearling and adult females in the population in year $t+1$ ($N_{Y,t+1}$ and $N_{A,t+1}$, respectively) consists of local survivors and recruits from the previous breeding season, as well as immigrant yearling (Imm_Y) and adult (Imm_A) females. The age-specific fecundity terms $F_{a,t}$ are products of breeding probability ($pB_{a,t}$), clutch size ($CS_{a,t}$), probability of nest success (pNS_t, probability of complete clutch failure = $1 - pNS_t$), and survival probabilities of every egg/nestling to fledging when there is no complete nest failure ($sN_{a,t}$, with a = age of the mother). Fledglings and yearlings/adults can survive to the next breeding season and remain within the population with annual survival probabilities sJ_t and sA_t, respectively.

Data on various aspects of reproductive output ($CS_{a,t}$, pNS_t, and $sN_{a,t}$) were analyzed within the IPM via generalized linear mixed models. Annual survival rates (sJ_t and sA_t), as well as breeding probabilities ($pB_{a,t}$) were estimated by specifying an age-structured Cormack-Jolly-Seber model for the mark-recapture data in which age- and year-specific recapture probability was set to equal the product of $pB_{a,t}$ (probability of breeding in a nest box) and a probability of capture and identification given breeding in a nestbox p_t^{CapB}. The latter was approximated as the proportion of nests in each breeding season t for which the breeding female had been identified.

2.4.2 Temporal variation in vital rates

We accounted for among-year variation in (age-specific) vital rates using environmental covariates and normally distributed random effects as described in Chapter 3 of the code manual.

Effects of post-hatching rainfall were modeled on nest success and survival to fledging, and an additional effect of temperature in the post-hatching period was included for the latter. Effects of rainfall and temperature in the 30-day period post fledging were modeled on juvenile annual survival. No environmental covariates were included for breeding probability, clutch size, or adult survival.

2.4.3 Bayesian implementation

We implemented the IPM for each study population separately in a Bayesian framework using R v4.0.3 (R Core Team 2020) and Nimble v0.12.1 (de Valpine *et al.* 2017) and estimated parameters via Markov chain Monte Carlo (MCMC). We used non-informative priors with biologically sensible upper bounds for all parameters and simulated initial values for all nodes to avoid initialization problems. Missing covariate values were imputed within the model where necessary. We ran four MCMC chains of 200,000 iterations, of which the first 50,000 were discarded as burn-in, and which were subsequently thinned to retain every 30th sample. Chain convergence was verified using visual inspection and the Gelman-Rubin statistic (Gelman & Rubin 1992).

2.5 Model testing

Since there are no global goodness-of-fit tests available for IPMs (Plard *et al.* 2019), we used three complementary approaches to assess our IPMs ability to produce biologically relevant estimates of vital rates and realistic representations of flycatcher population dynamics. For the model fit to each of the seven populations, we first plotted predictions of the numbers of breeders and breeding immigrants, and several measures of reproductive output, against relevant observational data to ensure that predictions were not substantially biased (Gelman *et al.* 2013). Second, we checked for major discrepancies among datasets and between datasets and the population model by comparing posterior distributions of vital rate parameters obtained from the IPM to those obtained from models estimating each vital rate independently (Kéry & Schaub 2012; Gelman *et al.* 2013). Lastly, we verified that models could make realistic predictions of population dynamics by running stochastic forward-projections based on posterior median estimates (Gabry *et al.* 2019). The three-step model testing procedure, including results, is further described in SI S2.

2.6 Transient life table response experiments (LTRE)

Life table response experiments (LTREs) are retrospective analyses that allow quantification of the relative contributions of changes in different vital rates to population dynamics

(Caswell 2000). Transient LTREs can further evaluate contributions from changes in population structure and are particularly suited for IPMs, which provide estimates of both vital rates and population size/structure (Koons *et al.* 2016; Koons, Arnold & Schaub 2017). We used transient LTREs to investigate the drivers of both short-term and longer-term changes in growth rates of all seven focal populations.

Two types of LTREs can be used to quantify relative contributions of changes in vital rates and population structure (represented by the proportion of yearlings and adults) to short-term population dynamics. The "random design LTRE" quantifies contributions of among-year variation in a vital rate / population structure components θ_i to the total annual variation in realized population growth rate, $var(\lambda_t)$:

$$Contribution_{\theta_i}^{var(\lambda_t)} \approx \sum_i cov(\theta_{i,t}, \theta_{j,t}) \frac{\delta\lambda_t}{\delta\theta_{i,t}} \frac{\delta\lambda_t}{\delta\theta_{j,t}}\bigg|_{\bar{\theta}}$$

where $cov(\theta_{i,t}, \theta_{j,t})$ is the covariance of the quantity of interest (θ_i) with all other quantities (θ_{i-}), and $\frac{\delta\lambda_t}{\delta\theta_{i,t}}$ is the sensitivity of λ_t with respect to $\theta_{i,t}$. We derive the sensitivities for all parameters in the IPM in SI S3. The same sensitivities are also used in the "fixed design LTRE" for calculating the contribution of a change in θ_i from year t to year $t+1$ to the change in annual growth rate over the same time interval ($\Delta\lambda_t$):

$$Contribution_{\theta_i}^{\Delta\lambda_t} \approx (\theta_{i,t+1} - \theta_{i,t}) \frac{\delta\lambda_t}{\delta\theta_{i,t}}\bigg|_{\bar{\theta}}$$

(Koons *et al.* 2016) introduced an additional LTRE design (here referred to as the "period design") which focuses on longer-term population changes by calculating contributions of changes in vital rate means (μ_i) and standard deviations (σ_i) to changes in geometric mean growth rates ($\Delta\lambda_g$) between two time-periods (P1 & P2):

$$Contribution_{\theta_i}^{log\Delta\lambda_g} \approx \left(log\mu_{i,P2} - log\mu_{i,P1}\right)\left(\bar{e}^{T}_{\mu_i} + \bar{e}^{\hat{n}}_{\mu_i}\right) + (log\sigma_{i,P2} - log\sigma_{i,P1})(\bar{e}^{T}_{\sigma_i} + \bar{e}^{\hat{n}}_{\sigma_i})$$

In addition to partitioning contributions into those due to changes in mean and standard deviation, the period design LTRE further distinguishes between direct effects of changes in the vital rate (expressed by real-time elasticities $\bar{e}^{T}_{\mu_i}$ and $\bar{e}^{T}_{\sigma_i}$) and indirect changes mediated by perturbation of population structure as a consequence of vital rate changes (real-time elasticities $\bar{e}^{\hat{n}}_{\mu_i}$ and $\bar{e}^{\hat{n}}_{\sigma_i}$). The two time-periods compared need to have the same duration, and we selected two equal length periods capturing different population trajectories for all seven study populations (Figure S1.1). Additional details on the period design LTRE are provided in SI S4 and we refer to Koons *et al.* (2016 & 2017) for more information.

The implementation of transient LTREs for IPMs as introduced by Koons, Arnold and Schaub (2017) assumes closed populations. Since the flycatcher IPM includes immigration, we accounted for this in the LTRE analyses. Calculating sensitivities for immigration rates for use in random- and fixed-design LTREs is straightforward (SI S3, see also Nater *et al.* 2021; Paquet *et al.* 2021). The derivation of real-time elasticities for immigration rates (for use in the period-design LTRE) is new, and we detail our approach in SI S4. Code for implementing and running all three types of LTRE is provided in the GitHub repository.

3 RESULTS

Comparison of model predictions to observed data suggested no major lack of fit of the IPM for any population (SI S2.1). Posterior distributions from independent and integrated models largely overlapped, although the IPM tended to estimate lower adult survival and, in some cases, adult clutch size and nest success probability (SI S2.2). Stochastic projections indicated that the IPMs were able to predict realistic population dynamics (S2.3).

The results presented here are based on the posterior samples of 3 out of 4 run chains for each population (the third chain was excluded from the posterior of all models since it did not converge within 200,000 iterations in the model for OKE, and convergence issues for this model persisted also when using different initial values and/or MCMC seeds) and are reported as Median[95% credible interval]. Posterior summaries for vital rate parameters are also provided in Table S1.2 (separate supplementary file “TableS2.csv”).

3.1 Temporal dynamics of seven populations

Across all seven populations total population sizes showed periods of increase, decrease and stability (Figure 2). Variation in breeding population size (defined as the number of females breeding in nestboxes in a given year) largely tracked the temporal pattern in total population size, with an average of between 68[65, 73]% (DIN) and 86[77, 95]% (OKE) of the total population being reproductively active. The two southernmost populations (TEI and EDM) showed overall positive trends in population sizes over their study periods (Figure 2, Table S1.3). Correlation coefficients indicated negative population trends for four populations (OKE, NAG, DIN, and KAT, Table S1.3) although most of these also saw a period of population increase early in their study periods (Figure 2). A post-hoc covariation analysis further provided evidence for substantial (primarily) positive associations of year-by-year changes in population size across study sites (Figure S1.2).

3.2 Time-average age-specific vital rates

Within populations, vital rates associated with both survival and reproduction were higher for older birds (Figures 3, S1.3-S1.9). In all populations, most immigrants were adults, with yearling immigration rates estimated below 0.2 (Figure 3). The degree of cross-population variation in average vital rates differed depending on the vital rate: breeding and juvenile survival probabilities, for example, varied substantially across populations while clutch size and nestling survival were more similar (Figures 3 & S1.10). There were no strong associations between vital rate averages and study site latitude, but more northern populations (DIN, NWA, KAT) tended to have higher nestling survival and lower adult annual survival. Furthermore, the two Welsh populations (DIN & NWA) were characterized by substantially lower nest success probabilities than the other populations.

3.3 Among-year variation in and environmental effects on vital rates

The degree of among-year variation in vital rates varied both across parameters and populations (Table S1.2, Figures S1.11-S1.18). Models estimated substantial variation in juvenile and adult annual survival, nest success probability, nestling survival, and adult immigration rates. Estimated breeding probabilities were relatively invariable in the more southern populations TEI, EDM, OKE, and NAG but showed more variation in Wales and Scotland (DIN, NWA, KAT, Figure S1.13). Clutch size and yearling immigration rates were relatively constant in all populations (Figures S1.14 & S1.17). Overall, there was very little evidence for time trends in vital rates; the exceptions were an indication of decreasing breeding probability and increasing immigration rate for DIN and increasing adult survival and decreasing nestling survival for NWA (Table S1.3).

Posterior estimates of the slope parameters for environmental effects provided mixed evidence for rainfall and temperature directly impacting nest success probabilities, nestling survival, and juvenile survival (Figure 4, Table S1.4). While the 95% credible intervals of all estimated effects in all populations overlapped with 0, their posterior distributions (also summarised through additional 90% and 50% credible intervals in Table S1.4) still provided insights into potential rainfall and temperature effects. Notably, almost all estimated effects of rainfall on vital rates had negative posterior medians, and for several, a decrease in the vital rate with increasing rainfall was clearly visible (Figure 4). Temperature effects, on the other hand, did not show a general direction and were estimated anywhere between moderately positive and moderately negative (Figure 4, Table S1.4).

3.4 Demographic contributions to year-by-year variation in population growth rate

Results from the random design LTRE indicated that among-year variation in annual population growth rates was driven primarily by changes in immigration rates, followed by changes in survival (Figure 5). Contributions from changes in reproductive parameters and local population structure, however, had little influence on short-term population growth rates in most locations (Figures 5, S1.19 & S1.20). For DIN and KAT, however, variation in annual survival and reproductive output (primarily nest success and breeding probability, respectively) were of similar importance. In all populations, contributions from changes in reproductive parameters of adults were larger than those of yearlings, and adult immigration was consistently more influential than yearling immigration (Figure S1.20). For survival contributions, juveniles made a bigger impact than adults in four populations (TEI, EDM, NAG, DIN), similar impact in one (NWA), and smaller impact in two (OKE, KAT, Figure S1.20).

Conclusions regarding relative importance of different demographic processes from the fixed-design LTRE generally aligned with those obtained from the random-design LTRE (above), but further revealed that “atypical” years, i.e. years in which changes in reproduction had more impact than changes in survival, occurred in all populations (Figures 6 & S1.21). Furthermore, population growth rate in some years was driven by opposing contributions from reproduction and survival (clearly visible for KAT where changes in breeding probability were often the opposite to other vital rates, Figure 6). The largest population growth rates tended to coincide with disproportionately large contributions from changes in adult immigration rates (Figure S1.21). Otherwise, patterns in relative contributions of different vital rates were not clearly related to the magnitude or direction of population change in any given year, nor were there any clear trends of longer-term changes in relative importance of different demographic components (Figure S1.22).

3.5 Demographic contributions to long-term trends in population growth rate

Results from the period-design LTREs indicated that changes in longer-term trends from one time-period to the next (Figure S1.1) were driven by similar relative contributions of changes in survival and reproduction as variation in short-term population growth rates, but that changes in immigration rates were much less influential at longer timescales (Figure 7). As in the random-design LTRE, changes in reproductive and immigration rates of adults were generally more influential than changes in the equivalent rates of yearlings (Figure S1.23). Survival contributions of juveniles and adults to changes in long-term trends, however, were more balanced in several populations (Figure S1.23). Among reproductive parameters, changes in nest success probability had the strongest effect on changes in long-term population trends except NAG and KAT (where nestling survival and breeding probability had stronger contributions, respectively; Figure S1.23). In all populations, direct changes in vital rate means were responsible for most changes in population trajectories from one time-period to the next; contributions from direct effects of changes in vital rate variation and from indirect effects (through perturbation of population structure) were negligible in comparison (Figure S1.24).

4 DISCUSSION

4.1 Diverse but covarying population trajectories

Across the seven study sites, populations showed periods of increase, decrease, and stability over the past 3-6 decades (Figure 2). The two southernmost populations, TEI and EDM, showed generally increasing trends throughout the study period (Table S1.3), which may be at least partially linked to expansion of these nestbox schemes. Consistent with this explanation, population declines in OKE and KAT also co-occurred with a reduction in nestboxes towards the end of the study periods (Figure 2). While this may – at first glance – make nestbox provision appear to be a simple and cost-effective measure to increase breeding numbers of flycatchers, it does not hold generally: populations NAG and DIN showed negative trends (Table S1.3) in line with national declines of flycatchers and other migratory passerines (Woodward *et al.* 2020) despite constant provision of nestboxes in excess, and NWA went through a period of decline even though the number of nestboxes was steadily increased (Figure 2). As some populations have large estimated fractions of non-breeders (Figures 2 & 3), it appears that large numbers of nestboxes alone are not sufficient to increase breeding populations. Non-breeding individuals are observed in flycatcher populations across the breeding range (Sternberg *et al.* 2002; Both *et al.* 2017), and Loman (2006) showed experimentally that flycatcher density only increased with nestbox availability in large but not small woodland patches. The latter may represent habitats or territories of lower quality, and birds may delay breeding when no high-quality territories are available (Stutchbury & Zack 1992). Hence, targeted provision of nestboxes in high-quality habitat/territory may enable more flycatchers to breed and – ultimately – contribute to local population growth.

By analyzing population dynamics in multiple breeding locations simultaneously, we were also able to compare trajectories across populations. Population sizes in breeding locations ranging from the south of England to Scotland were positively correlated, and covariation was not necessarily strongest for neighboring locations in all cases (Figure S1.2). This points towards large-scale drivers impacting British-breeding populations of flycatchers beyond breeding sites. While some drivers may act at a national scale during the breeding season, weak connectivity (i.e. different breeding populations mixing during migration and/or in non-breeding areas) is common among long-distance migrants (Finch *et al.* 2017) and may generate population synchrony via conditions encountered on shared migration routes and/or non-breeding areas. This may well be the case for British-breeding flycatchers since they have a small non-breeding distribution relative to the species' entire non-breeding range (Bell *et al.* 2022).

4.2 Local, regional, and general environmental effects

We found substantial variation in both averages of, and environmental impacts on, key demographic parameters across breeding locations (Figures 3 & 4). Populations located further north (KAT, NWA, DIN) tended to have – on average – higher nestling survival (Figure 3), which may be related to longer photoperiods providing more time for parents to forage and provision nestlings (Lundberg & Alatalo 1992). Generally wetter conditions in Wales may explain the relatively lower average nest success probability in DIN and NWA (Figure 3).

The relationships between reproductive parameters and temperature varied substantially across breeding sites, suggesting localized effects (Figure 4). Consistent with other studies (e.g. Siikamaki 1996; Burgess 2014), higher rainfall was predicted to have predominantly negative effects on nest success probability and nestling survival. Importantly, we found that the same held for the post-fledging period: in all seven study populations, wetter weather in the 30 days following fledging resulted in lower survival of fledglings to the next year (Figure 4). The post-fledging period of songbirds is highly selective and associated with high mortality, yet it is understudied compared to other parts of the annual life cycle due to the difficulty of following young as they disperse after fledging (Cox *et al.* 2014; Naef-Daenzer & Grüebler 2016). High or prolonged rainfall between fledgling and southward migration can be detrimental for fledglings through affecting foraging efficiency, or increasing predation risk due to lowered body condition (Cox *et al.* 2014). Rainfall in the post-fledging period may therefore be a common but rarely identified cause of mortality in songbirds in locations where rainfall in this period can be high or prolonged, such as Britain.

4.3 Population dynamics driven by survival and dispersal

For all study populations, LTRE results consistently showed that both short-term fluctuations and longer-term trends in population size were primarily driven by changes in survival and immigration (Figures 5-7, S1.19-S1.23). In comparison, changes in reproduction played a small role, which is consistent with cross-population covariation indicating large-scale drivers likely acting outside the breeding season (section 4.1). Taken together, these results provide compelling evidence that the key drivers of flycatcher population dynamics primarily operate outside breeding areas, and that this applies across the British breeding distribution (and not only a single population in Southern England, as shown earlier in Goodenough, Elliot & Hart 2009). Mallord *et al.* (2016) arrived at a similar conclusion for flycatchers, and three other Afro-Palearctic migratory bird species breeding across the UK, and further found that structural changes in breeding habitat could not explain population declines.

Another mechanism often invoked as a cause of declines is a breeding season trophic mismatch between the peak food requirements of nestlings and the peak availability of seasonal invertebrate prey (see Both *et al.* 2006 for a link to flycatcher declines in the Netherlands). Our results show relatively small contributions of reproduction to population growth rates, and an absence of time trends in reproductive output (Table S1.3), suggesting that trophic mismatch is unlikely to explain declines of British-breeding flycatchers. This is not surprising, given little recent or historic phenological matching of the British flycatcher nestling period with peak caterpillar abundance in oak woodlands (Burgess *et al.* 2018).

DIN and KAT were the only populations in which reproduction contributed similarly to both short- and long-term population dynamics as survival (Figures 5 & 7, S1.19). Notably, these two populations not only declined markedly, but also represent the two sites with the lowest nestbox density (per area). They may therefore be small relative to the environment's carrying capacity, a state that Sæther *et al.* (2016) found to lead to relatively larger contributions of reproduction in birds generally. For all other populations survival contributions mostly outweighed reproduction substantially (Figures 5 & 7, S1.19), suggesting that the drivers of variation in annual survival rates are also important drivers of population dynamics. Unfortunately, these drivers are difficult to study in long-distance migrants such as flycatchers, as they may act during migration, at stop-over sites, and in the non-breeding areas (e.g. Howard *et al.* 2020; Selonen *et al.* 2021). Further studies of conditions, resource requirements, and fitness constraints during the non-breeding season are required to identify the mechanisms underlying changes in annual survival.

4.4. Immigration: crucial and cryptic

Our LTRE analyses revealed that immigration rates were more crucial than survival for local population dynamics, at least with regards to fluctuations in annual population growth rates (Figure 5). While this is commonly found for birds (Millon *et al.* 2019) transient LTREs frequently overestimate contributions of immigration to population dynamics when immigration rates are estimated as latent parameters within IPMs (Paquet *et al.* 2021). The IPMs in our analysis, however, estimate immigration based on observed counts of newly marked individuals, which limits the amount of unexplained variation that can be absorbed into immigration rates and hence results in more robust LTRE estimates. Contributions of immigration to population dynamics still need to be interpreted carefully as immigration rates are inherently scale-dependent (Schaub, Jakober & Stauber 2013; Reichert, Fletcher &

Kitchens 2021). First, when nestlings are marked in nestboxes only, any bird hatched in a natural cavity will be considered an immigrant, even if the natural cavity is within or very close to a study site (Millon *et al.* 2019). This is likely rare in our seven study populations as natural cavities were relatively scarce (Burgess 2014), and flycatchers have a strong preference for breeding in nestboxes when available (Slagsvold 1987) and these were provided in excess. Second, the smaller the spatial scale at which immigration contributions are considered, the larger these are likely to be (e.g. Schaub, Jakober & Stauber 2013). This can, for example, explain the relatively higher and more influential immigration rates in the three relatively smaller study sites in Devon (TEI, EDM, OKE, Figures 1 & 5). Third, our results also highlight that assessments of the importance of immigration need to consider temporal scales in addition to spatial ones, as changing immigration rates were less important for longer-term population trends than for short-term fluctuations (Figures 5 & 7). All caveats considered, our study still provides evidence for an important role of dispersal for flycatcher population dynamics across British breeding sites and highlights a need for studying the drivers of dispersal and immigration.

4.5 Moving forward: IPMs for comparative and range-wide studies

While the present study focused on British breeding sites, large-scale declines of flycatcher populations are a pan-European phenomenon (PECBMS 2020) and the British breeding range is small relative to the species' entire breeding range (Keller *et al.* 2020). SPI-Birds alone hosts data from over 30 additional breeding sites across Europe, and the standardized modelling framework and analysis workflow presented in this paper were designed to allow for straightforward inclusion of additional data. Importantly, this not only allows to extend population-specific analyses – as done in this study – to more sites, but also opens new possibilities for data integration beyond the population level. Datasets from many sites can be linked in multi-population models to enable demographic studies at range-wide scales thanks to shared hyperparameters (e.g. Horswill *et al.* 2019) and/or to improve conservation through estimating and matching actions to large-scale spatio-temporal variation in demography and population dynamics (Morrison *et al.* 2022). Similarly, the generalized IPM could also be extended into an integrated meta-population model by formally linking data sets from different sites through movement parameters (McCrea *et al.* 2010; Paquet *et al.* 2020). This is particularly relevant for identifying drivers and consequences of dispersal dynamics. Estimated contributions of immigration to population dynamics at small spatial scales may, for example, not necessarily be informative at regional and larger scales (Reichert, Fletcher & Kitchens 2021) and local and range-wide management may have to consider both flow and direction of dispersal (Paquet *et al.* 2020). In practice, estimating movement parameters for a meta-population model could benefit from extending data sources beyond SPI-Birds and integrating with other large-scale databases such as the EURING bird ringing database (Du Feu *et al.* 2016). Standardized integrated population models integrating data from both SPI-Birds and EURING will not only be able to formally estimate dispersal dynamics, but also overcome one of the key challenges with comparative demographic studies: making rates of survival, emigration, and immigration comparable across populations by disentangling them from each other and from sizes and features of local study areas (e.g. Kendall, Conn & Hines 2006). Given the large potential for future extensions of our generalized IPM into multi-population, meta-population, and even multi-species frameworks (e.g. Quéroué *et al.* 2021), we have strived to increase accessibility and re-usability of not just the model but the entire workflow through publishing our entire analysis toolbox including detailed, dynamic, and user-friendly documentation.

CONCLUSIONS

Our study shows that both annual variation in population growth rate and long-term population trends of pied flycatchers across the British breeding range are driven by survival and dispersal dynamics. While reproductive parameters were sensitive to temperature and rainfall, little is known about the factors generating variation in survival and immigration rates. Future study and conservation efforts therefore need to focus on migratory routes and non-breeding areas and consider connectivity among different breeding populations. The latter will be greatly facilitated by the link of our IPM to the SPI-Birds database and resulting ease with which data from additional breeding sites can be included into further analyses. Beyond that, the well-documented and generalized modelling framework can serve as a starting point for a multitude of larger-scale comparative and range-wide population analyses of both single and multiple bird species.

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Conflict of interest

The authors have no conflicts of interest.

AUTHOR CONTRIBUTIONS

CN, MB, and RR conceived and designed the study; MB, PC, BH, FL, DP and MR collected substantial parts of the data; CN analysed the data; CN and MB wrote the manuscript and share first authorship. All authors contributed critically to the drafts and gave final approval for publication.

DATA AND CODE ACCESSIBILITY

Processed data will be made available via Zenodo. Original data can be requested from SPI-Birds. Code for formatting data, implementing and running models and analyses, and plotting results is available on GitHub: https://github.com/SPI-Birds/SPI-IPM. An up-to-date version of the code manual is published here: https://spi-birds.github.io/SPI-IPM/.

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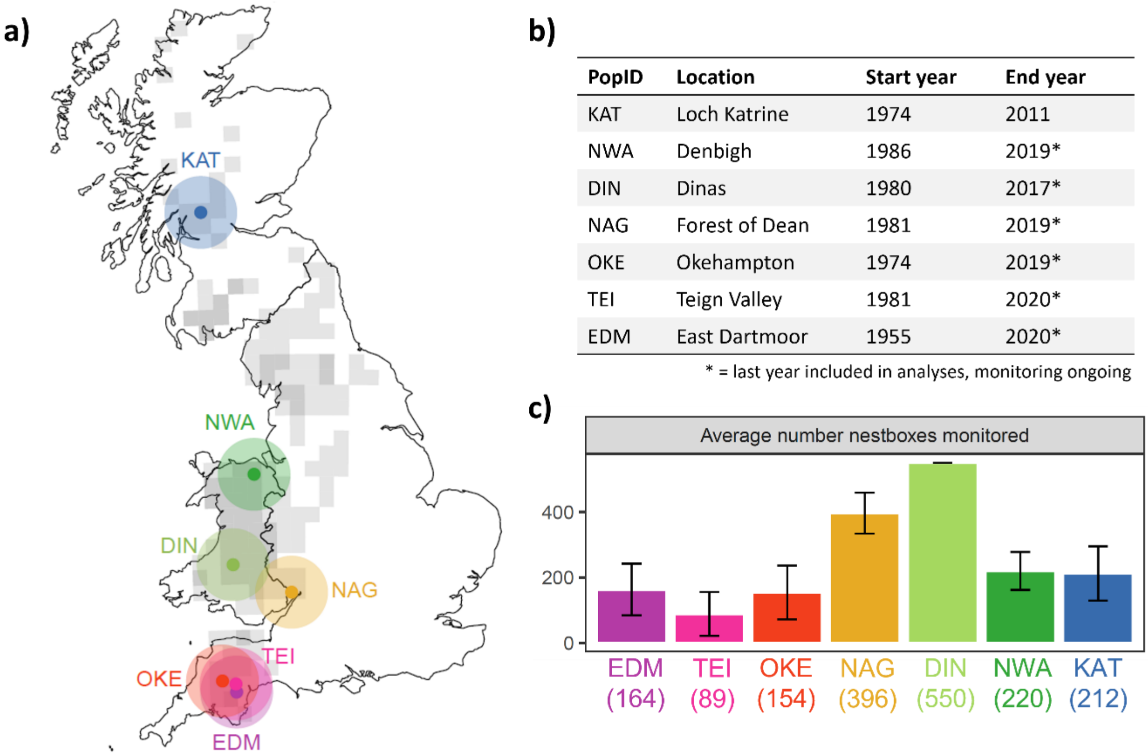
Figure 1



PopID	Location	Start year	End year
KAT	Loch Katrine	1974	2011
NWA	Denbigh	1986	2019*
DIN	Dinas	1980	2017*
NAG	Forest of Dean	1981	2019*
OKE	Okehampton	1974	2019*
TEI	Teign Valley	1981	2020*
EDM	East Dartmoor	1955	2020*

* = last year included in analyses, monitoring ongoing

Figure 1: (a) Geographical location of flycatcher study populations (colored dots) relative to the British breeding distribution (grey, with darker shading indicating higher relative abundance, data from EBBA, Keller et al. 2020). (b) Overview of location names and sampling years. (c) Mean number of nestboxes monitored per year in each study site (black bars indicate mean ± SD).

765 **Figure 2**

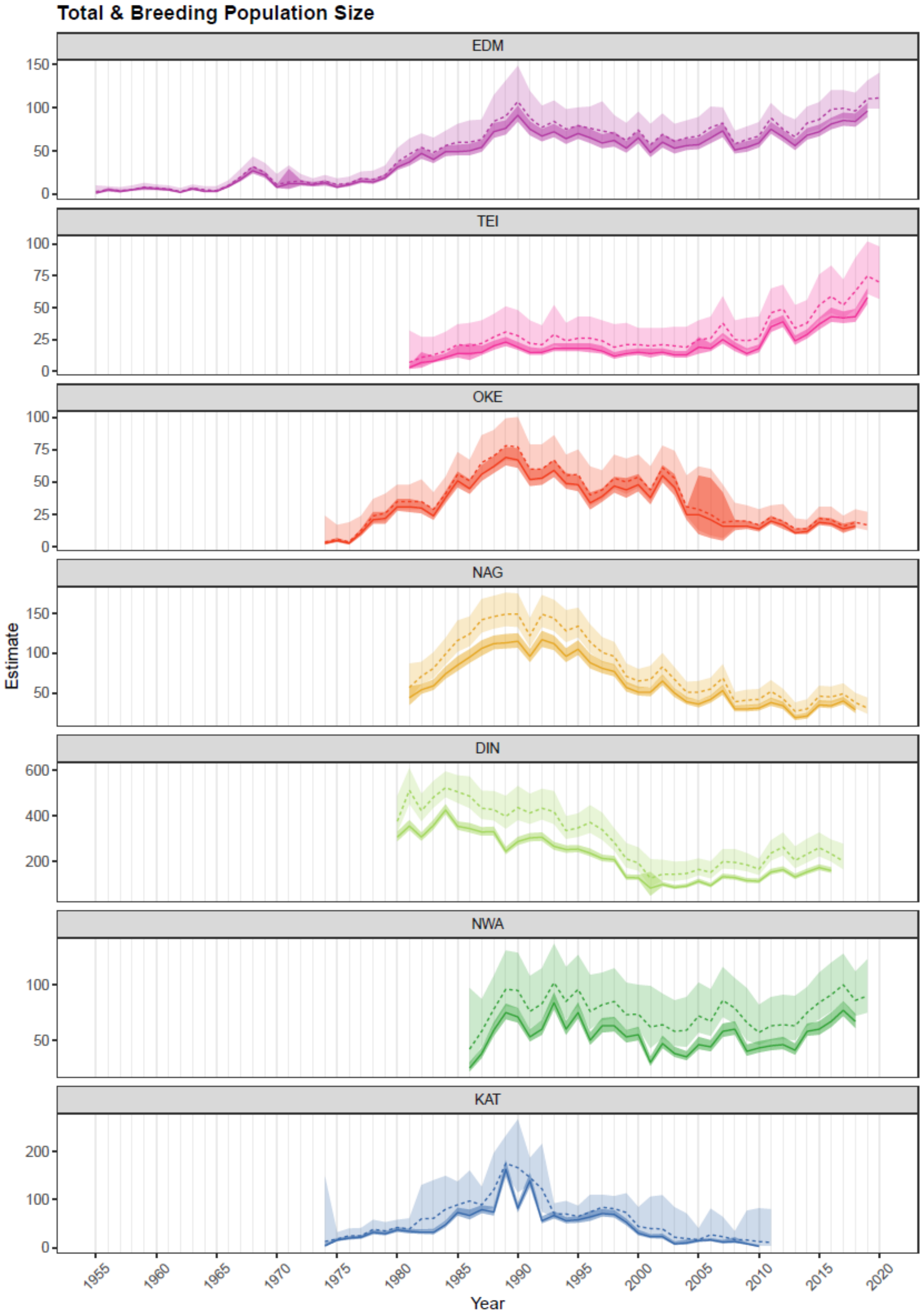


Figure 2: Annual estimates of the total number of females (dashed line) and the number of females breeding in nestboxes (solid line) for all seven study populations. Lines represent the posterior median estimates, ribbons mark the 95% credible interval.

Figure 3

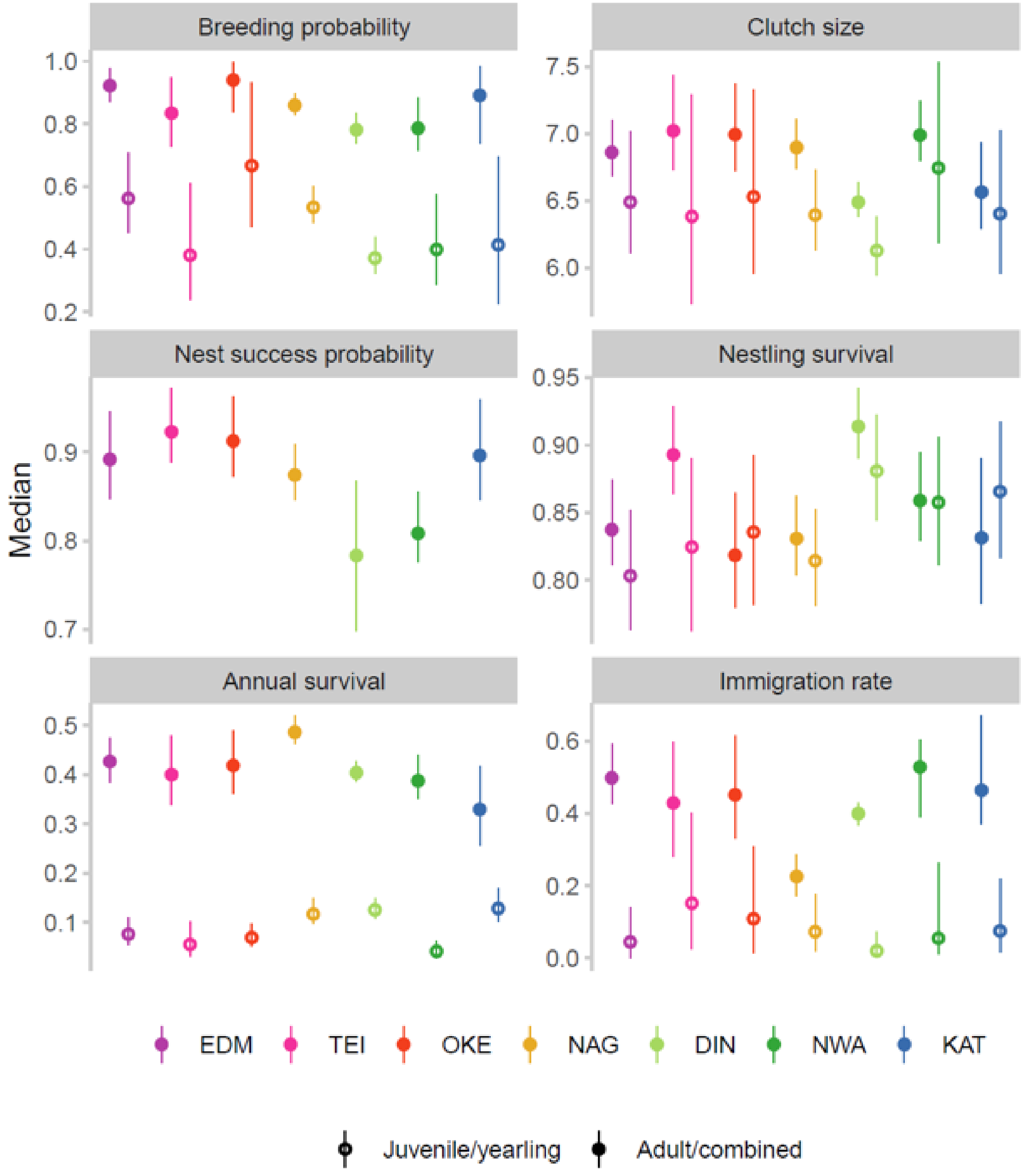


Figure 3: Posterior medians (dots) and 95% credible intervals (lines) for estimated time-average vital rates for the seven study populations. Open symbols = younger age class (juveniles for annual survival, yearlings otherwise). Filled symbols = adults (combined age class for nest success probability). For numerical summaries, see Table S1.2.

Figure 4

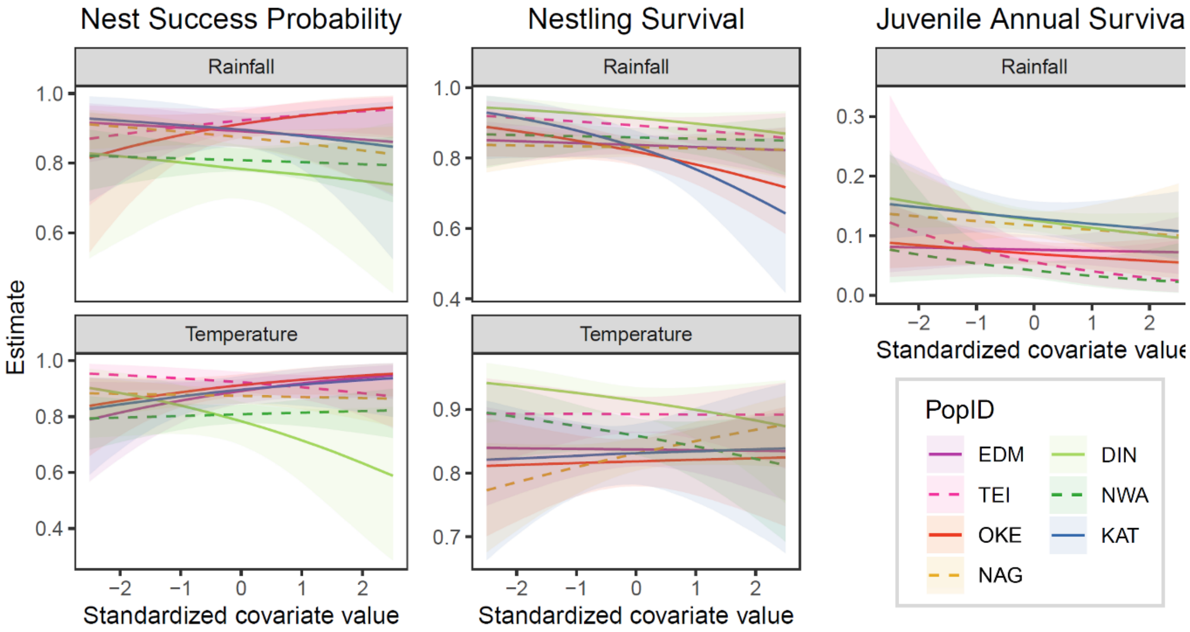


Figure 4: Effects of rainfall (top row) and temperature (bottom row) on nest success probability, nestling survival, and juvenile annual survival (columns) of the seven study populations. For nest success probability and nestling survival, environmental covariates represented conditions during a 16-day window post hatching. For juvenile annual survival, the rainfall covariate covered a 30-day period post-fledging. Environmental variables are plotted on a standardized scale for easier comparison across populations.

773 **Figure 5**

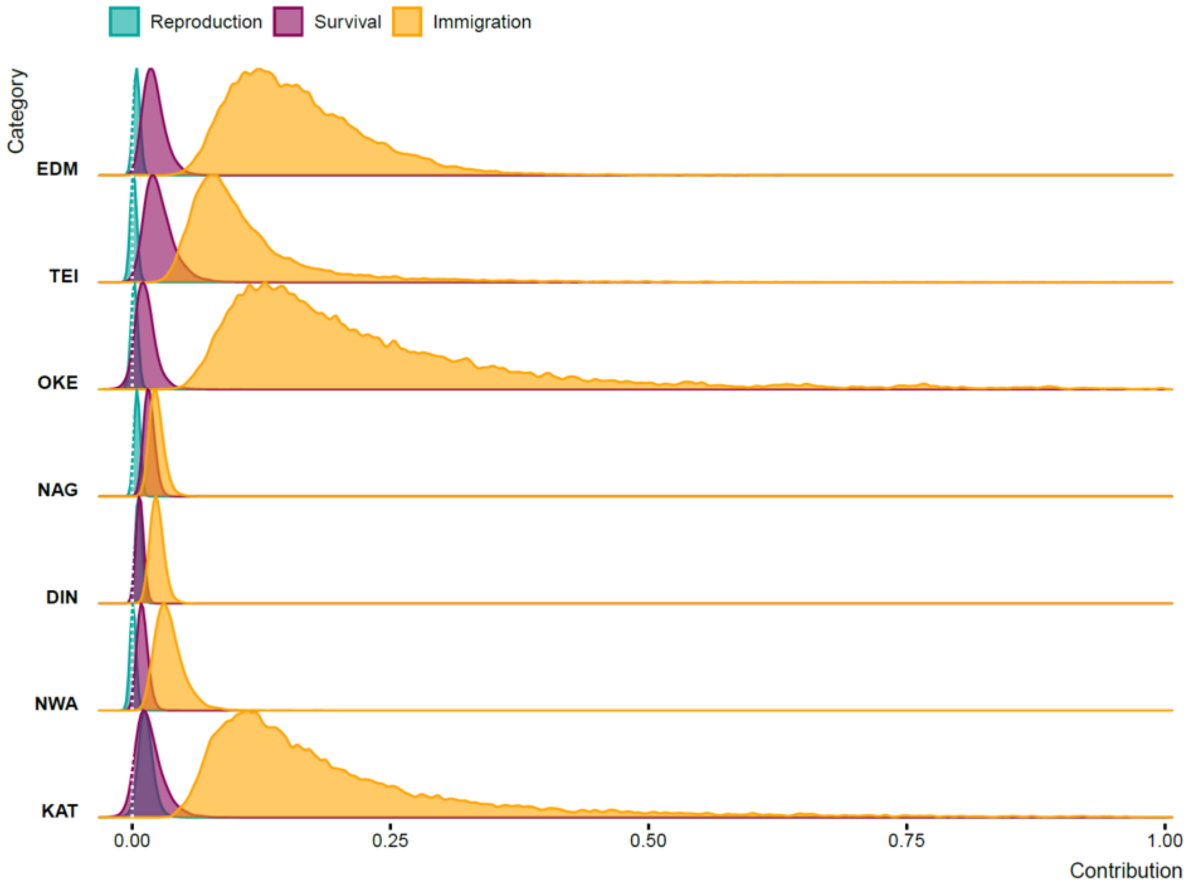


Figure 5: Posterior distributions of the contributions of reproduction (breeding probability, nest success probability, nestling survival probability), survival (juvenile and adult annual survival), and immigration rates to variation in realized annual population growth rates. Contributions from local population structure were negligible and are omitted here (but see Figure S1.20).

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776 **Figure 6**

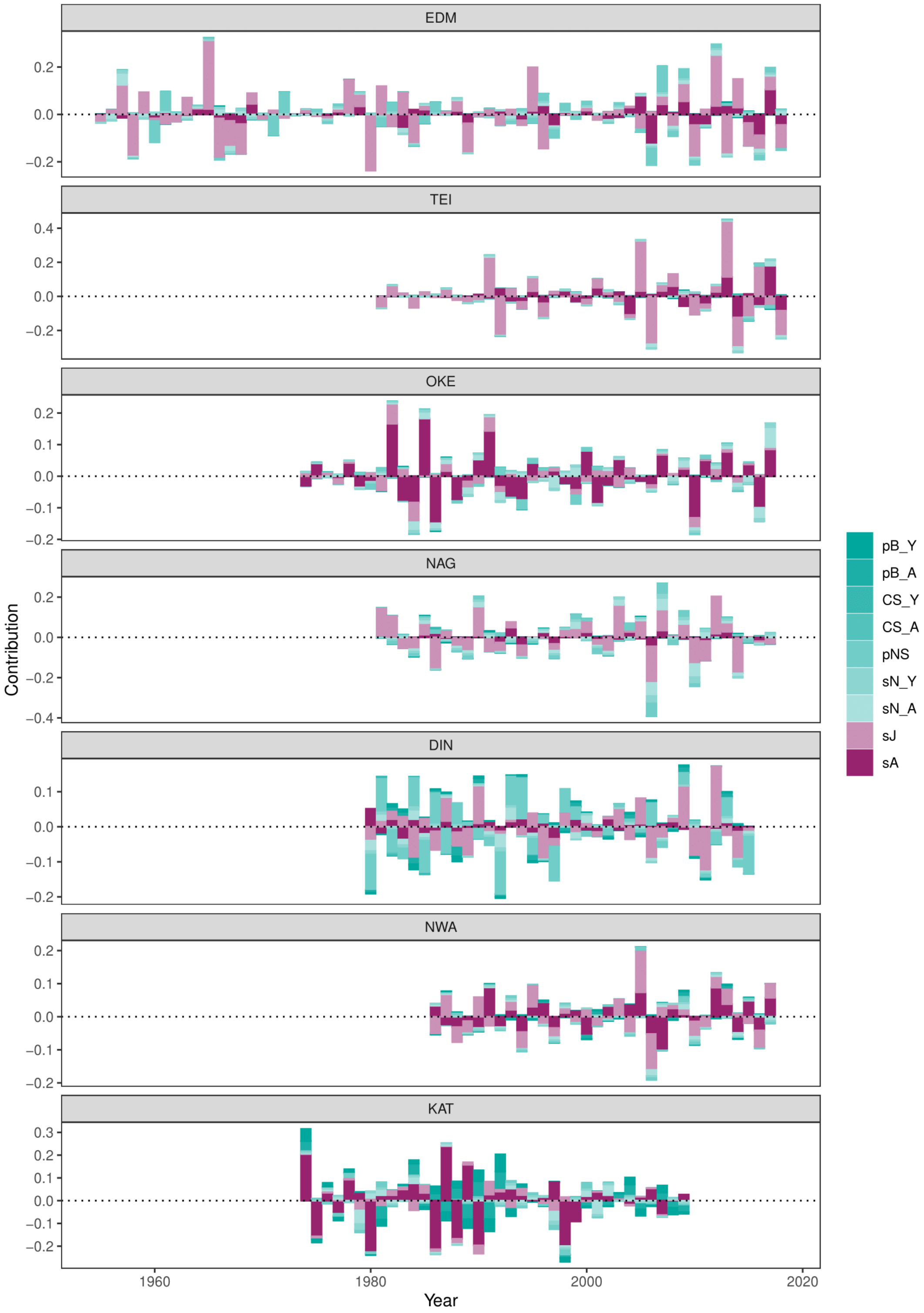

Figure 6: Posterior medians of stacked contributions of vital rates representing reproduction (turquoise shades) and survival (pink shades) to year-by-year changed in annual population growth rate over time for each study population. The sum of all contributions approximates the total rate of change in population size from one year to the next. Contributions from local population structure and immigration are omitted here to facilitate comparison of reproduction vs. survival contributions but see Figure S1.21 for the same figure including all types of contributions.

777 Figure 7

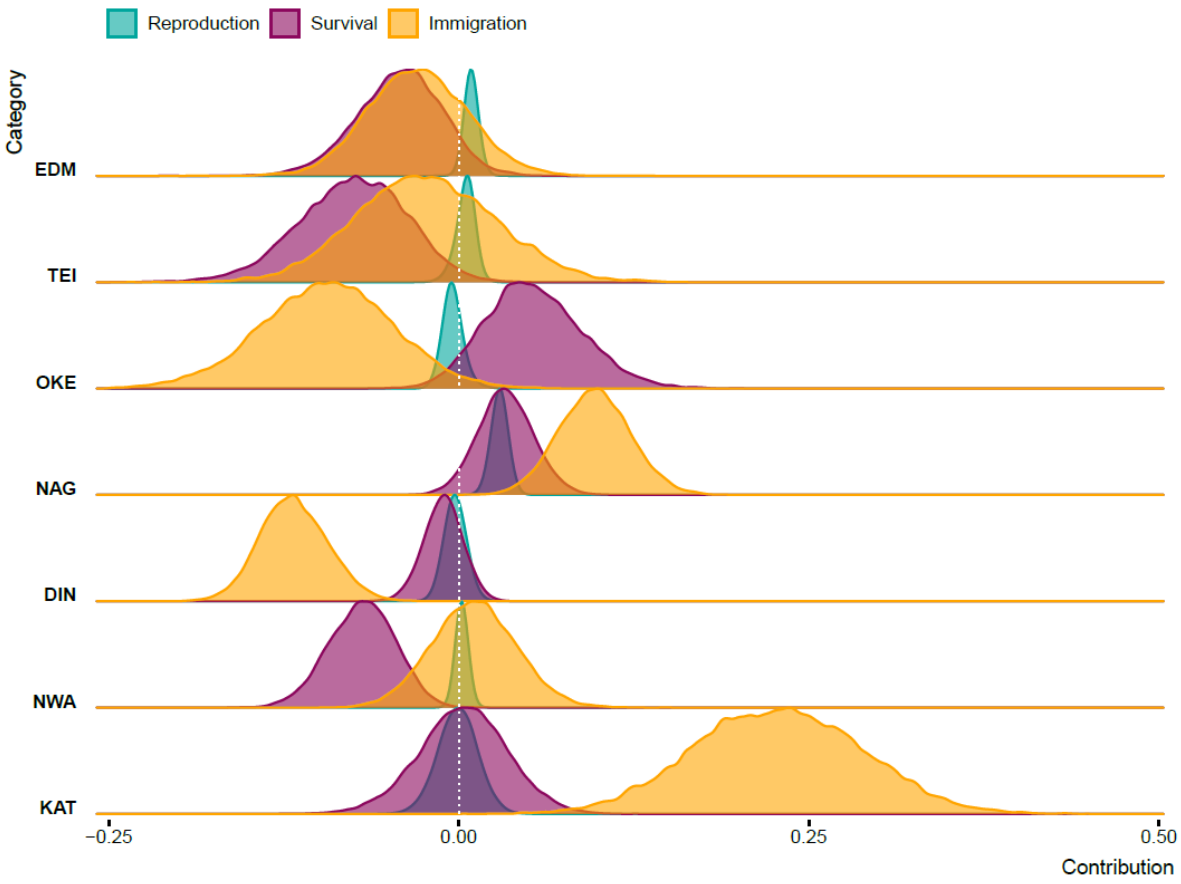

Figure 7: Posterior distributions of the contributions of reproduction (breeding probability, nest success probability, nestling survival probability), survival (juvenile and adult annual survival), and immigration rates to changes in longer-term population trends within the study period. The time periods compared for each population are shown in Figure S1.1. Contributions include both effects of direct changes in vital rates and indirect effects caused by perturbation of population structure due to vital rate changes.

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