RESEARCH ARTICLE

Demographic drivers of collapse in an island population of Tree Swallows

Liam U. Taylor,[1]* Bradley K. Woodworth,[2,3] Brett K. Sandercock,[4] and Nathaniel T. Wheelwright[1]

[1] Department of Biology, Bowdoin College, Brunswick, Maine, USA
[2] Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada
[3] School of Biological Sciences, The University of Queensland, Brisbane, Queensland, Australia
[4] Department of Terrestrial Ecology, Norwegian Institute for Nature Research, Trondheim, Norway
* Correspondence author: liam.taylor@yale.edu

ABSTRACT
Diagnosing causes of population declines requires an understanding of the contributions of demographic vital rates to interannual variability and long-term changes in population size. At Kent Island, New Brunswick, Canada, an isolated population of Tree Swallows (*Tachycineta bicolor*) collapsed between 1987 and 2010, providing a unique opportunity to reconstruct how demographic rates drive population dynamics. We fit an integrated population model to 24 yr of population count, reproductive success, and capture–recapture data to generate annual estimates of productivity, juvenile and adult survival, immigration, and the finite rate of population change (λ). The Kent Island population declined from 202 to 12 breeding adults over 24 yr, with a geometric mean decline of 11.6% per year. Annual apparent survival of adults averaged 56% across sexes, whereas annual survival and recruitment of juveniles never exceeded 6%. Transient life table response experiments revealed that variation in male and female immigration rates were the major contributors to both overall and interannual variation in λ, followed by female and male adult survival. Local recruitment and reproductive rates had little effect on variation in λ. Given broad-scale regional declines in Tree Swallows, our study shows how declines of isolated populations can be driven by reductions in immigration, especially when coupled with variation in adult survival and low local recruitment.

Keywords: aerial insectivore, immigration, integrated population models, life table response experiments, population dynamics, recruitment, survival

Controladores demográficos del colapso de una población insular de *Tachycineta bicolor*

RESUMEN
El diagnóstico de las causas de la disminución poblacional requiere un entendimiento de las contribuciones de las tasas vitales demográficas sobre la variabilidad interanual y los cambios a largo plazo en el tamaño poblacional. En la Isla Kent, New Brunswick, Canadá, una población aislada de *Tachycineta bicolor* colapsó entre 1987 y 2010, brindando una oportunidad única para reconstruir cómo las tasas demográficas controlan las dinámicas poblacionales. Ajustamos un modelo poblacional integrado para 24 años de datos de conteo poblacional, éxito reproductivo y de captura-recaptura para generar estimaciones anuales de productividad, supervivencia juvenil y adulta, inmigración y tasa finita de cambio poblacional (λ). La población de la Isla Kent disminuyó de 202 a 12 adultos reproductivos a lo largo de 24 años, con una disminución media geométrica de 11.6% por año. La supervivencia aparente anual de los adultos promedió 56% entre sexos, mientras que la supervivencia anual y el reclutamiento de juveniles nunca superaron el 6%. Los experimentos de respuesta de tablas de vida transitoria revelaron que los cambios en las tasas de inmigración de machos y hembras fueron la principal causa de variación global e interanual en λ, seguida de la supervivencia de hembras y machos adultos. El reclutamiento local y las tasas reproductivas tuvieron poco efecto en la variación en λ. Dadas las disminuciones regionales a gran escala de *T. bicolor*, nuestro estudio muestra cómo las disminuciones en poblaciones aisladas pueden ser controladas por reducciones en la inmigración, especialmente cuando se combinan con variaciones en la supervivencia de los adultos y con un bajo reclutamiento local.

Palabras clave: dinámicas poblacionales, experimentos de respuesta de tablas de vida, inmigración, insectívoro aéreo, modelos poblacionales integrados, reclutamiento, supervivencia

INTRODUCTION

Diagnosing causes of population declines requires understanding the demographic mechanisms underlying inter-annual variability and long-term changes in population size. The first step is quantifying demographic vital rates and their relationship to the rate of population change (Caswell 2001). Vital rates such as reproductive success, adult survival, or immigration directly contribute to patterns of population change (e.g., Hitchcock and Gratto-Trevor 1997, Newton 2004, Ward 2005). Vital rates may also be correlated with one another, either positively, such as when a suite of rates is driven by shared environmental covariates, or negatively, such as through life-history tradeoffs or density-dependent competition (Lack 1954, 1966). By quantifying the demographic contributors to population change, we can better assess how threats to reproduction and survival impact populations and species.

Populations of many aerial insectivores, including Tree Swallows (*Tachycineta bicolor*), have been declining in northeastern North America since at least the 1980s (Sauer et al. 2017). The ecological and demographic mechanisms of ongoing declines are unclear but appear to be species- and region-specific (Nebel et al. 2010, Smith et al. 2015, Michel et al. 2016, Imlay et al. 2018). At broad scales, climate change may create a phenological mismatch between breeding and food availability, requiring Tree Swallows to adjust their breeding strategies or suffer population declines (Dunn and Winkler 1999, but see Dunn et al. 2011, Imlay et al. 2018). At more local scales, weather conditions may influence adult survival or reproductive success (Weegman et al. 2017), and chemical contaminants such as mercury and neonicotinoids can disrupt food availability or reproduction (Hallinger and Cristol 2011, Hallmann et al. 2014). Declines in body mass as a result of foraging conditions at nonbreeding sites could also play a role in the deterioration of some populations (Paquette et al. 2014). However, the extent to which threats such as climate change or pesticides contribute to population declines depends on which vital rates they are impacting and the relative contributions of the impacted vital rates to population change.

A long-term study of Tree Swallows breeding on Kent Island, New Brunswick, Canada, presented an opportunity to characterize the demographic drivers of collapse of an aerial insectivore population. As with the populations of Bank (*Riparia riparia*), Barn (*Hirundo rustica*), and Cliff (*Petrochelidon pyrrhonota*) swallows at Kent Island (N.T. Wheelwright personal observation), the Tree Swallow population experienced a rapid decline beginning in the 1980s. To quantify the demography of this Tree Swallow population, we fit an integrated population model (IPM) to 24 yr of population count, reproductive success, and capture–recapture data. By incorporating multiple data-sets, IPMs allow for simultaneous, high-precision estimates of a full suite of population size and vital rate parameters in a Bayesian framework (Kéry and Schaub 2011, Schaub and Abadi 2011, Zipkin and Saunders 2018). In particular, IPMs can be used to estimate latent parameters such as immigration, a vital rate for which direct data are difficult to obtain (Abadi et al. 2010, Schaub and Fletcher 2015). Increasingly, these models are being utilized to study the demography and conservation of both widespread and threatened taxa (Zimmerman et al. 2017, Arnold et al. 2018, Coates et al. 2018, Ross et al. 2018).

With IPM estimates of annual rates of population change and vital rates (productivity, sex-specific survival, and sex-specific immigration), we conducted transient life table response experiment (LTRE) analyses to decompose the contributions of variation in individual vital rates to overall and annual variation in the rate of population change (Koons et al. 2016, 2017). We also evaluated correlations among vital rates to provide insight into the demographic mechanisms underlying the population decline.

METHODS

Study Species and Study Site

Tree Swallows are migratory aerial insectivores with a breeding range that spans North America from the Canadian subarctic to the central United States (Winkler et al. 2011). The natural nesting habitat is cavities created by woodpeckers and other hole-excavating birds, but Tree Swallows generally prefer artificial nest boxes adjacent to open fields (Rendell and Robertson 1990).

We studied Tree Swallows nesting at the Bowdoin Scientific Station at Kent Island, an isolated island in the Bay of Fundy, New Brunswick, Canada (44.582°N, 66.756°W) from 1987 to 2010 (Figure 1). Upwelling of the Labrador Current in this area results in cool foggy weather during much of the summer. The nearest other sites where Tree Swallows breed are White Head Island (~5 km away), Grand Manan Island (~10 km away), and mainland sites on the coast of Maine, New Brunswick, and Nova Scotia (30–50 km away). The southern two-thirds of Kent Island consists of open fields, whereas the northern third of the island is covered in boreal forest, chiefly white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), heart-leafed birch (*Betula cordifolia*), and mountain ash (*Sorbus americana*).

Tree Swallows begin to arrive at Kent Island in mid- to late April and nest construction begins in mid-May to early June (Paynter 1954). The earliest eggs are laid in late May. Females in this population lay 3–8 eggs per clutch (mean ± SD: 5.6 ± 1.0), eggs are incubated for an average of 15.8 ± 1.5 days, and nestlings remain in the nest for an
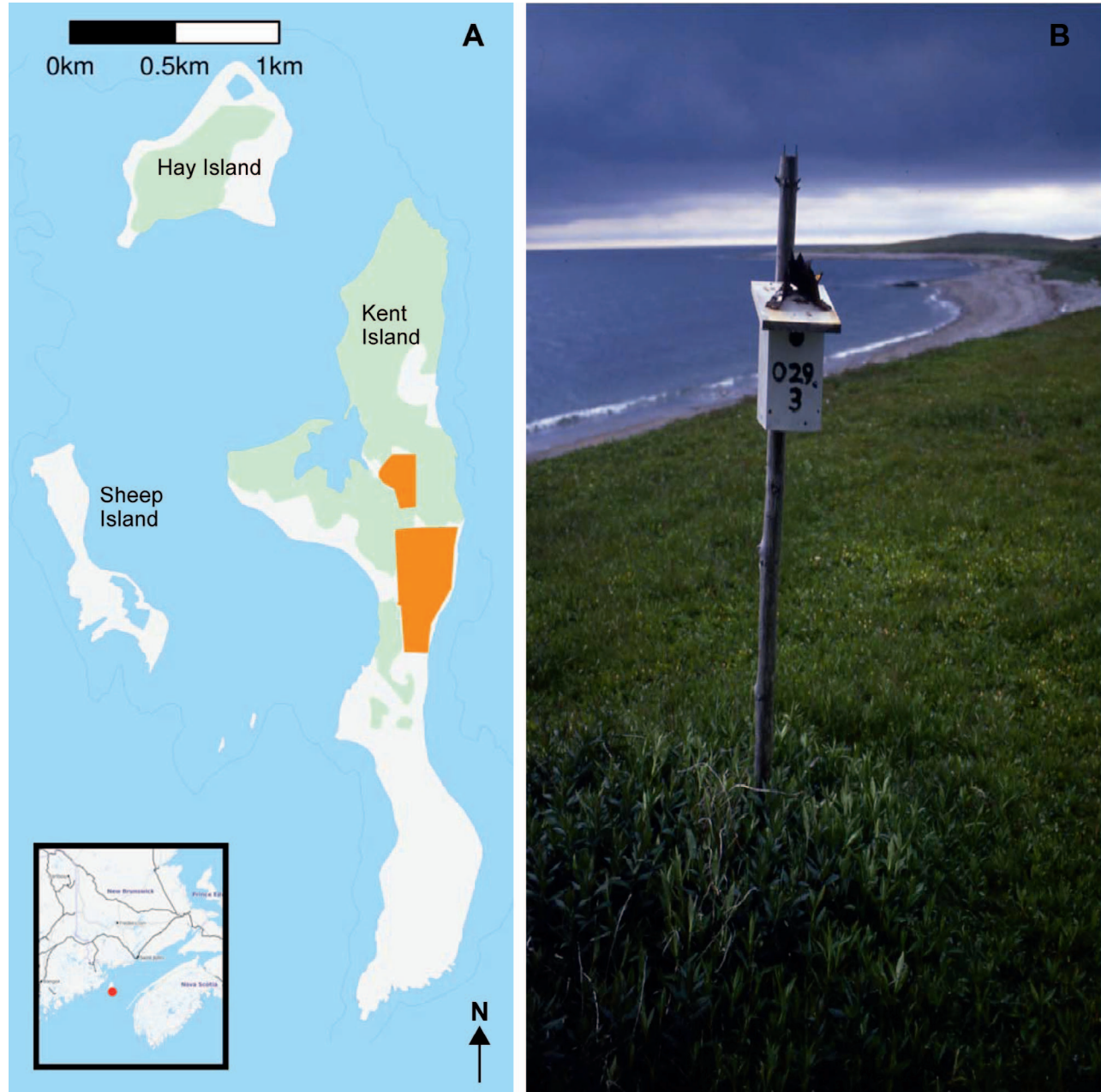
Figure 1. (**A**) Map of the Kent Island study site and neighboring Hay and Sheep Islands, New Brunswick, Canada, with the location of the 3 islands in the Bay of Fundy (inset). Tree Swallows nest in boxes distributed across 2 open fields (orange), but not in forested areas (green). Maps retrieved using the ggmap and OpenStreetMap packages in R (Kahle and Wickham 2013, Fellows and Stotz 2016). (**B**) Tree Swallow nest box and open field habitat on Kent Island.

average of 19.2 ± 0.8 days before fledging (Paynter 1954). Compared to mainland populations at the same latitude, Tree Swallows at Kent Island begin nesting several weeks later and have longer incubation periods (Wheelwright et al. 1991, Winkler et al. 2011).

Woodpeckers do not breed on Kent Island, so Tree Swallows are restricted to nesting in artificial boxes (Wheelwright et al. 1991), which were first erected on the island in 1934 (Gross 1936). Nest boxes were maintained at roughly 30 m intervals across 2 open fields in the center of the island. Although we lack precise data on the number of accessible nest boxes across the time series, 100–110 nest boxes were available from 1987 to 2005, and at least 50 nest boxes were available from 2006 to 2010. Data from Shutler et al. (2012) indicate that nest box occupancy rates at Kent Island declined from >80%
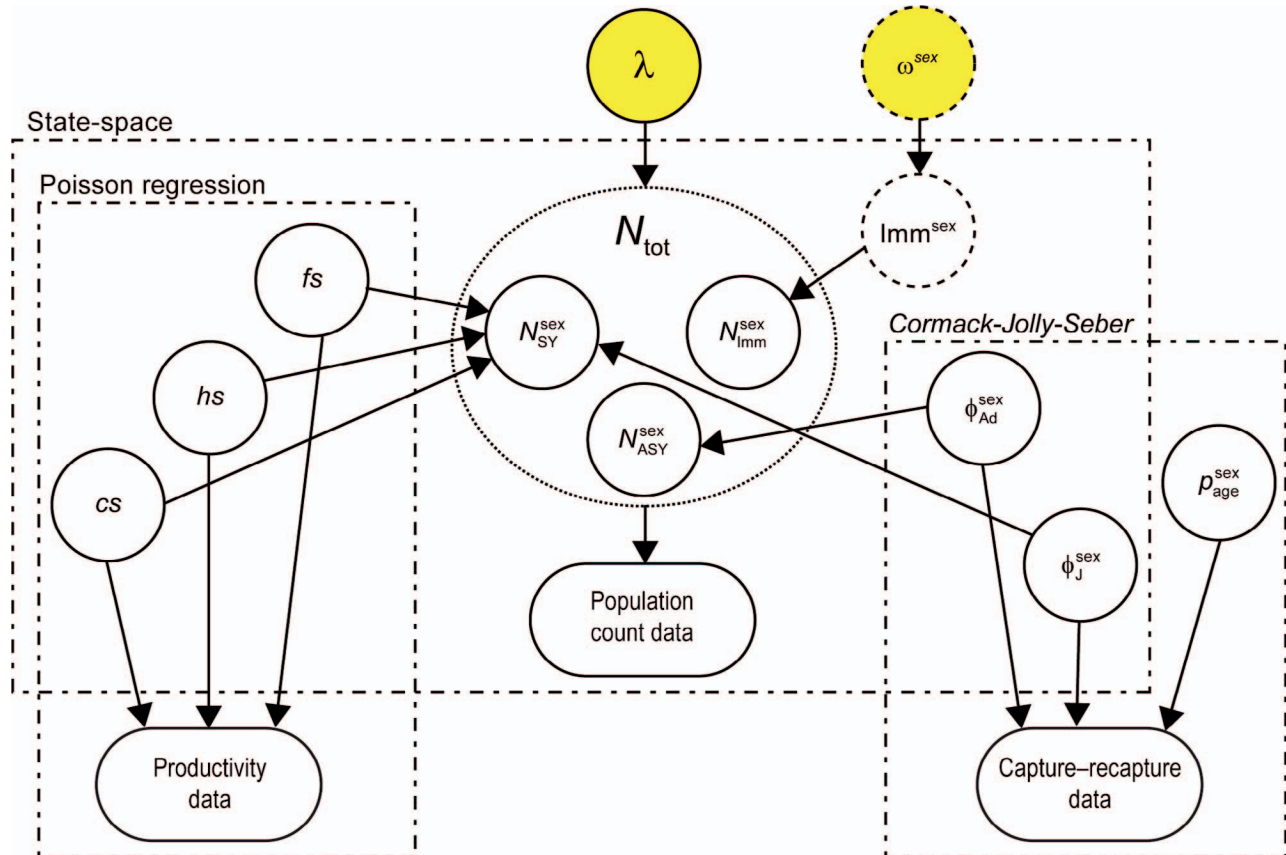
Figure 2. IPM used to describe the relationships between data, parameters, and models for Tree Swallows nesting on Kent Island (following figure 1 in Abadi et al. 2010). (Left) Poisson regressions modeled productivity parameters from nest box monitoring. (Center) A state space model connected population sizes with counts of breeding adults. (Right) A Cormack–Jolly–Seber model described the relationship between capture–recapture of banded birds and apparent survival and recapture parameters by sex and age classes. All parameters were linked with population size estimates across models, which allowed immigration to be estimated as a latent parameter. Yellow nodes were calculated directly from other values. See Table 1 for symbols and definitions.

in 1987 to <20% by 2006, so decreasing nest box availability could not explain the decline of this population.

Each year, all nest boxes on the island were surveyed starting in late May and throughout June. If there were indications of nest-building, boxes were checked every other day until eggs appeared. After counting eggs to determine clutch size, we left nests undisturbed until nest checks resumed several days before the first eggs were estimated to hatch. After hatching, nestlings were counted and then banded at 11–16 days of age. Several days after the first young fledged, we checked the nest to record any nestlings that failed to fledge. Throughout the breeding season, we captured adults and marked them with a USFWS aluminum band on one leg and a single split-color plastic band on the other. Adult females were captured on the nest during incubation. Most adult males were mist-netted or captured in the nest box while feeding nestlings, although we were unable to capture a few individuals every year. We determined the sex of adults by the presence of a cloacal protuberance (male), brood patch (female), or brownish plumage (second-year female; Hussell 1983).

Over a 24 yr period, we recorded 920 nesting attempts resulting in 5,049 eggs, 4,071 hatchlings, and 3,034 fledglings. In total, 4,152 Tree Swallows were banded, 3,229 of them as hatchlings and 923 as adults. Of the 814 banded breeding adults, 492 were female and 321 were male. One breeding adult of unknown sex was removed from all analyses.

Integrated Population Model

We combined 3 datasets to construct an integrated population model (IPM; Figure 2) for the Kent Island population of Tree Swallows: (1) counts of males and females breeding in nest boxes; (2) reproductive success (total number of eggs, hatchlings, and fledglings for each nest); and (3) individual encounter histories based on mark–recapture of banded adults at or near nest boxes. Population counts consisted of the total number of banded and unbanded parents at nest boxes each year. Because

Table 1. Demographic parameters for the Kent Island Tree Swallow population.

Parameter	Definition
Clutch size (cs)	Number of eggs laid per nest in year t
Hatching success rate (hs)	Probability that eggs survived to become hatchlings in year t
Fledging success rate (fs)	Probability that hatchlings survived to fledge in year t
Juvenile survival rate (ϕ_J^{sex})	Sex-specific probability of local fledgling survival and return from year t to year $t + 1$
Adult survival rate (ϕ_{Ad}^{sex})	Sex-specific probability of adult survival and return from year t to year $t + 1$
Count of immigrants (Imm^{sex})	Sex-specific number of immigrants in year $t + 1$
Per capita immigration rate (ω^{sex})	Sex-specific ratio of Imm^{sex} to the number of individuals (N^{sex}) in year t
Recapture rate (p_{age}^{sex})	Sex-specific probability of recapture of a banded bird in year t

Tree Swallows at Kent Island are single-brooded, and male floaters are uncommon during the breeding season (Conrad et al. 2001), we assumed that all unbanded parents were single, unique individuals.

At the core of the IPM was a state space model that projected age- and sex-specific population sizes (Kéry and Schaub 2011, Schaub and Abadi 2011, Schaub et al. 2015). The population was divided into 3 age classes for each sex: (1) after-second-year (ASY) adults (N_{ASY}^{sex}) that had bred in the study population in a previous year; (2) second-year (SY) adults that had been banded in the study area as nestlings the previous year (N_{SY}^{sex}, "local recruits"); and (3) individuals of either age class breeding in the population for the first time (N_{Imm}^{sex}, "immigrants").

Vital rates and observation parameters were modeled with static mean μ and annual residuals $\varepsilon[t]$ (see Table 1 for parameter symbols and definitions). Sex-specific immigration was modeled as a count parameter (number of immigrants, Imm^{sex}) and later converted to a per capita rate (ω^{sex}) by dividing by the sex-specific population size from the preceding year (Schaub and Fletcher 2015). Demographic losses from the population could be due to mortality or permanent emigration, so our survival parameters are "apparent survival" parameters representing the combination of both processes.

The state process modeled the relationship between population size and underlying vital rates. We could not determine the sex of fledglings (Fl) in the field, so fledglings that never returned to breed were assigned as male or female using a binomial distribution based on a 1:1 sex ratio (Equations 1–3). To incorporate demographic stochasticity, the 6 demographic classes in the population were projected with binomial or Poisson distributions for each year t (Equations 4–6).

$$Fl[t] = N^{\female} \times cs[t] \times hs[t] \times fs[t] \qquad (1)$$

$$Fl^{\female}[t] \sim Binomial(Fl[t], 0.5) \qquad (2)$$

$$Fl^{\male}[t] = Fl[t] - Fl^{\female}[t] \qquad (3)$$

$$N_{SY}^{sex}[t + 1] \sim Binomial(Fl^{sex}[t], \phi_J^{sex}[t]) \qquad (4)$$

$$N_{ASY}^{sex}[t + 1] \sim Binomial(N^{sex}[t], \phi_{Ad}^{sex}[t]) \qquad (5)$$

$$N_{Imm}^{sex}[t + 1] \sim Poisson(Imm^{sex}[t]) \qquad (6)$$

Sex-specific (N^{sex}) population sizes were calculated as the annual sum of age classes for each sex, and total population size (N_{tot}) was the annual sum of all breeding males and females. Finite rate of population change (λ) in year t was then derived as the ratio of total population sizes in consecutive years $t + 1$ and t (Equation 7).

$$\lambda[t] = \frac{N_{tot}[t + 1]}{N_{tot}[t]} \qquad (7)$$

The observation component of the state space model linked population count data for each sex (Y^{sex}) to the estimate of sex-specific population size with a Poisson regression (Equation 8).

$$Y^{sex}[t] \sim Poisson(N^{sex}[t]) \qquad (8)$$

Per capita clutch size, hatching success rate, and fledging success rate were modeled with Poisson regressions using productivity data (number of nests, R; number of eggs, E; number of hatchlings, H; number of fledglings, F) for each year t (Equations 9–11).

$$E[t] \sim Poisson(R[t] \times cs[t]) \qquad (9)$$

$$H[t] \sim Poisson(E[t] \times hs[t]) \qquad (10)$$

$$F[t] \sim Poisson(H[t] \times fs[t]) \qquad (11)$$

Unlike survival and immigration rates, which were transitions between years, productivity rates could be estimated for the final year of the study.

Capture–recapture data were summarized in m-array format and used to estimate annual apparent survival and recapture probabilities for each age class and sex by modeling multinomial likelihoods with a Cormack–Jolly–Seber (CJS) model (Kéry and Schaub 2011).

IPM Implementation

We implemented our IPM in JAGS using the R environment and the jagsUI package (Plummer 2003,
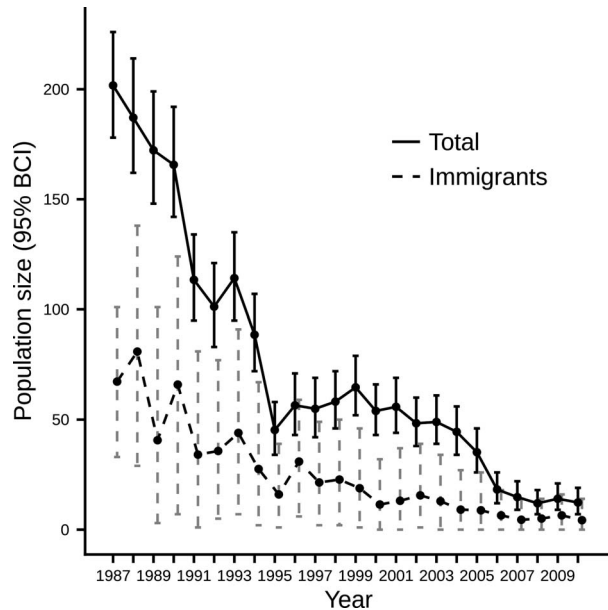
Figure 3. IPM estimates of total annual population size and number of immigrants across both sexes.

Kellner 2015, R Core Team 2017). All data, model code (including priors), and analysis code are available online (https://github.com/ltaylor2/TRES_IPM). The sampling process was run for 600,000 iterations with 3 independent chains, a burn-in period of 300,000 iterations, and a thinning value of 20 (i.e. 45,000 iterations sampled). We interpreted convergence across the chains using the Gelman–Rubin $\hat{R}$ statistic, for which values approaching 1.0 indicate confidence about convergence (Brooks and Gelman 1998). All output parameters for our model achieved $\hat{R} < 1.03$. We also examined output trace plots to confirm effective burn-in and chain mixing. We applied posterior predictive checks to test for model goodness-of-fit to individual datasets (Appendix). We used the R packages ggplot2, plyr, and dplyr for summarizing and visualizing model output (Wickham 2009, 2011; Wickham and Francois 2015).

Life Table Response Experiments

Life table response experiments (LTREs) allow for analyses of the contribution of variation in individual demographic parameters to the variation in λ (Caswell 1989). We used transient LTREs to assess the contribution of variation in each parameter, θ_i, for each of 9 vital rates (cs, hs, fs, $\phi_J^\female$, $\phi_J^\male$, $\phi_{Ad}^\female$, $\phi_{Ad}^\male$, $\omega^\female$, $\omega^\male$), and the proportional abundances of each sex, to variance in λ across the entire time series (eq. 1 in Koons et al. 2017, or Equation 12 below). Within each sex, adults, local recruits, and immigrants contributed to productivity equally in our model (without age-specific performance), and we did not assess the contribution of within-sex age structure.

$$\text{contribution}_{\theta_i}^{\text{var}(\lambda_t)} \approx \sum_j \text{cov}(\theta_{i,t}, \theta_{j,t}) \frac{\partial \lambda_t}{\partial \theta_{i,t}} \frac{\partial \lambda_t}{\partial \theta_{j,t}} \bigg|_{\bar\theta} \quad (12)$$

We then assessed the contribution of each parameter to the annual change in λ for each interval, t and $t+1$, from $t = 1987$ to $t = 2008$ (eq. 2 in Koons et al. 2017, or Equation 13 below).

$$\text{contribution}_{\theta_i}^{\Delta\lambda_t} \approx (\theta_{i,t+1} - \theta_{i,t}) \frac{\partial \lambda_t}{\partial \theta_{i,t}} \bigg|_{\bar\theta_i} \quad (13)$$

Last, to investigate relationships among vital rates such as adult response to breeding success, we extracted Pearson r correlation coefficients from the LTRE covariance matrices.

All results were calculated from 45,000 iterations comprising the posterior distributions for each model parameter and are summarized as means followed by lower and upper limits of the 95% Bayesian credible interval (BCI). A μ subscript indicates the modeled static mean parameter.

RESULTS

Rate of Population Change and Vital Rate Estimates

The population of Tree Swallows at Kent Island declined precipitously from 202 breeding adults (95% BCI: 178, 226) in 1987 to only 12 breeding adults (7, 19) in 2010, or 5.9% of the initial population size (Figure 3). At no point during the 24 yr study did the population size equal or exceed the initial population size. The population declined ($\lambda < 1.0$) in 16 of 23 intervals, with the greatest declines in 1990–1991, 1994–1995, and 2005–2006 (Figure 4G). The geometric mean annual rate of population decline was −11.6% (−13.8%, −9.6%). The interval of most severe population decline, 1994–1995, was notable for complete fledging failure (despite normal clutch sizes and hatching success) and the lowest probability of adult female survival of any year ($\lambda_{1994} = 0.52$ [95% BCI = 0.37, 0.70], $cs_{1994} = 5.38$ [4.74, 6.07], $hs_{1994} = 0.77$ [0.67, 0.88], $fs_{1994} = 0.01$ [0.00, 0.03], $\phi_{Ad,1994}^\female = 0.24$ [0.12, 0.38]). The highest rate of population growth occurred in 1995–1996 ($\lambda_{1995} = 1.27$ [0.87, 1.82]) when the population increased from 45 (34, 58) to 56 (43, 71) breeding adults.

Vital rates were generally similar for males and females. Annual probabilities of juvenile survival never exceeded 6% ($\phi_{J,\mu}^\female = 0.05$ [0.03, 0.06], $\phi_{J,\mu}^\male = 0.04$ [0.02, 0.05], $P(\phi_{J,\mu}^\female > \phi_{J,\mu}^\male) = 0.87$; Figure 4D). In contrast, probabilities of adult survival averaged over 50% ($\phi_{Ad,\mu}^\female = 0.53$ [0.17, 0.87], $\phi_{Ad,\mu}^\male = 0.58$ [0.20, 0.90], $P(\phi_{Ad,\mu}^\female > \phi_{Ad,\mu}^\male) = 0.43$; Figure 4E). Recapture rates were generally high but variable, ranging from 0.90 (0.78, 0.99) for ASY females in 1999 to 0.45 (0.13, 0.75) for SY males in 1988. Recapture probability for SY males was similar to that of SY females
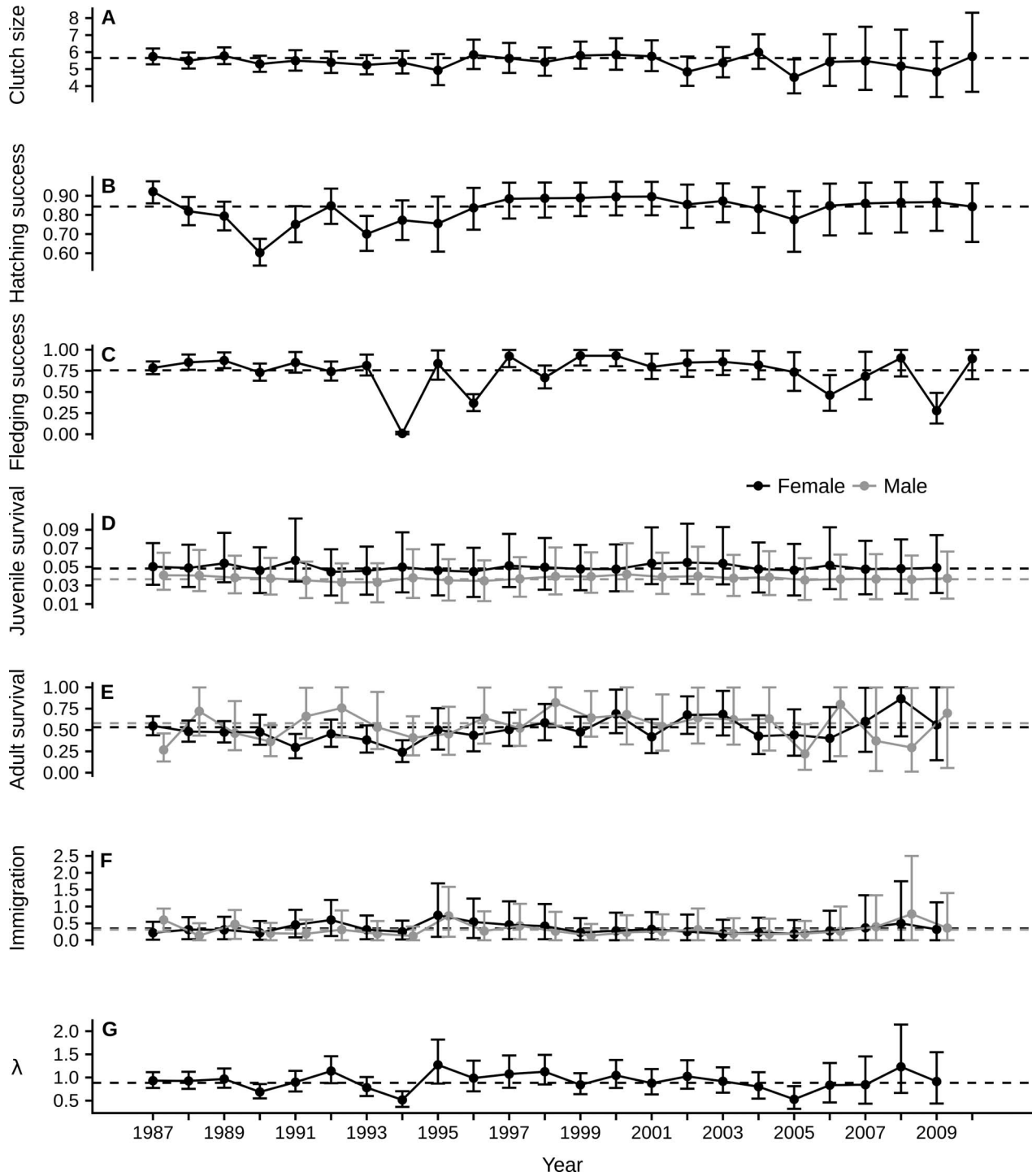
Figure 4. (**A–F**) Vital rate estimates and (**G**) rate of population change (λ). All parameters are per capita rates except for clutch size, which is a count. Horizontal dashed lines indicate mean estimates. Vertical bars show 95% BCI.

($p^{\female}_{SY,\mu} = 0.57$ [0.41, 0.74], $p^{\male}_{SY,\mu} = 0.63$ [0.38, 0.87], $P(p^{\female}_{SY,\mu} > p^{\male}_{SY,\mu}) = 0.35$), whereas recapture rates were 21% higher for ASY females than ASY males ($p^{\female}_{ASY,\mu} = 0.87$ [0.79, 0.94], $p^{\male}_{ASY,\mu} = 0.66$ [0.53, 0.79], $P(p^{\female}_{ASY,\mu} > p^{\male}_{ASY,\mu}) = 0.99$).

Per capita immigration rates were approximately 0.30 for both sexes with wider annual uncertainty intervals than other vital rates, particularly in the final years of the study (derived arithmetic mean $\omega^{\female} = 0.35$ [0.27, 0.44], $\omega^{\male} = 0.32$
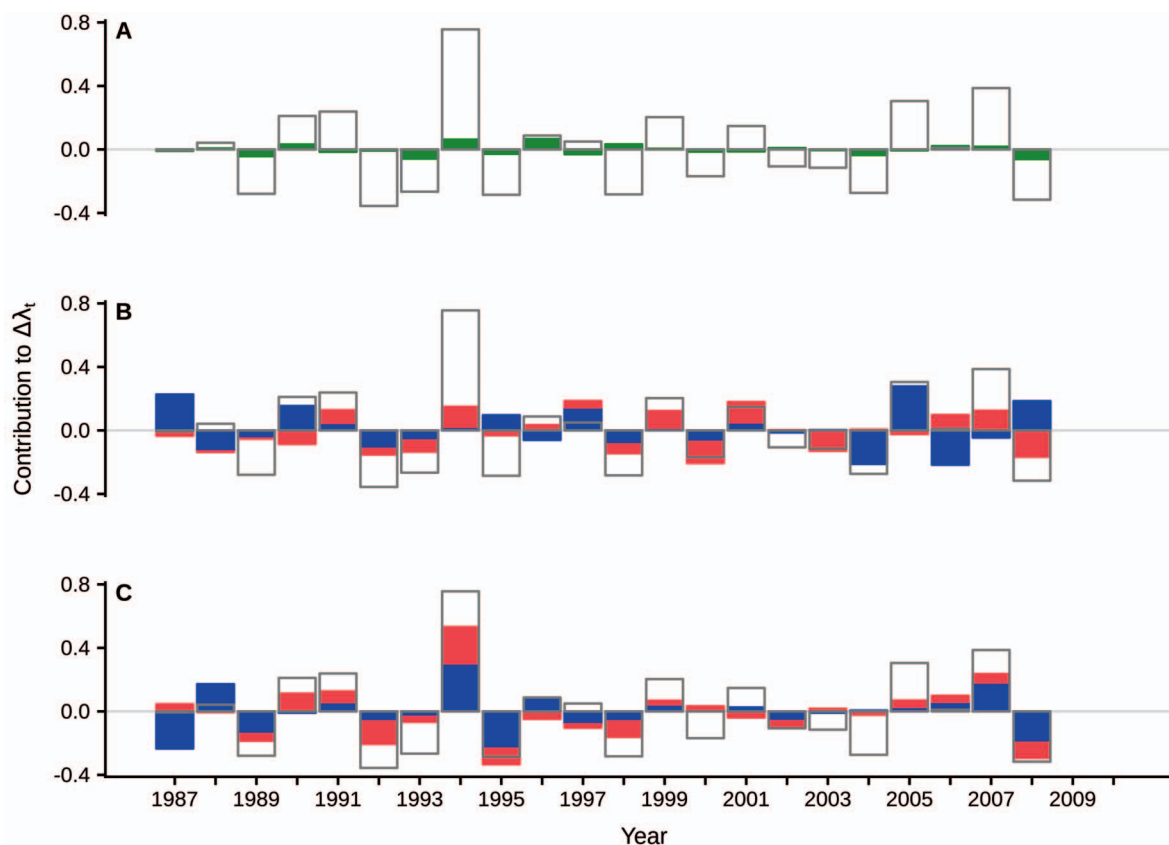
Figure 5. Contributions of variation in demographic parameters to the annual difference in rate of population change ($\Delta\lambda_t$) between all consecutive intervals (t and $t + 1$) from $t = 1987$ to $t = 2008$ estimated from life table response experiments. (**A**) Sum of mean contributions from clutch size, hatching success, fledging success, and juvenile survival of both sexes (green). (**B**) Mean contributions from female (red) and male (blue) adult survival. (**C**) Mean contributions from female (red) and male (blue) per capita immigration. The contributions from all parameters approximately sum to $\Delta\lambda_t$, displayed as a gray box for each starting year t.

Table 2. Contributions of variation in demographic parameters to overall variance in rate of population change (λ) over 24 yr estimated from life table response experiments. The sum of all contributions approximates the variance in λ_t.

Parameter	Mean LTRE contribution (95% BCI)	Normalized mean % contribution to var(λ_t)
cs	0.00003 (−0.00103, 0.00106)	0.04 %
hs	0.00053 (−0.00014, 0.00125)	0.71 %
fs	0.00161 (−0.00061, 0.00388)	2.20 %
$\phi_J^{\female}$	0.00003 (−0.00115, 0.00133)	0.04 %
$\phi_J^{\male}$	0.00001 (−0.00098, 0.00104)	0.01 %
$\phi_{Ad}^{\female}$	0.01040 (0.00134, 0.02280)	14.22 %
$\phi_{Ad}^{\male}$	0.00957 (−0.00399, 0.02390)	13.09 %
$\omega^{\female}$	0.02450 (0.00519, 0.06530)	33.49 %
$\omega^{\male}$	0.02660 (0.00444, 0.08160)	36.36 %
$N^{\female} / N_{tot}$	−0.00006 (−0.00053, 0.00013)	−0.08 %
$N^{\male} / N_{tot}$	−0.00006 (−0.00053, 0.00013)	−0.08 %

[0.22, 0.42]; Figure 4F). The number of immigrants declined from 22 females (1, 51) and 59 males (27, 87) in the second year of the study to 2 females (0, 7) and 2 males (0, 7) by the final year (Figure 3).

Life Table Response Experiments

Our first set of LTREs examined the contribution of variation in vital rates to overall temporal variance in λ (var(λ_t) $\approx$ 0.07; Table 2). Across sexes, immigration rates contributed to a normalized mean of ~70% of overall variance in λ compared to ~27% for adult survival probabilities, ~2% for fledging success rate, and <1% for all other contributions combined. Contributions from male and female parameters were similar.

Our second set of LTREs examined the contribution of changes in vital rates to the changes in λ between consecutive-year intervals (Figure 5, Appendix Figure 7). The most important demographic driver (the vital rate with the highest contribution to $\Delta\lambda_t$ in the same direction as $\Delta\lambda_t$) was male immigration in 41% of intervals, female

Table 3. Correlations among same-year vital rates across 24 yr. Pearson r correlation coefficients were calculated from covariances estimated from life table response experiments. Each cell shows Pearson r correlation coefficients (maximum density value from the posterior distribution), 95% BCI in parentheses, and $P(r > 0)$ across 45,000 iterations in brackets. High-probability correlations are in bold.

	hs	fs	$\phi_J^♀$	$\phi_J^♂$	$\phi_{Ad}^♀$	$\phi_{Ad}^♂$	$\omega^♀$	$\omega^♂$
cs	0.15 (−0.19, 0.47) [0.81]	0.13 (−0.29, 0.43) [0.68]	0.00 (−0.40, 0.42) [0.52]	0.05 (−0.38, 0.45) [0.58]	−0.09 (−0.50, 0.41) [0.38]	0.13 (−0.35, 0.51) [0.66]	−0.06 (−0.44, 0.41) [0.45]	−0.09 (−0.49, 0.40) [0.40]
hs		0.07 (−0.19, 0.35) [0.70]	0.04 (−0.37, 0.43) [0.59]	0.12 (−0.35, 0.46) [0.64]	**0.31 (−0.06, 0.55) [0.95]**	0.18 (−0.15, 0.44) [0.84]	0.00 (−0.36, 0.31) [0.48]	0.10 (−0.25, 0.40) [0.71]
fs			0.09 (−0.40, 0.43) [0.58]	0.07 (−0.41, 0.43) [0.58]	**0.34 (−0.04, 0.59) [0.96]**	−0.08 (−0.36, 0.33) [0.39]	0.03 (−0.39, 0.34) [0.54]	0.19 (−0.29, 0.41) [0.75]
$\phi_J^♀$				0.04 (−0.39, 0.43) [0.53]	0.01 (−0.41, 0.41) [0.49]	0.03 (−0.38, 0.43) [0.55]	−0.10 (−0.44, 0.37) [0.38]	−0.02 (−0.40, 0.42) [0.48]
$\phi_J^♂$					0.07 (−0.37, 0.46) [0.59]	0.00 (−0.40, 0.41) [0.51]	−0.09 (−0.44, 0.37) [0.39]	−0.03 (−0.41, 0.39) [0.43]
$\phi_{Ad}^♀$						−0.06 (−0.43, 0.38) [0.40]	−0.18 (−0.51, 0.38) [0.29]	0.25 (−0.21, 0.60) [0.83]
$\phi_{Ad}^♂$							0.08 (−0.35, 0.47) [0.61]	**−0.44 (−0.65, 0.10) [0.06]**
$\omega^♀$								0.13 (−0.29, 0.62) [0.72]

adult survival in 32% of intervals, male adult survival in 18% of intervals, and female immigration in 9% of intervals (4.5% ≈ 1 interval). Male immigration and male and female adult survival were the top demographic drivers in intervals with both positive and negative changes in λ, whereas female immigration was the top driver only in negative intervals. The only other vital rates among the highest 2 demographic drivers for any interval were fledging success (second highest in 2 intervals) and female juvenile survival (second highest in 1 interval).

Correlations Among Vital Rates

LTRE covariance matrices revealed strong positive relationships between female adult survival and both hatching success and fledging success, and a strong negative relationship between male adult survival and male immigration (Table 3).

DISCUSSION

Between 1987 and 2010, the Tree Swallow population at Kent Island declined by 94.1%, an average of −11.6% per year. Variation in immigration of both sexes contributed the most to variation in the rate of population change, followed by adult survival. Variation in fledging success made minor contributions to demographic changes in some years, but local reproductive rates contributed only slightly to overall dynamics. In any case, for reproductive rates to have a strong effect on population change, juvenile Tree Swallows born on the island would have had to recruit into the local breeding population at much higher rates. Given that juvenile survival was low (<6%) and unrelated to patterns of population change, it is unlikely that the dynamics of local productivity were a major factor in population changes. Our study population was dependent on immigration instead of local recruitment and was therefore a sink population (Pulliam 1988).

Immigration can rescue local populations from decline, even in the face of high mortality (Schaub et al. 2010, 2013; Duarte et al. 2016), and is known to play a strong role in maintaining another breeding population on Kent Island, Savannah Sparrows (*Passerculus sandwichensis*; Woodworth et al. 2017). However, immigration from other Tree Swallow populations was too low to prevent the decline of the population on Kent Island. Immigration is also likely to be crucial for maintaining some mainland populations. For example, a Tree Swallow population in Ontario with similarly low recruitment maintained a growth rate of only 0.59 when immigrants were excluded from calculations (Cox et al. 2018). Even such large and apparently stable sites can thus be "cryptic sinks" dependent upon immigration, as has been described in Greenland Greater White-fronted Geese (*Anser albifrons flavirostris*; Weegman et al. 2016).

Region-wide declines of Tree Swallows have likely reduced the number of potential immigrants to Kent Island. Both North American Breeding Bird Survey data and nest box occupancy rates show dramatic declines in Tree Swallow populations in northeastern North America (Shutler et al. 2012, Sauer et al. 2017). A regional reduction in potential immigrants may be exacerbated by the isolation of Kent Island, at distances of 5–10 km from possible island nesting sites and >30 km from the mainland, as well as the island's harsh maritime climate. Swallows nesting at Kent Island exhibit reproductive traits typical of more northerly latitudes, including later egg-laying dates, longer incubation periods, and absence of double-brooding (Paynter 1954, Wheelwright et al. 1991, Monroe et al. 2008). Thus, in contrast to some locations in the southern United States where Tree Swallow populations are expanding (Sauer et al. 2017), Kent Island may be both a low-probability and low-desirability target for immigrants from mainland populations.

As with all studies that use integrated population models, lack of direct immigration data limited the precision of our immigration estimates (Abadi et al. 2010). Furthermore, given that immigration is a latent parameter in these models, systematic bias in other vital rate estimates can result in inverse systematic bias of immigration estimates (Schaub and Fletcher 2015). In particular, failures to perfectly model annual variation in non-immigration vital rates may exaggerate the relationships between immigration rates and rate of population change. Such structural modeling issues need to be addressed—perhaps through the development of more diagnostic goodness-of-fit analyses—if IPMs are to produce more accurate and precise immigration estimates (Zipkin and Saunders 2018).

Variation in adult survival was also linked to the decline of the Tree Swallow population on Kent Island. These results mirror the impact of adult survival on population change at mainland sites in Saskatchewan (Weegman et al. 2017) and Ontario (Cox et al. 2018), but the ecological forces affecting adult mortality remain unclear. One possibility is that survival is reduced by diminishing food availability or quality during migration or on the wintering grounds (Paquette et al. 2014). Local conditions, such as weather, may also play an important role in limiting survival as well as the weaker demographic contributor, reproductive success (Weegman et al. 2017). A strong positive correlation between female adult survival and both hatching and fledging success suggests that adult mortality and reproductive success may be driven by shared environmental covariates. For example, a major storm on Kent Island in 1994 that killed nestlings may also have compromised adult condition, making breeding females more vulnerable to overwintering mortality and contributing to the long-term population decline. Kent Island has a shorter breeding period than more southerly sites, so the population may also be limited in its ability to compensate for stochastic weather events (e.g., by renesting). Further, a shorter breeding window could make it more difficult for Kent Island Tree Swallows to shift the timing of breeding in response to long-term climate trends, which may exacerbate phenological mismatches with the availability of insects (Dunn and Winkler 1999, Dunn et al. 2011, Imlay et al. 2018).

Unlike female survival, male survival showed no relationship with reproductive rates. Instead, there was an inverse annual relationship between male survival and male immigration. Although the availability of unoccupied nest boxes in most years of the study indicates that there was little or no competition for nest sites (Holroyd 1975), territoriality across multiple nest boxes may explain the negative correlation between male survival and immigration (Robertson and Gibbs 1982). Female Tree Swallows also defend nest sites (Leffelaar and Robertson 1985, Stutchbury and Robertson 1985) but female immigration showed no tradeoff with adult survival, suggesting that the male population was limited by the number of females.

Emigration may play an important role in the decline of isolated populations, but standard mark–recapture methods preclude detailed analysis of this vital rate. Given that Tree Swallows show high levels of natal dispersal, first-year emigration from Kent Island (rather than mortality) may be largely responsible for our low estimates of juvenile survival relative to earlier studies (20.9% across North America; Butler 1988). Natal dispersal may compound the population's sensitivity to immigration by suppressing potential population growth via local recruitment. Further, adult Tree Swallows emigrate at much higher rates in response to breeding failures (Winkler et al. 2004, Lagrange et al. 2017). Indeed, the positive relationship between adult female (apparent) survival and reproductive success in the Kent Island population may demonstrate an emigration response rather than mortality. Given that older Tree Swallows are more successful breeders (Wheelwright and Schultz 1994, Robertson and Rendell 2001), permanent emigration of younger birds as a response to reproductive failure could contribute to a positive feedback cycle of population decline.

Tree Swallow populations are expanding in some southern and western parts of their range, but declines in northeastern North America may increase risks of stochastic population collapse and lead to contractions of northerly distributions (Howe et al. 1991, Duarte et al. 2016). The sharp decline of Tree Swallows on Kent Island over a 24 yr period was a product of decreasing immigration (a regional effect) against a backdrop of variation in adult survival and low recruitment (local or remote effects). Our study represents just one population collapse in a species with many asynchronously changing

populations (Michel et al. 2016, Weegman et al. 2017) and a complex migratory network (Knight et al. 2018). Uncovering the causes of the decline of Tree Swallows will depend on a multi-population approach examining demographic drivers, environmental variables, and the links among these factors.

ACKNOWLEDGMENTS

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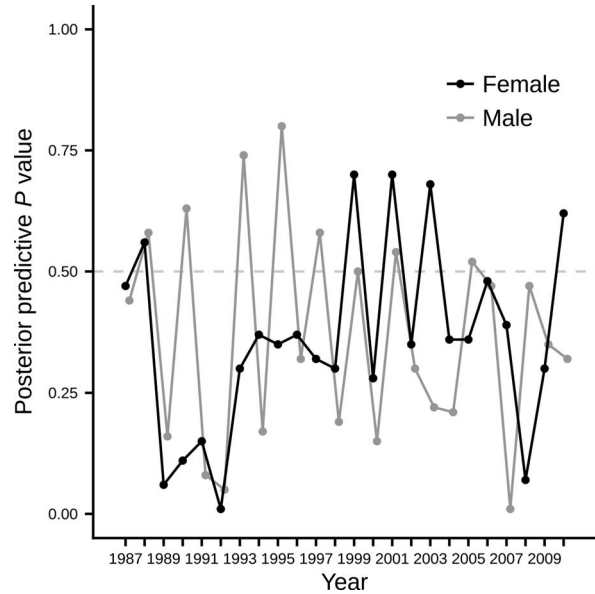
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APPENDIX

We assessed the goodness-of-fit of the parameters from the Cormack–Jolly–Seber (CJS) and Poisson regression models to their individual respective datasets using posterior predictive checks (Schaub et al. 2015). Standardized methods to evaluate the fit of the state space model and of the entire integrated population model (IPM) have yet to be established (Schaub et al. 2015, Zipkin and Saunders 2018). To evaluate goodness-of-fit, we produced a series of simulated, single-dataset values for capture–recapture (CR) and productivity datasets. The discrepancy measures of these simulated values were compared to the
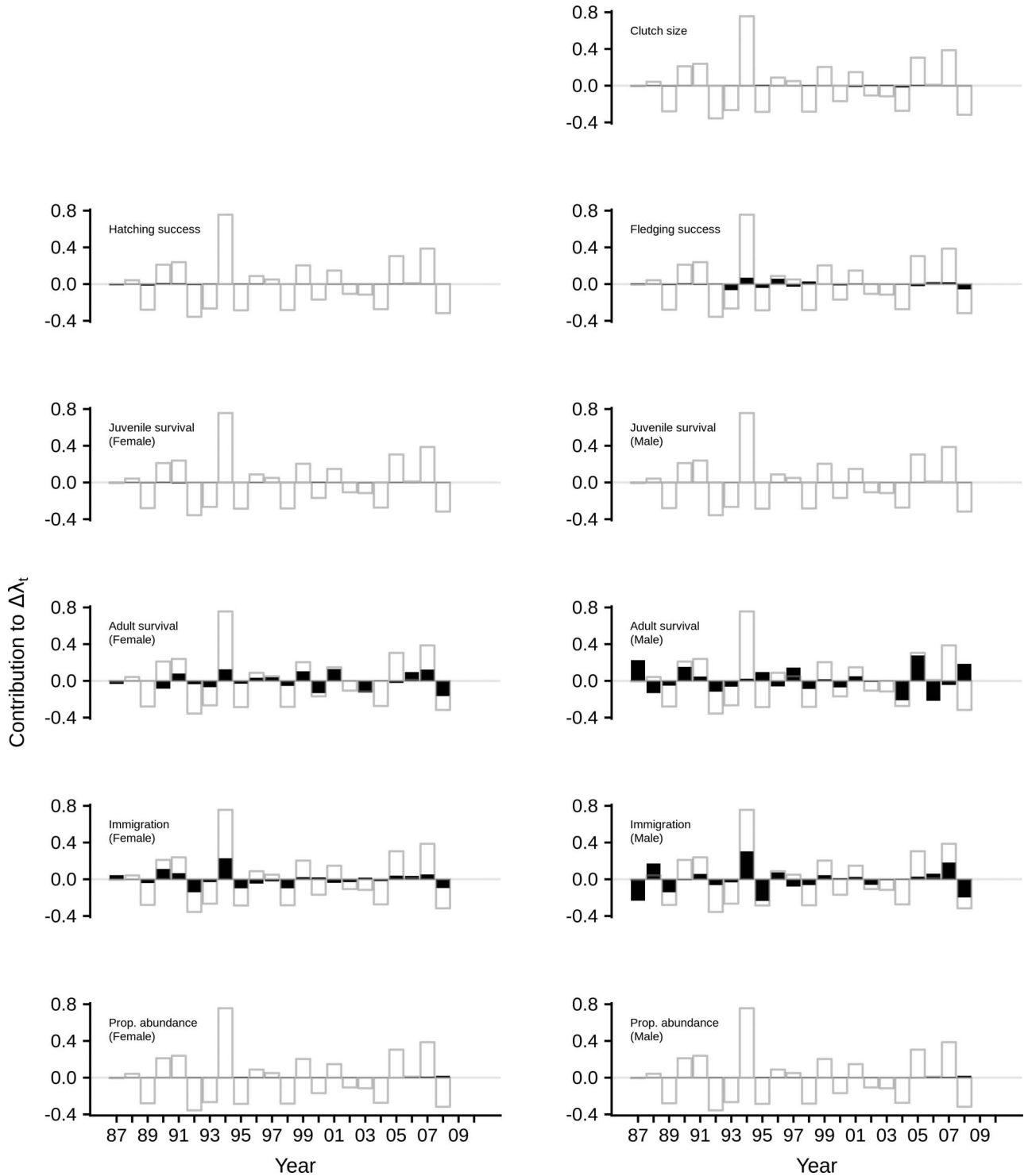

Appendix Figure 6. Posterior predictive *P* values (*PPP*) for adult survival parameters estimated from CJS discrepancy values, separated by year.

discrepancy of datasets extracted from full model (i.e. from multiple datasets) estimates. To assess the fit of CJS parameters to the capture–recapture data, we used the Freeman–Tukey discrepancy measure (Brooks et al. 2000, Schaub et al. 2015). To evaluate the fit of Poisson regressions parameters to productivity data, we used the χ^2 statistic.

The goodness-of-fit test is represented as a posterior predictive *P* value (*PPP*), equal to the probability that the simulated (from single dataset) values have higher discrepancy from the true dataset than those drawn from the posterior of the full model. One aim is that the discrepancy of the simulated values does not systematically differ from the discrepancy of the values produced by the full models. Therefore, we expect a 50% chance (*PPP* = 0.5) that the simulated discrepancy is higher than the discrepancy of the model (Gelman 2013).

When considered across all years, juvenile CJS parameters and Poisson regression parameters had *PPP* values near 0.5. On the other hand, adult CJS parameters demonstrated consistently lower discrepancy in the full model as compared to the simulated dataset (Appendix Table 4). However, when we calculated *PPP* for each individual year (rather than across all years), adult CJS *PPP* fluctuated more closely around 0.5 (Appendix Figure 6).

Appendix Table 4. Posterior predictive *P* values (*PPP*) for parameters estimated from CJS or Poisson regression model discrepancy across all years. *PPP* was calculated as the probability that a simulated (from single dataset) version of the data had a higher discrepancy than a dataset drawn from the full IPM.

Parameter	Model	Discrepancy statistic	*PPP* value
cs	Poisson	χ^2	0.49
hs	Poisson	χ^2	0.67
fs	Poisson	χ^2	0.50
$\phi_J^{\female}$	CJS	Freeman–Tukey	0.45
$\phi_J^{\male}$	CJS	Freeman–Tukey	0.33
$\phi_{Ad}^{\female}$	CJS	Freeman–Tukey	0.03
$\phi_{Ad}^{\male}$	CJS	Freeman–Tukey	0.02

Appendix Figure 7. Contributions of variation in individual demographic parameters (upper-left of each plot) to the annual difference in rate of population change ($\Delta\lambda_t$) between all consecutive intervals (t and $t+1$) from $t = 1987$ to $t = 2008$ estimated from life table response experiments. Some contributions are negligible. The contributions from all parameters approximately sum to $\Delta\lambda_t$, displayed as a gray box for each starting year t.