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Article

Geographic variation and environmental correlates of apparent survival rates in adult tree swallows *Tachycineta bicolor*

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Determining demographic rates in wild animal populations and understanding why rates vary are important challenges in population ecology and conservation. Whereas reproductive success is reported frequently for many songbird species, there are relatively few corresponding estimates of annual survival for widespread populations of the same migratory species. We incorporated mark–recapture data into Cormack–Jolly–Seber models to estimate annual apparent survival and recapture rates of adult male and female tree swallows *Tachycineta bicolor* in eight local breeding populations across North America for periods of 7–33 yr. We found strong site-specific and annual variation in apparent survival rates of adult swallows, and evidence of higher survival or site fidelity among males than females. There were no strong associations between putative overwintering region and survival. Strength and patterns of winter climate-apparent survival relationships varied across four sites monitored for >15 yr; at one site, spring pond conditions, local spring precipitation and, to a lesser extent, winter North Atlantic Oscillation Index were credible predictors of annual apparent survival. Further work is needed to evaluate how survival is related to environmental conditions throughout the annual cycle and how these factors affect population dynamics of swallows and related species of conservation concern.

Keywords: aerial insectivore, climate cycles, population ecology, recapture rates

Introduction

Population growth rates are driven by variation in reproductive success and survival rates which, in turn, are related to environmental factors interacting with biological properties of individuals (Blums et al. 2005, Pelletier et al. 2009). Determining why and how populations respond to environmental perturbations is a fundamental

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challenge for ecologists, and the answers to these questions are central to many conservation efforts. Thus, an improved understanding of the environmental factors determining reproductive and survival rates is essential for reliably evaluating hypotheses about causes of population changes. For most migratory songbird species, considerable information about reproductive success has been available for decades, but knowledge of spatiotemporal or sex-specific variation in survival rates has grown only more recently (Sillett and Holmes 2002, Mazerolle et al. 2005, Schaub and von Hirschheyd 2009). Populations of widespread species can experience dramatically different environmental conditions through the breeding season, potentially influencing an individual's performance directly via mortality, or indirectly via effects on timing of breeding or body condition. Regional breeding subpopulations also may segregate by wintering areas or migration routes and timing, resulting in individuals from different parts of a breeding range experiencing divergent conditions of weather, food supply, or predation. Thus, changes in sizes of regional subpopulations could be related to conditions on breeding or wintering areas, or more likely both, amplifying the complexity of pinpointing causes of fluctuations in their densities (Newton 2004).

Survival rates of many bird species can vary with sex (Stutchbury et al. 2009, Rymešová et al. 2012), owing to differences in sex-specific costs of territorial defense, gamete production, parental care, body size and thermoregulation, and migration distances and tempo (Promislow et al. 1992, Schaub and von Hirschheyd 2009). Higher reproductive costs could lower survival rates, a hypothesis that predicts lower survival for the sex that invests most in reproduction, although breeding-season costs for one sex could be offset by higher mortality of the opposite sex at other times of the year. In many studies, apparent survival is estimated because it is not possible to distinguish between permanent dispersal and mortality, and presumed sex differences in true survival could actually be related to sex-specific breeding dispersal (Greenwood and Harvey 1982, Lagrange et al. 2014). Thus, annual variation in survival rates likely depends on a dynamic interplay between effects of reproductive investment and environmental conditions on males and females – and their respective dispersal responses – at stages throughout the annual life-cycle.

Here, we use a large data set to estimate apparent annual survival rates for adult male and female tree swallows *Tachycineta bicolor* breeding in nest boxes at eight sites across North America. Tree swallows are small (~20 g) migratory songbirds that prey principally on aerial insects. There are few estimates of apparent survival in tree swallows (Shutler et al. 2006; Table 5 in Winkler et al. 2011) and no estimates of true survival; rather, most studies have reported return rates, which usually underestimate survival because they do not account for recapture failures (Williams et al. 2002). Annual variation in apparent survival rates of adult female tree swallows ranged from 0.29 to 0.54 in the eastern U.S. (Custer et al. 2007, 2012, Hallinger et al. 2011). Annual estimates of apparent survival were somewhat lower among adult females (range = 0.31 to 0.53) but overlapped those of males (range = 0.40 to 0.57) in Québec (Lagrange et al. 2014). Whether these estimates from eastern North America are broadly applicable to tree swallows across their entire breeding range is unknown.

Several species of aerial insectivore have declined in some areas of North America (Nebel et al. 2010, Michel et al. 2016) for reasons that are not entirely clear. For most of these species, including tree swallows, the strongest declines have been recorded in the northeastern region of the continent (Shutler et al. 2012, Michel et al. 2016). Population declines have been attributed to changes in climate and land use at different stages of the annual cycle, changes in predation or food availability, or nest site or other habitat losses but, to our knowledge, these hypotheses have not been fully evaluated. As in previous studies of tree swallows (Winkler et al. 2002, Dunn et al. 2011), we used data from long-term studies of individually marked adults to explore spatiotemporal patterns in apparent survival rates. We began by determining whether apparent survival rates varied annually, among sites, between neighboring sites (presumed to share similar wintering areas), and by sex. If winter climate is an important correlate of variation in apparent survival, then we expected that adults inhabiting similar wintering regions would have similar yearly patterns in survival. We also tested whether apparent survival was related to winter climate cycles (LaManna et al. 2012, McKellar et al. 2015) and environmental conditions at breeding sites (Salewski et al. 2013, García-Pérez et al. 2014).

Methods

Tree swallows were monitored at eight sites in Canada and the USA (Fig. 1): Wolfville, Nova Scotia (45.05°N, 64.25°W; Shutler et al. 2004, Hainstock et al. 2010); Long Point and Mud Creek, Ontario (near 42.64°N, 80.46°W; Hussell 2003); Ithaca, New York (42.4°N, 76.50°W; Winkler and Allen 1996); Saukville, Wisconsin (43.38°N, 88.02°W; Whittingham and Dunn 2000); Allendale, Michigan (42.95°N, 85.88°W; Lombardo and Thorpe 2010); St Denis, Saskatchewan (52.20°N, 106.08°W; Shutler et al. 2006); and Prince George, British Columbia (53.79°N, 122.77°W; O'Brien and Dawson 2005). Swallows at all sites nested in wooden boxes, placed on metal or wooden posts about 1.25 m above ground, with nest holes generally facing southeast. Site descriptions and nest-box monitoring procedures are provided by Shutler et al. (2012).

Swallows were banded and recaptured annually for periods ranging from 7 to 33 yr. Accordingly, numbers of females and males marked on each site depended on the number of monitored nest boxes, local site fidelity, and study period length (Fig. 1). Most adult swallows were captured soon after the last egg had hatched in a nest box, banded (if not previously banded), and sexed (cloacal protuberance in males, brood patch in females; Winkler et al. 2011). Depending on the site, some females were captured and banded opportunistically

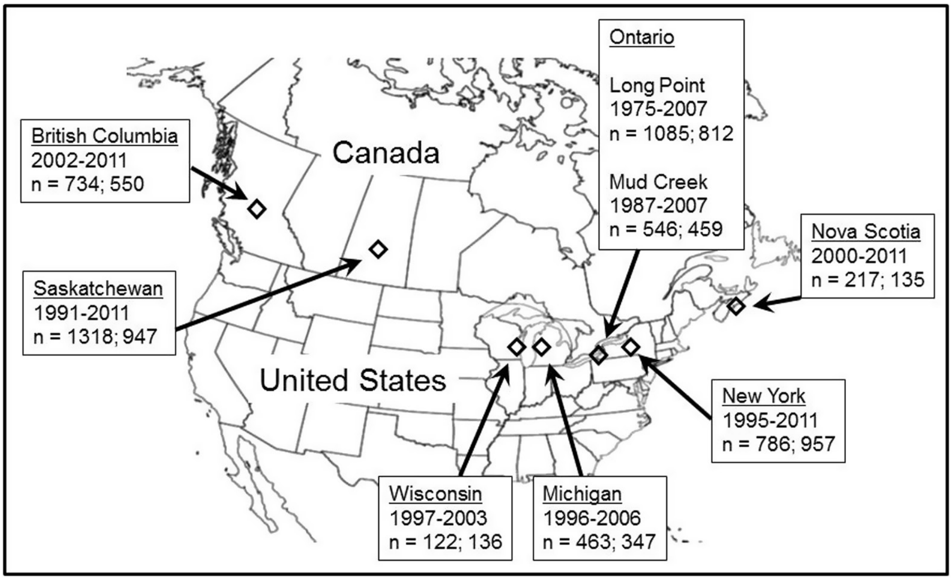

Figure 1. Study site locations in North America (open diamonds). Shown for each site are years of study and numbers of ringed birds (n = females; males).

during routine nest-monitoring before eggs hatched. Yearly banding and recapture data were used to create encounter histories for individual adults, and these data were used to estimate apparent survival and recapture rates (details below). We did not distinguish apparent survival of female swallows marked as yearlings (i.e. in their second year of life) from those of older (after-second year) birds, but recognize that survival could be age-specific (Custer et al. 2012). Unlike females, yearling and older male tree swallows have similar plumage characteristics, so it was not possible to reliably partition survival estimates by age group in a consistent manner for both sexes.

Mark–recapture analyses

Apparent survival (Φ) and recapture (p) rates were estimated using live-encounter, Cormack–Jolly–Seber (CJS) models, implemented in program MARK (Lebreton et al. 1992, White and Burnham 1999). We began by analyzing data for all sites, 1991–2011, with values coded as missing (‘.’) in the time series for sites that lacked mark–recapture information in some years. The time series was started in 1991 to include the Saskatchewan site because years prior to 1991 were represented by only two adjacent sites in Ontario (Fig. 1). We ended the time series in 2011 because in that year we began to mark previously-banded adult swallows with light-level geolocators at many sites which would further complicate survival estimation (Gómez et al. 2014). The candidate set included models that incorporated additive and interaction effects of time (t; year), site, and sex on Φ and p. Here and in subsequent modeling steps, we employed an information theoretic approach to select best approximating models (Burnham and Anderson 2002), ranking them by Akaike’s information criterion adjusted for sample size ($\mathrm{AIC_c}$). We calculated model weights (w_i) and differences between $\mathrm{AIC_c}$ of the best approximating model and $\mathrm{AIC_c}$ of other models in the candidate set ($\Delta\mathrm{AIC_c}$), and reported number of estimable parameters (k), as appropriate. We conducted systematic comparisons to test for differences in Φ between nearest adjacent sites, reasoning that neighbouring sites should have similar survival rates because swallows would be exposed more often to common conditions during the annual cycle relative to swallows from more distant breeding populations. We also assigned each breeding site (Fig. 1) to one of three provisional wintering regions on the basis of recently-acquired movement data to determine whether variation in apparent survival was associated with overwintering region (Knight et al. 2018): southeastern USA and eastern Caribbean (NS, NY, ON, MI, WI); southern USA, central Caribbean and southcentral Mexico (SK); southwestern USA and western Mexico (BC).

Then, a common set of models was evaluated with data from each study site, separately, and this set incorporated effects of t, sex, $t \times$ sex, and $t +$ sex on Φ and p, as well as combinations of models aggregating across t or sex; a logit link function was specified to facilitate covariate modeling described below. At New York and British Columbia, the only sites where there were two closely neighbouring sub-sites (< 10 km and < 20 km apart, respectively), Φ and p were initially estimated separately for each sub-site and then combined because estimates for sub-sites were indistinguishable. Sites at Ontario (Long Point, Mud Creek) were ~30 km apart, located in distinct environments, and involved different time series lengths (Fig. 1); data for these two sites were analyzed separately because annual variation in Φ was site-specific (details below).

We simplified models at each site (beginning with p) to derive the best supported models yielding estimates of Φ and p. Model fit was assessed using a median $\hat{c}$ method, derived from a global model that allowed Φ and p to vary by t and sex in program MARK. When $\hat{c}$ exceeded 1.0 (lower confidence interval > 1.0), we adjusted AIC_c for lack of model fit, using quasi-AIC_c (i.e. $QAIC_c$) to rank models (Burnham and Anderson 2002). At Wisconsin (7-yr time series), due to model selection uncertainty, Φ and p and their unconditional standard errors (SE_{uncond}) were estimated via model-averaging over models within 4 AIC_c units of the best-approximating model (Burnham and Anderson 2002); results did not change when we averaged over models within 8 AIC_c units.

Apparent survival, winter climate indices, and local spring conditions

We related Φ to winter climate conditions, as indexed by the North Atlantic Oscillation Index (NAOI) and Bivariate El Niño Time-Series (BEST), using the time series of climate indices relevant to each site studied for at least 10 yr (details below; Wisconsin excluded). Monthly index values were averaged over the period from December to March each year, and standardized (mean = 0, variance = 1). To assess the effects of climatic variables on survival, we incorporated in the best model a logistic regression containing both linear and quadratic terms, following Grosbois et al. (2008) and Frederiksen et al. (2014). We replaced time with a linear and quadratic term for each standardized index into the best-approximating model that had incorporated time variation in Φ at each site, while retaining the most parsimonious structure for p. Given ample data, covariate models rarely out-perform fully time-dependent models (Frederiksen et al. 2008). Therefore, we also inspected parameter estimates and errors to gauge covariate effects, compared covariate models with (Q)AIC_c and ANODEV (F-tests) in program MARK while retaining a consistent p structure, and calculated the proportion of temporal variation attributed to the best approximating covariate model with the deviance method (Grosbois et al. 2008); we interpreted covariate relationships cautiously for ANODEV F-tests with $p < 0.15$ between appropriate null and covariate models (Yoccoz 1991). We implemented variance components analysis of global models in program MARK (method of moments) to estimate mean Φ and to derive separate estimates of sampling and process variation (Appendix D [by K. Burnham] in Cooch and White 2014).

At the Saskatchewan site, we had information about spring weather (temperature, precipitation) and pond counts on the site in early May; swallows rely heavily on flying insects originating from ponds (Winkler et al. 2011, Harriman et al. 2017), so we modeled survival variation in relation to winter climate, spring mean temperature and total precipitation during a 20-d spring arrival period just prior to the onset of nesting (i.e. 26 April to 15 May), and pond count in the previous and current year (all local variables were standardized, as described above for climate indices). Current and previous May pond counts were correlated ($r = 0.63$, $p = 0.003$, $n = 20$) and never included in the same model; none of the other environmental covariates were correlated ($r < |0.27|$, $p > 0.25$).

Markov chain Monte Carlo simulations

Markov chain Monte Carlo (MCMC) simulations with a logit link function were run in program MARK following details in Cooch and White (2014: Appendices D and E) to estimate Φ and p (with 95% credible intervals), while accounting for effects of sampling error. Following recommendations in Cooch and White (2014) for minimum sample sizes, Φ and p were estimated for sites with at least 10 yr of data (i.e. excluding Wisconsin). For analyses of survival in relation to winter climate or local conditions (SK) we used sites with > 15 yr of data. MCMC was performed with 5000 tuning and 10 000 burn-in samples, and parameters (credible intervals based on highest posterior densities) were estimated from 80 000 values of the posterior distribution (120 000 values for covariate models). For covariate models, we used the hyperdistribution design matrix to model means and variances of hyperdistributions with linear models and obtain estimates of covariate effects on apparent survival rates using step sizes of 0.1, defined values for prior distributions of means ($\mu \sim \text{normal}(0, 10)$) and default values for variances ($1/\sigma \sim \text{gamma}(0.001, 0.001)$).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.f2d0df0> (Clark et al. 2018).

Results

Large-scale variation in apparent survival and recapture rates

Strong annual variation in Φ was evident during 1991–2011, as were differences in survival patterns among sites and between sexes, whereas recapture rates varied by site and sex (Table 1; effective sample size = 15 550). The best-approximating model {Φ(t × site) + sex, p(site × sex)} was more plausible ($\Delta AIC_c = 55.37$) than a model that included interactive sex effects on Φ ({Φ(t × site × sex), p(site × sex)}). The additive effect of sex indicated that apparent survival of males was ~0.04 (95% confidence interval = 0.02, 0.06) higher than that of females on an annual basis across all sites. Models that lacked t, site, or sex-specific effects on Φ received no support ($\Delta AIC_c > 200$).

In general, annual patterns in Φ were unique to each site. Whereas there was evidence that Nova Scotia and New York had similar temporal variation in Φ ($\Delta AIC_c = 1.32$), relative to the model {Φ(t × site) + sex, p(site × sex)}, annual variation in Φ differed between Long Point and Mud Creek, Ontario ($\Delta AIC_c = 11.85$), located ~30 km apart (Table 1). Stronger differences in annual patterns were detected in all other comparisons of Φ from adjacent sites ($\Delta AIC_c > 30$; models not shown), indicative of distinct processes underlying patterns of survival variation or permanent dispersal movements for most sites. A model in which Φ was associated with the three

Table 1. Model selection results for the combined analysis of apparent survival (Φ) and recapture (p) rates of adult tree swallows from eight sites in North America (Fig. 1), 1991–2011, in relation to time (t), site, and sex. Shown are Akaike's information criterion adjusted for sample size (AIC$_c$), difference in AIC$_c$ between the best-approximating model and other models in the candidate set (ΔAIC$_c$), model weight (w_i), number of estimable parameters (k), and model deviance. NS is Nova Scotia, NY is New York, and MC and LP refer, respectively, to Mud Creek and Long Point, Ontario (Fig. 1). WINTER signifies the assignment of each breeding site to one of three nonbreeding season regions (see text for explanation).

Model	AIC$_c$	ΔAIC$_c$	w_i	k	Deviance
{$\Phi(t \times \text{site}) + \text{sex}$, $p(\text{site} \times \text{sex})$}	24702.63	0	0.512	122	3150.87
{$\Phi(t \times \text{site}) + \text{sex}$, NS = NY), $p(\text{site} \times \text{sex})$}	24703.94	1.32	0.265	111	3174.52
{$\Phi(t \times \text{site})$, $p(t \times \text{site} \times \text{sex})$}	24704.70	2.08	0.181	304	2778.72
{$\Phi(t \times \text{site})$, $p(\text{site} \times \text{sex})$}	24709.10	6.47	0.020	120	3161.40
{$\Phi(t \times \text{site}) + \text{sex}$, MC = LP), $p(\text{site} \times \text{sex})$}	24714.48	11.85	0.001	106	3195.20
{$\Phi(t \times \text{site} \times \text{sex})$, $p(\text{site} \times \text{sex})$}	24757.99	55.37	0	224	2997.60
{$\Phi(t \times \text{site} \times \text{sex})$, $p(t \times \text{site} \times \text{sex})$}	24780.76	78.13	0	400	2653.77
{$\Phi(t \times \text{WINTER region}) + \text{sex})$, $p(\text{site} \times \text{sex})$}	24820.88	118.25	0	67	3382.49
{$\Phi(t + \text{sex})$, $p(\text{site} \times \text{sex})$}	24967.42	264.79	0	37	3587.42
{$\Phi(\text{site})$, $p(\text{site} \times \text{sex})$}	24992.74	290.12	0	24	3638.85
{$\Phi(t)$, $p(\text{site} \times \text{sex})$}	24999.11	296.49	0	36	3621.13
{$\Phi(\text{sex})$, $p(\text{site} \times \text{sex})$}	25077.54	374.91	0	18	3735.68
{$\Phi(.)$, $p(\text{site} \times \text{sex})$}	25109.88	407.26	0	17	3770.03
{$\Phi(.)$, $p(.)$}	25295.99	593.36	0	2	3986.17

putative wintering regions was ~146 AIC$_c$ units less than a model that lacked site effects on Φ, {$\Phi(t + \text{sex})$, $p(\text{site} \times \text{sex})$}, suggesting possible spatial structure in survival patterns; an estimated 47% of site-specific variation in Φ was associated with wintering region affiliation ($F_{29,56} = 1.71$, $p = 0.04$).

Site-specific components of variation in apparent survival and recapture rates

The best-approximating model for the Nova Scotia data set indicated that Φ varied annually (Table 2, Fig. 2; effective sample size = 498), and p varied in parallel between sexes over time or differed between sexes (females: 0.78 ± 0.07 SE; males: 0.59 ± 0.07 SE). Median $\hat{c}$ (1.12 ± 0.08 SE) indicated acceptable model fit. Two competitive models (ΔAIC$_c$ < 2) suggested that sex differences in Φ varied in a similar manner from year-to-year, with lower Φ observed in females. Apparent survival rates varied among years at Long Point, Ontario (Table 2, Fig. 3A; effective sample size = 3575), and males had higher Φ estimates than females; median $\hat{c}$ was 0.99 (± 0.01 SE). Despite some indication that p differed among years, a more plausible model suggested that p was constant at 0.77 ± 0.01 (SE). At Mud Creek, Ontario, Φ also varied among years (Table 2, Fig. 3B; effective sample size = 1855), and the second-ranked model suggested higher Φ in males; median $\hat{c}$ was 1.00 ± 0.01 SE). Recapture rate was nearly constant (0.83 ± 0.02 SE) and sex differences were trivial (females: 0.83 ± 0.02 SE; males: 0.83 ± 0.02 SE).

Apparent survival rates varied annually and by sex (males > females) at Saskatchewan (Table 2, Fig. 4A; effective sample size = 5135); median $\hat{c}$ was 1.00 ± 0.01 (SE). Estimates of p were annually variable, and marginally higher among females than males. At British Columbia, Φ varied with t and additively with sex, being consistently lower in females than males (Table 2, Fig. 4B; effective sample size = 2075); estimates of p were somewhat higher in females than males from year-to-year or varied annually. Median $\hat{c}$ was 1.03 ± 0.02 (SE).

At New York, Φ for males and females varied annually (Table 2, Fig. 2; effective sample size = 2576). Estimates of p varied among years in different ways for males and females. Median $\hat{c}$ was 1.13 ± 0.01 (SE), so models were ranked with QAIC$_c$. A model in which Φ estimates of females were marginally higher than males each year received some support (Table 2). At Michigan, estimates of Φ were year-specific (Fig. 3B), with no difference between sexes (Table 2, Fig. 3B; effective sample size = 1329). Median $\hat{c}$ was 1.39 ± 0.03 (SE), so models were ranked with QAIC$_c$. Estimates of p were either constant (0.83 ± 0.03 SE) or sex-specific (females, 0.86 ± 0.04 SE; males, 0.80 ± 0.04 SE). Apparent survival rates were constant (0.62 ± 0.04 SE), varied annually or were sex-specific in Wisconsin, where model selection uncertainty was observed (Table 2; effective sample size = 498); median $\hat{c}$ was 2.79 (± 0.07 SE). Model-averaged annual estimates of Φ ranged from 0.54 (± 0.13 SE$_{\text{uncond}}$) to 0.67 (± 0.11 SE$_{\text{uncond}}$) in females and from 0.55 (± 0.14 SE$_{\text{uncond}}$) to 0.69 (± 0.11 SE$_{\text{uncond}}$) in males; model-averaged p estimates were 0.91 ± 0.06 SE$_{\text{uncond}}$ and 0.87 ± 0.06 SE$_{\text{uncond}}$ for females and males, respectively.

MCMC estimates of Φ and p (model-averaged estimates for Wisconsin) are presented in on-line supplementary material (Supplementary material Appendix 1 Table A1). Variance components analysis of global models {$\Phi(t \times \text{sex})$ $p(t \times \text{sex})$} for sites studied at least 10 yr produced mean Φ estimates that ranged from 0.41 at Nova Scotia to 0.55 at Long Point, Ontario (Supplementary material Appendix 1 Table A2). At all sites except Michigan (0.84), the proportion of temporal variance attributed to sampling variance was < 0.50 and ranged from 0.24 at Saskatchewan to 0.44 at Long Point.

Table 2. Model diagnostics and model-ranking results for Cormack–Jolly–Seber models of apparent survival (Φ) and recapture (p) rates of female and male tree swallows at sites in North America. Shown are Akaike's information criterion adjusted for sample size (AIC$_c$), difference in AIC$_c$ between the best-approximating model and other models in the candidate set (ΔAIC$_c$), model weight (w_i), number of estimable parameters (k), and model deviance; quasi-AIC$_c$ (QAIC$_c$) and quasi-deviance (QDev) shown for New York, Michigan and Wisconsin (see Results). Results are shown for models within 4 Δ(Q)AIC$_c$ units of the best approximating model, the top-ranked environmental covariate model(s), and the null and fully parameterized models. NAOI refers to North American Oscillation Index in the most recent winter; BEST signifies Bivariate El Niño-Southern Oscillation Time-Series in the most recent winter; Ponds and Precip refer to previous May pond count and current spring precipitation, respectively, at Saskatchewan (see text for details). Site locations and number of study years are shown in Fig. 1.

Site: model structure	AIC$_c$	ΔAIC$_c$	w_i	k	Deviance
Nova Scotia					
$\{\Phi(t), p(t+\text{sex})\}$	734.12	0	0.212	20	117.11
$\{\Phi(t), p(\text{sex})\}$	734.18	0.06	0.206	13	132.18
$\{\Phi(t+\text{sex}), p(\text{sex})\}$	734.66	0.54	0.162	14	130.54
$\{\Phi(t+\text{sex}), p(t+\text{sex})\}$	735.36	1.24	0.114	21	116.17
$\{\Phi(t), p(.)\}$	736.48	2.35	0.065	12	136.58
$\{\Phi(\text{NAOI}+\text{NAOI}^2), p(t+\text{sex})\}$	736.58	2.46	0.062	14	132.46
$\{\Phi(.), p(t+\text{sex})\}$	737.19	3.07	0.046	12	137.30
$\{\Phi(.), p(.)\}$ NULL	749.32	15.20	0	2	170.04
$\{\Phi(t \times \text{sex}), p(t \times \text{sex})\}$	770.50	36.32	0	42	103.32
Ontario – Long Point					
$\{\Phi(t+\text{sex}), p(.)\}$	6398.89	0	0.779	34	1198.71
$\{\Phi(t+\text{sex}), p(t)\}$	6401.69	2.80	0.192	64	1137.74
$\{\Phi(\text{sex}), p(.)\}$	6418.84	19.95	0	3	1281.33
$\{\Phi(\text{BEST}+\text{sex}), p(.)\}$	6420.58	21.69	0	4	1281.06
$\{\Phi(\text{NAOI}+\text{sex}), p(.)\}$	6420.82	21.93	0	4	1281.31
$\{\Phi(.), p(.)\}$ NULL	6428.32	29.43	0	2	1292.81
$\{\Phi(t \times \text{sex}), p(t \times \text{sex})\}$	6448.55	49.66	0	127	1053.61
Ontario – Mud Creek					
$\{\Phi(t), p(.)\}$	3073.70	0	0.425	21	528.00
$\{\Phi(t+sex), p(.)\}$	3074.43	0.74	0.294	22	526.69
$\{\Phi(t), p(\text{sex})\}$	3075.72	2.03	0.154	22	527.98
$\{\Phi(t+sex), p(\text{sex})\}$	3076.29	2.60	0.116	23	526.50
$\{\Phi(\text{NAOI}+\text{NAOI}^2), p(.)\}$	3115.84	42.14	0	4	604.62
$\{\Phi(\text{NAOI}), p(.)\}$	3116.03	42.34	0	3	606.82
$\{\Phi(\text{BEST}+\text{BEST}^2), p(.)\}$	3118.38	44.69	0	4	607.17
$\{\Phi(.), p(.)\}$ NULL	3119.82	46.12	0	2	612.62
$\{\Phi(t \times \text{sex}), p(t \times \text{sex})\}$	3127.34	53.65	0	78	461.21
Saskatchewan					
$\{\Phi(t+\text{sex}), p(t+\text{sex})\}$	8469.50	0	0.435	40	770.31
$\{\Phi(t+\text{sex}), p(t)\}$	8469.79	0.29	0.376	39	772.63
$\{\Phi(t \times \text{sex}), p(t+\text{sex})\}$	8472.95	3.45	0.078	59	735.01
$\{\Phi([\text{Ponds}+\text{Precip}+\text{NAOI}]+\text{sex}), p(t+\text{sex})\}$	8483.71	14.21	0	26	812.88
$\{\Phi(t \times \text{sex}), p(t \times \text{sex})\}$	8484.02	14.51	0	78	707.03
$\Phi([\text{Ponds}+\text{Precip}]+\text{sex}), p(t+\text{sex})\}$	8494.35	24.84	0	25	825.54
$\{\Phi([\text{Ponds}]+\text{sex}), p(t+\text{sex})\}$	8496.78	27.28	0	24	829.99
$\{\Phi(.), p(t+\text{sex})\}$	8513.70	44.20	0	22	850.96
$\{\Phi(\text{sex}), p(t+\text{sex})\}$	8514.52	45.02	0	23	849.75
$\{\Phi(.), p(.)\}$ NULL	8650.71	181.21	0	2	1028.16
British Columbia					
$\{\Phi(t+\text{sex}), p(t+\text{sex})\}$	3148.71	0	0.469	20	315.65
$\{\Phi(t+\text{sex}), p(t)\}$	3149.96	1.25	0.251	18	320.97
$\{\Phi([\text{BEST}]+\text{sex}), p(t+\text{sex})\}$	3151.81	3.10	0.100	13	332.98
$\{\Phi([\text{BEST}+\text{BEST}^2]+\text{sex}), p(t+\text{sex})\}$	3152.59	3.88	0.067	14	331.73
$\{\Phi(\text{sex}), p(t+\text{sex})\}$	3159.01	10.30	0.003	12	342.20
$\{\Phi(t \times \text{sex}), p(t \times \text{sex})\}$	3161.32	12.61	0.001	33	301.57
$\{\Phi(.), p(t+\text{sex})\}$	3177.06	28.35	0	11	362.28
$\{\Phi(.), p(.)\}$ NULL	3186.93	38.22	0	2	390.27
$\{\Phi(t \times \text{sex} \times \text{subsite}), p(t \times \text{sex} \times \text{subsite})\}$	3195.23	46.52	0	68	261.90

(*Continued*)

Table 2. (Continued)

Site Model structure	QAIC$_c$	ΔQAIC$_c$	w_i	k	QDev
New York					
$\{\Phi(t), p(t \times \text{sex})\}$	3486.79	0	0.695	46	548.22
$\{\Phi(t+\text{sex}), p(t \times \text{sex})\}$	3488.84	2.04	0.250	47	548.19
$\{\Phi(\text{NAOI}+\text{NAOI}^2), p(t \times \text{sex})\}$	3497.56	10.77	0.003	34	583.76
$\{\Phi(t \times \text{sex}), p(t \times \text{sex})\}$	3501.23	14.43	0.001	62	529.25
$\{\Phi(.), p(t \times \text{sex})\}$	3502.72	15.92	0	33	590.97
$\{\Phi(t \times \text{sex} \times \text{subsite}), p(t \times \text{sex} \times \text{subsite})\}$	3557.45	70.65	0	124	451.94
$\{\Phi(.), p(.)\}$ NULL	3641.88	155.09	0	2	793.01
Michigan					
$\{\Phi(t), p(.)\}$	1477.69	0	0.362	11	185.66
$\{\Phi(t), p(\text{sex})\}$	1478.57	0.88	0.233	12	184.51
$\{\Phi(t+\text{sex}), p(\text{sex})\}$	1478.79	1.10	0.209	13	182.69
$\{\Phi(t+\text{sex}), p(.)\}$	1479.00	1.31	0.189	12	184.93
$\{\Phi(\text{NAOI}+\text{NAOI}^2), p(.)\}$	1489.76	12.06	0.001	4	211.89
$\{\Phi(.), p(.)\}$ NULL	1493.57	15.87	0.000	2	219.73
$\{\Phi(t \times \text{sex}), p(t \times \text{sex})\}$	1506.05	28.37	0.000	38	157.93
Wisconsin					
$\{\Phi(.), p(.)\}$ NULL	223.59	0	0.248	2	85.72
$\{\Phi(t), p(.)\}$	224.25	0.67	0.177	7	76.18
$\{\Phi(.), p(\text{sex})\}$	224.53	0.94	0.155	3	84.63
$\{\Phi(\text{sex}), p(.)\}$	225.01	1.51	0.116	3	85.20
$\{\Phi(t), p(\text{sex})\}$	225.17	1.58	0.112	8	75.03
$\{\Phi(\text{sex}), p(\text{sex})\}$	225.58	2.00	0.091	4	83.66
$\{\Phi(t+\text{sex}), p(.)\}$	225.96	2.37	0.075	8	75.82
$\{\Phi(t \times \text{sex}), p(t \times \text{sex})\}$	243.79	20.21	0	19	70.36

Associations between apparent survival, winter climate indices, and local spring conditions

At Nova Scotia (Table 2), the most plausible climate model incorporated nonlinear effects of winter NAOI ($\beta_{\text{NAOI}} = -0.618 \pm 0.308$ SE, $\beta_{\text{NAOI}^2} = -0.373 \pm 0.168$ SE) and explained ~24% of the temporal variance in Φ. However, this model differed by only 0.61 AIC$_c$ units from model $\{\Phi(.), p(t+\text{sex})\}$ (ANODEV: $F_{2,6} = 0.96$, $p = 0.44$). Likewise, about 23% of the temporal variance in Φ was accounted for by nonlinear effects of NAOI at Michigan ($\beta_{\text{NAOI}} = -0.066 \pm 0.087$ SE, $\beta_{\text{NAOI}^2} = 0.150 \pm 0.057$ SE; Table 2). This model was 3.81 AIC$_c$ units less than model $\{\Phi(.), p(.)\}$ yet NAOI effects were unsubstantiated ($F_{2,7} = 1.04$, $p = 0.40$). At British Columbia (Table 2), Φ was negatively related to winter climate ($\beta_{\text{BEST}} = -0.205 \pm 0.069$ SE), where an estimated 66% of temporal variation in Φ was explained by the BEST index ($F_{2,7} = 5.92$, $p = 0.03$).

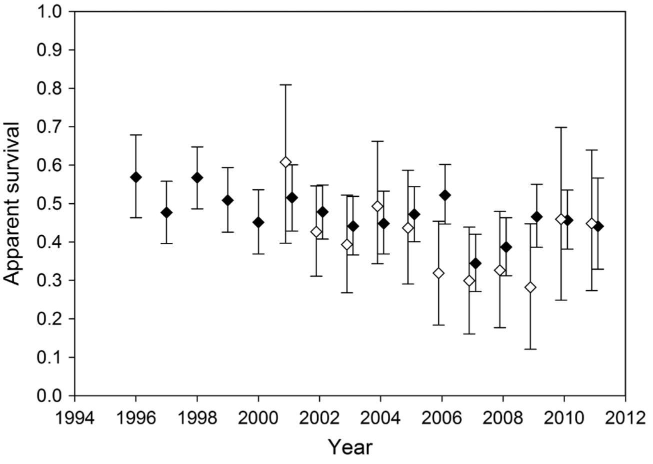

Figure. 2. Estimates of annual apparent survival rates (95% credible intervals) for adult tree swallows from Nova Scotia (2000–2011; open diamonds) and New York (1995–2011; closed diamonds). Estimates were derived by Markov chain Monte Carlo simulation.

The best-approximating covariate model at New York included nonlinear effects of winter NAOI and explained ~17% of the temporal variance in Φ ($F_{1,12} = 2.43$, $p = 0.14$); the difference in AIC$_c$ from model $\{\Phi(.), p(t \times \text{sex})$ was 5.15 lower ($F_{1,12} = 2.43$, $p = 0.14$) and was 2.44 AIC$_c$ units less than a linear NAOI model. Parameters estimated with MCMC suggested weak nonlinear effects of winter climate ($\beta_{\text{NAOI}} = -0.192$ [95% credible interval $= -0.397$, 0.011], $\beta_{\text{NAOI}^2} = -0.080$ [-0.174, 0.018]). At Long Point, the longest time series, the best-approximating winter climate models explained ~13% of temporal variance ($F_{2,30} = 2.14$, $p = 0.13$). Models incorporating effects of BEST and NAOI were indistinguishable (Table 2) and covariate effects uncertain ($\beta_{\text{BEST}} = -0.014$ [-0.180, 0.156]; $\beta_{\text{NAOI}} = -0.024$ [-0.191, 0.137]). A model incorporating effects of winter NAOI explained ~9.5% of temporal variation at Mud Creek ($F_{2,17} = 0.88$, $p = 0.43$) and was 3.99 AIC$_c$ units less than model $\{\Phi(.), p(.)\}$. Corresponding covariate estimates were imprecise for nonlinear ($\beta_{\text{NAOI}} = 0.120$ [-0.102, 0.345]; $\beta_{\text{NAOI}^2} = 0.093$ [-0.057, 0.238]) and linear ($\beta_{\text{NAOI}} = 0.121$ [-0.103, 0.351]) patterns of NAOI effects.

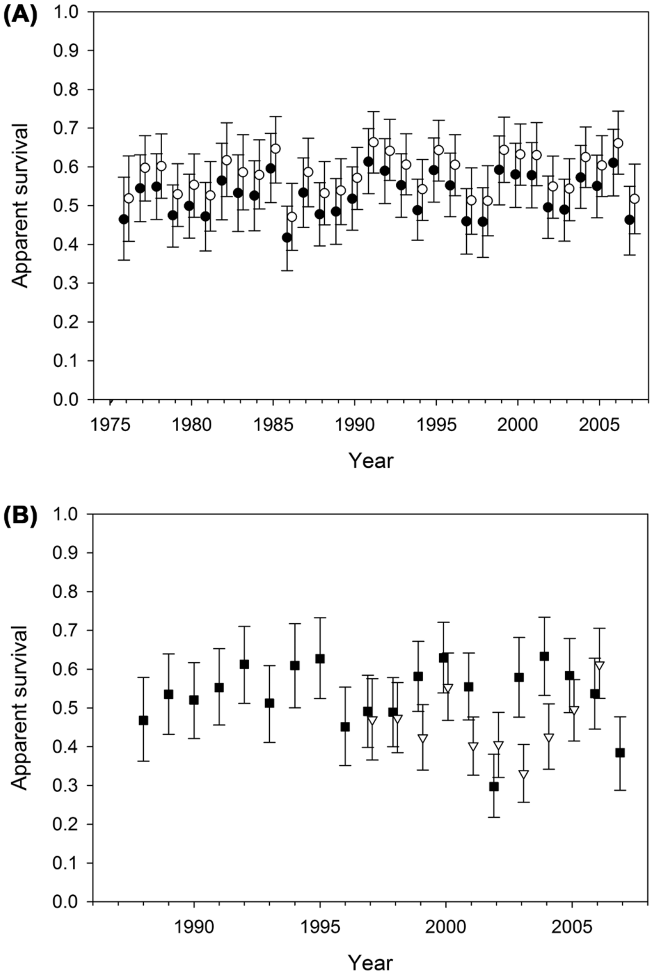

Figure 3. Estimates of annual apparent survival rates (95% credible intervals)) for adult female (closed circles) and male (open circles) tree swallows from Long Point (1975–2007) in (A), and adult swallows from Mud Creek (solid squares; 1987–2007), Ontario, and Michigan (open inverted triangles; 1996–2006) in (B). Estimates were derived by Markov chain Monte Carlo simulation.

At Saskatchewan, a model that allowed sexes to respond similarly to linear forms of three environmental covariates was most plausible among covariate models (Table 2, Fig. 5) and collectively explained 47% of temporal variation in Φ ($F_{4,14} = 3.13$, $p = 0.05$). Based on MCMC simulations, this model indicated that previous pond count had a positive effect on subsequent Φ ($\beta_{\text{Prev-Ponds}} = 0.138$ [0.020, 0.262]), whereas Φ was negatively related to amount of early spring precipitation ($\beta_{\text{SpringPrecip}} = -0.166$ [−0.292, −0.031]) and, possibly, winter NAOI ($\beta_{\text{NAOI}} = -0.112$ [−0.234, 0.014]). Models containing other covariates with linear or nonlinear terms received less support; the most plausible of these incorporated a linear effect of previous pond count (Table 2), which explained an estimated 26% of temporal variation in Φ ($F_{2,16} = 2.81$, $p = 0.09$), and a model with previous pond count and spring precipitation ($F_{3,15} = 2.30$, $p = 0.12$; 32% of temporal variation explained).

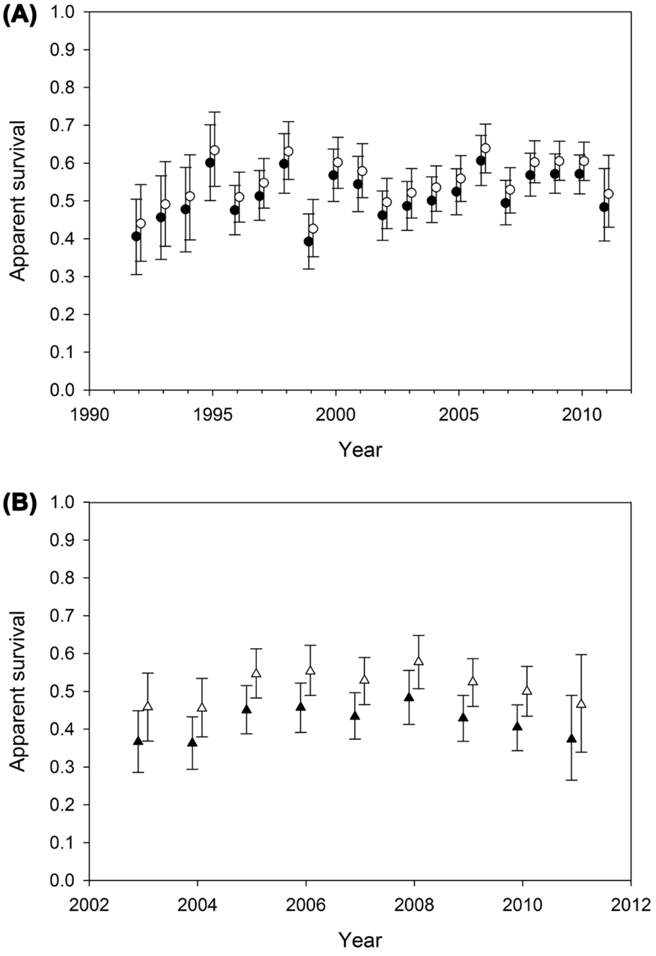

Figure 4. Estimates of annual apparent survival rates (95% credible intervals) for adult female (closed circles) and male (open circles) tree swallows from Saskatchewan (1991–2011) in (A), and for adult female (closed triangles) and male (open triangles) tree swallows from British Columbia in (B). Estimates were derived by Markov chain Monte Carlo simulation.

Discussion

Large-scale and generally unique patterns in apparent survival of adult tree swallows suggest that environmental conditions specific to local breeding populations may be strong drivers of demographic rates. These results are generally consistent with analyses showing that populations of tree swallows follow different trajectories over time across broad regions of North America (Michel et al. 2016). Winter climate conditions (or correlates of these conditions) were associated with only ~9–13% (NAOI) of temporal variation at the Ontario sites, yet as much as 66% (BEST) in British Columbia. García-Pérez et al. (2014) also reported that apparent survival of adult barn swallows *Hirundo rustica* was related to global climate indices at a breeding colony along the Pacific coast of Washington State but not among barn swallows nesting in southern Ontario. Apparent survival of purple martins *Progne subis* breeding near Lake Ontario was not associated with the mean annual Southern Oscillation Index values (Stutchbury et al. 2009). In some cases, we detected nonlinear relationships between climate indices and apparent survival. At New York, and possibly Nova Scotia, apparent survival tended to be higher during years with benign winter conditions and lower when the NAOI was strongly negative or positive, similar to relationships between the Southern Oscillation Index and apparent survival rates of female American redstarts *Setophaga ruticilla* (McKellar et al. 2015). Climate indices were related linearly to apparent survival at Saskatchewan (NAOI) and British Columbia (BEST), whereas climate–survival relationships at Ontario and Michigan were uncertain. Collectively, results of our work and others highlight that impacts of environmental factors on survival rates of resident and migratory songbirds are not necessarily consistent from site to site or across species (Salewski et al. 2013).

Survival rates of swallows are related to spring weather conditions, as suggested from reports of high mortality of adults during periods of inclement weather (Dence 1946, Weatherhead et al. 1985, Custer et al. 2012) and our precipitation results for Saskatchewan (Fig. 5). Custer et al. (2012) estimated survival of adult female tree swallows, and suggested that poor spring weather caused low female survival (0.29) in one of four years (range = 0.29–0.54). Low apparent survival observed at Mud Creek, Ontario, in 2002 and 2007 (Fig. 3B) probably resulted from severe cold periods that reduced aerial insect abundance at that site to a greater extent than at the Long Point site located along Lake Erie (DJTH unpubl.; also see Winkler et al. 2013). In contrast, Swiss populations of barn swallows separated by distances ranging from 19 to 224 km had very similar year-to-year patterns in adult apparent survival possibly due to close associations of these birds throughout the entire annual cycle (Schaub et al. 2015).

We were able to rigorously evaluate competing environmental covariate models at Saskatchewan using an MCMC simulation framework because of the rich capture–recapture data set with the largest effective sample size and relatively long time series (Fig. 1). Apparent survival was positively associated with pond abundance in the previous May (and, to a lesser extent, current May ponds; result not shown), which broadly reflects food supply or quality during the previous breeding season (Fast 2007, Twining et al. 2016), and possibly either lower survival costs of reproduction or reduced dispersal among breeding adult swallows. Higher precipitation in early spring as swallows arrived to this breeding site had adverse effects on survival. Large precipitation events in

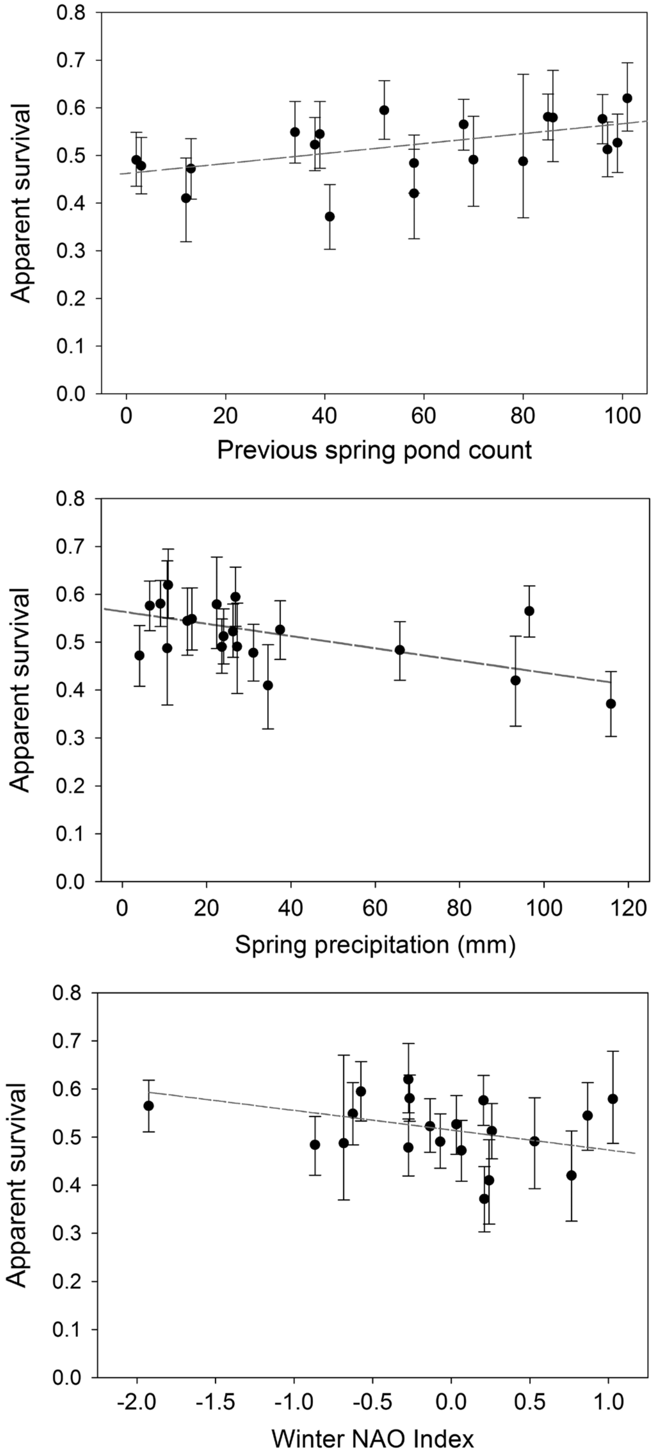

Figure 5. Estimates of annual apparent survival rates (95% credible intervals) for adult female tree swallows (closed circles) at Saskatchewan in relation to May pond count in the previous spring (top panel), total precipitation during early spring, from 20 April to 15 May (middle panel), and winter North Atlantic Oscillation Index (bottom panel). Estimates were derived by Markov chain Monte Carlo simulations. Predicted apparent survival rate for females, holding other covariates at their mean values (i.e. 0), is indicated with dashed lines. The linear equation was: apparent

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Figure 5. Continued

survival rate = 0.227 (intercept) – 0.149 (female sex effect) + 0.138 × (previous May ponds) – 0.166 × (spring precipitation) – 0.112 × (winter NOAI), and standard errors for each model term were 0.068, 0.057, 0.061, 0.066, 0.062, respectively. For ease of interpretation, estimates are plotted against observed (i.e. unstandardized) environmental covariate values. Apparent survival for adult males is ~0.04 greater than each female estimate (not shown).

late April and early May often produce snowfall, lowering food availability and even causing direct mortality (RGC unpubl.). While less certain, negative effects of winter NAOI suggested that survival is higher during drier, cooler winters when fewer storms occur along the Atlantic coast of North America. Although local conditions directly and indirectly affecting food supply at the Saskatchewan breeding site had somewhat stronger effects than NAOI, effects of winter climate conditions were evident at several sites.

Some of our most intriguing results involved remarkably low estimates of apparent survival rates for adult swallows at sites in Nova Scotia and New York in several years (Fig. 2), and consistently low female apparent survival rates compared with males in British Columbia (Fig. 4). Overall, low apparent survival rates at Nova Scotia during the mid-2000s mirrored a general temporal pattern observed in New York. Nest box occupancy rates at Nova Scotia and New York (Shutler et al. 2012) were positively correlated (Ps < 0.02) with respective apparent survival estimates in the preceding year at these two sites but not the others (RGC unpubl.). Although low adult survival rates could contribute to population declines reported in northeastern North America (Nebel et al. 2010), we caution that population change could also result from temporal changes in first-year survival, dispersal, or reproductive rates (Szép 1995, Siriwardena et al. 1999, Weegman et al. 2017). For instance, if reproductive failure provokes dispersal to nests located outside our study sites (Winkler et al. 2004, Lagrange et al. 2017), apparent survival estimates would be biased downward.

One of the most important confounds of survival rate estimates based on live recaptures is permanent emigration. When a bird fails to return, it could have died or left the study area to breed elsewhere and our global analysis indicated that breeding dispersal may be more common among females than males. In British Columbia, females usually had much lower apparent survival rates than did males, and these estimates for females also were generally lower than corresponding rates from other locations except Nova Scotia. We suspect that this difference did not arise from higher emigration rates by females in British Columbia because there was almost no evidence of temporary emigration (i.e. one-year absences) for any individuals of either sex in this population (RDD unpubl.). Still, breeding female swallows, as in other passerines, are more likely to disperse to other breeding sites than males (Winkler et al. 2004, Schaub et al. 2015), and the area around the British Columbia study site has natural cavities available in local woodland edges. Alternatively, low female survival at this site could reflect challenging environmental conditions that females encounter during the breeding season. Only female swallows incubate eggs, and the mountainous British Columbia location receives abundant spring–summer rainfall and cool temperatures compared with other study sites (Dawson 2008), and typically produces lower aerial insect biomass compared with the Saskatchewan site (Bortolotti et al. 2011, Harriman et al. 2017). Also, swallows at this site seemed susceptible to cold, wet conditions on wintering areas, as inferred from the negative relationship between BEST and survival of both males and females from British Columbia. García-Pérez et al. (2014) also reported a negative relationship between BEST and apparent survival of barn swallows in Seattle, Washington.

Annual variation in apparent survival was characteristic of all sites (Table 2) which may reflect variability in food abundance among years within sites as well as food resource differences (Dunn et al. 2011) during the annual cycle. We cannot determine the extent to which our findings reflect differences in true survival versus permanent emigration (Cilimburg et al. 2002), although we argue above that females in British Columbia may incur more severe costs of reproduction via lower survival rather than exhibit higher dispersal rates (Schaub and von Hirschheyd 2009). Variation in recapture estimates may be related to site variation in capture effort and success, availability of nest boxes and natural nest cavities, and ability of swallows to disperse between natural and artificial nests (Shutler and Clark 2003, Winkler et al. 2004, 2011), or in the case of males their presence during the breeding season as floaters (Kempenaers et al. 2001). Although we cannot rule out the possibility that banded adult swallows began to vacate the Nova Scotia (or New York) site during the mid-2000s, producing a false pattern of low adult survival, we have no biological or methodological explanation for why this would have occurred and only at this site.

Estimates of demographic rates and information about seasonal migrations and connectivity are critical for developing integrated models that may be used to evaluate hypotheses about key drivers of population dynamics, and identify information gaps, conservation actions, and research needs (Schaub and Abadi 2011, Weegman et al. 2017). Further work should address environmental correlates of spatiotemporal variation in other demographic rates, attempt to distinguish bird movements from mortality, and improve estimates of season-specific survival (Paxton et al. 2017). Temporal variation in apparent survival rates was clearly evident overall, and in the best-supported models at most sites (Table 2). Apparent survival rates are related to local weather conditions during the pre-breeding period, as shown previously, and these conditions presumably vary independently among our widely-separated sites. That these swallow populations respond differently to specific climatic covariates indicates that it may be unwise to extrapolate climate relationships from one local population to another. Recent results of movement analyses obtained with light-level geolocator data (Laughlin et al. 2013, Knight et al. 2018) will further refine our understanding of the environmental conditions that are most relevant to swallows from each of the study populations throughout their distinctive annual cycles of movement.

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Permits – Work on swallows at all study populations was approved by institutional animal care committees, and conformed with animal use regulations and laws of Canada and the USA.

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Supplementary material (Appendix JAV-01659 at <www.avianbiology.org/appendix/jav-01659>). Appendix 1.