Breeding phenology and performance for four swallows over 57 years: relationships with temperature and precipitation

Tara L. Imlay [ID],[1],† Joanna Mills Flemming,[2] Sarah Saldanha,[1]
Nathaniel T. Wheelwright,[3] and Marty L. Leonard[1]

[1]*Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4R2 Canada*
[2]*Department of Mathematics and Statistics, Dalhousie University, Halifax, Nova Scotia B3H 4R2 Canada*
[3]*Department of Biology, Bowdoin College, Brunswick, Maine 04011 USA*

Abstract.   Climate change can drive population declines for many species, often through changes to their food supply. These changes can involve a mis-timing between periods of high food demand and peak food availability, typically from advances in breeding phenology, and/or an overall reduction in food availability. Aerial insectivores, birds that feed on insects caught in flight, are experiencing steep population declines possibly because of shifts in the timing and/or abundance of aerial insects. We determined whether changes in breeding performance over time could account for declines in Bank *Riparia riparia*, Barn *Hirundo rustica*, Cliff *Petrochelidon pyrrhonota,* and Tree *Tachycineta bicolor* Swallows, and if so, whether changes were related to shifts in breeding phenology and/or climate change. We compared breeding performance and phenology in Maritime Canada before (1962–1972) and after (2006–2016) the onset of steep population declines during the mid-1980s, to determine whether breeding performance was reduced or phenology was advanced. Then, we modeled relationships between temperature, precipitation, breeding phenology, and performance for Barn and Tree Swallows, the only species with sufficient data, from 1960 to 2016, to determine whether phenology and performance were related to climatic conditions. Between the two time periods, we found significantly lower performance in Bank Swallows, higher performance in Barn and Tree Swallows, and unchanged performance in Cliff Swallows. We also found clutch initiation dates advanced by 8–10 d for all species except Bank Swallows. On the breeding grounds, warmer winter temperatures for Tree Swallows and less winter precipitation for Barn and Tree Swallows in a given year were associated with earlier breeding, and for Tree Swallows, changes in nestling survival. Otherwise, Barn and Tree Swallow breeding performance was unaffected by winter temperature and precipitation. Our results suggest that in this region poorer breeding performance could contribute to population declines for Bank Swallows but not for the other three species.

Key words: citizen science; climate change; *Hirundo rustica;* historical ecology; insect availability; *Petrochelidon pyrrhonota;* reproductive success; *Riparia riparia; Tachycineta bicolor.*

† **E-mail:** tara.imlay@gmail.com

INTRODUCTION

Climate change has altered weather patterns across the planet, from gradual warming trends (Hayhoe et al. 2007, Hartmann et al. 2013) to temperature and precipitation extremes that result in worsening droughts, heavier rainfall, reduced snow cover, and more frequent and intense storms (Easterling et al. 2000, Hayhoe et al. 2007, Levinson and Bromirski 2007, Hartmann et al. 2013).

Changes to weather patterns have wide-reaching impacts on the population dynamics and persistence of many taxa. These effects can include changes in species distributions, predator–prey interactions, demography, and phenology (reviewed in McCarty 2001, Walther et al. 2002, Crick 2004, Parmesan 2006, Selwood et al. 2015).

One well-documented effect of warmer spring temperatures is a change in avian breeding phenology (i.e., the timing of breeding). Birds of a variety of species are arriving on the breeding grounds and nesting earlier than in the past (Dunn and Winkler 1999, Butler 2003, Sanz 2003, Donnelly et al. 2009, Townsend et al. 2013), which in turn can affect breeding performance (Dunn and Møller 2014). For some species, early breeding results in more young fledged (Møller 2008, Vatka et al. 2011), higher nestling mass (Vatka et al. 2011), and increased rates of double-brooding (i.e., raising two or more broods each year, Townsend et al. 2013). In most species, however, early breeding results in poor nestling body condition, lower nestling survival, and reduced rates of double-brooding (Visser et al. 2006, Both et al. 2009, Husby et al. 2009). The effects of early breeding are often mediated through a shift in food availability, especially for species that largely exploit a single prey item during breeding (Visser et al. 2006, Both et al. 2009, Husby et al. 2009, Vatka et al. 2011). Specifically, reduced food supply during breeding, from a mismatch between peak food abundance and peak food demand or an overall reduction in food abundance, results in lower performance and in turn drives population declines and increased risk of extinction (Both et al. 2006, Møller et al. 2008).

Aerial insectivores, including swallows (Hirundinidae), swifts (Apodidae), nightjars (Caprimulgidae), and tyrant flycatchers (Tyrannidae), experienced severe and widespread population declines beginning in the mid-1980s in North America, particularly so in the northeast (Nebel et al. 2010, Shutler et al. 2012, Smith et al. 2015, but see Michel et al. 2016). Although the causes of the declines are unknown, like many other species, aerial insectivores face a variety of shared threats, including habitat loss, pesticides, pollution, road mortality, and climate change (Nebel et al. 2010). The latter threat, in particular, is a likely driver of these declines, because the rapid warming trend in North America (e.g.,

mid-1970s) began in close proximity to population declines (Hansen et al. 2006, National Research Council 2007). Given their common food source, one way that climate change might drive declines is by shifting the timing or abundance of aerial insects (Shutler et al. 2012).

Warmer temperatures are linked to both earlier first emergence and timing of peak abundance for a variety of insects (Visser et al. 2006, Bartomeus et al. 2011, Brooks et al. 2014, Kharouba et al. 2014). In addition, changes in winter temperature and precipitation also affect the annual abundance and diversity of insects (Finn and Poff 2008, Templer et al. 2012). In turn, reductions in insect availability during breeding have been repeatedly associated with lower reproductive performance in the Tree Swallow, as measured by decreased clutch sizes, fewer fledglings, and reduced nestling body condition (Quinney et al. 1986, Hussell and Quinney 1987, McCarty and Winkler 1999, Nooker et al. 2005).

Although decreased breeding performance can contribute to population declines in aerial insectivores (Ambrosini et al. 2011), there is little information on whether breeding performance has declined during the period of population declines. While earlier breeding appears related to warmer spring temperatures (Dunn and Winkler 1999, Butler 2003, Sparks and Tryjanowski 2007, Møller 2008, 2011, but see Hussell 2003), it is not clear whether early breeding could negatively affect performance. It is also unclear whether these patterns are consistent across species, suggesting a common driver of decline. Thus, research investigating changes in breeding performance before and after the onset of steep population declines is needed to determine whether the declines result from reduced breeding performance, and if so, whether changes in breeding phenology and climatic conditions could contribute to changes in performance.

Here we take a comparative, multi-species approach to determine whether changes in breeding phenology and performance (i.e., clutch size, brood size, and nestling survival) over time could account for declines in Bank *Riparia riparia,* Barn *Hirundo rustica,* Cliff *Petrochelidon pyrrhonota,* and Tree Swallows *Tachycineta bicolor* in the Maritime provinces of Canada, an area where aerial insectivores have experienced steep declines (Sauer et al. 2014). The climate in this region has changed since the mid-1900s, with increases in annual

temperature, particularly during the winter, and rainfall, and decreases in snowfall and snow depth (Mekis and Vincent 2011, Vincent et al. 2012, 2015), and thus could be implicated in the observed population declines. To determine whether there have been changes in breeding phenology and performance over time, we used historical data to compare each before (1962–1972) and after (2006–2016) the onset of steep population declines (i.e., during the mid-1980s, Nebel et al. 2010, Smith et al. 2015). Although the population trends during the before period are unknown, it is clear that populations of all four species were larger during the before period than during the after period (Sauer et al. 2014, A. C. Smith, *personal communication*). To help inform our understanding of the potential effect of climate change on population declines, we also related temperature and precipitation, two variables known to affect performance in aerial insectivores (McCarty and Winkler 1999, Ambrosini et al. 2011, Winkler et al. 2013), on the breeding grounds to breeding phenology and performance from 1960 to 2016 in Barn and Tree Swallows, the two species with adequate data. Our comparative, multi-species approach allows us to determine whether there is a common pattern across species, which could help to explain declines in aerial insectivores as a larger group.

MATERIALS AND METHODS

We compiled most of the Bank, Barn, Cliff, and Tree Swallow nest-monitoring information from historical nest-monitoring data (1960–2013) found in the Maritime Nest Records Scheme (MNRS). MNRS volunteers in New Brunswick and Nova Scotia recorded data on the number of eggs and nestlings in the nests of all four species during one or more nest checks over the breeding season. We also included nest-monitoring data for Tree Swallows from two long-term study sites on Kent Island, New Brunswick (1987–2006; Wheelwright and Schultz 1994) and near Wolfville, Nova Scotia (1988–1990, 1994–2013; Leonard and Horn 1996), and for all four species from several sites around Sackville, New Brunswick (2014–2016; Saldanha 2016, Imlay et al. 2017). At these latter sites, nests were typically checked every 1–3 d during the breeding season.

From the monitoring data, we recorded two variables that relate to breeding phenology (clutch initiation and hatching dates) and five variables that represent different components of breeding performance (clutch size, brood size, hatching success [whether or not at least one egg hatched], nestling survival [the number of surviving nestlings], and nest success [whether or not at least one young survived]). We applied several decision rules to ensure that these variables were consistently recorded (see Appendix S1 for details). Ultimately, we had at least one phenology or performance variable for 689 Bank, 2177 Barn, 687 Cliff, and 4515 Tree Swallow breeding records. See Fig. 1 for the spatial and temporal distribution of breeding records.

Changes in breeding phenology and performance

We compared breeding phenology and performance for the four species between two time periods: 1962–1972 and 2006–2016. Our comparisons were across two periods rather than continuous because the data for Bank and Cliff Swallows were concentrated in the earlier and later years (Fig. 1). We used linear regressions to compare clutch initiation dates (up to and including the median clutch initiation date for each year; see Appendix S1) to compare phenology for all four species from 1962–1972 to 2006–2016. We also used generalized linear models with a zero-truncated poisson distribution (for clutch size, brood size, and nestling survival in successful nests) or binomial distribution (for hatching and nest success) to compare performance for all four species from 1962–1972 to 2006–2016.

Effects of climate on Barn and Tree Swallow phenology and performance

We examined the effect of climatic variables on Barn and Tree Swallow breeding phenology and performance over the 57-yr time-span. Comparable data for Bank and Cliff Swallows were not available and so these species are excluded from the following analyses. For this analysis, we modeled the relationships between climate and swallow breeding phenology and performance.

First, using ArcGIS version 10.3.1, we identified the closest weather station within an arbitrarily selected distance of 50 km (19.1 km $\pm$ 0.15 SE) of each breeding record with temperature and precipitation data. We retrieved temperature and precipitation data from Environment and Climate Change Canada: http://climate.weather.gc.ca/
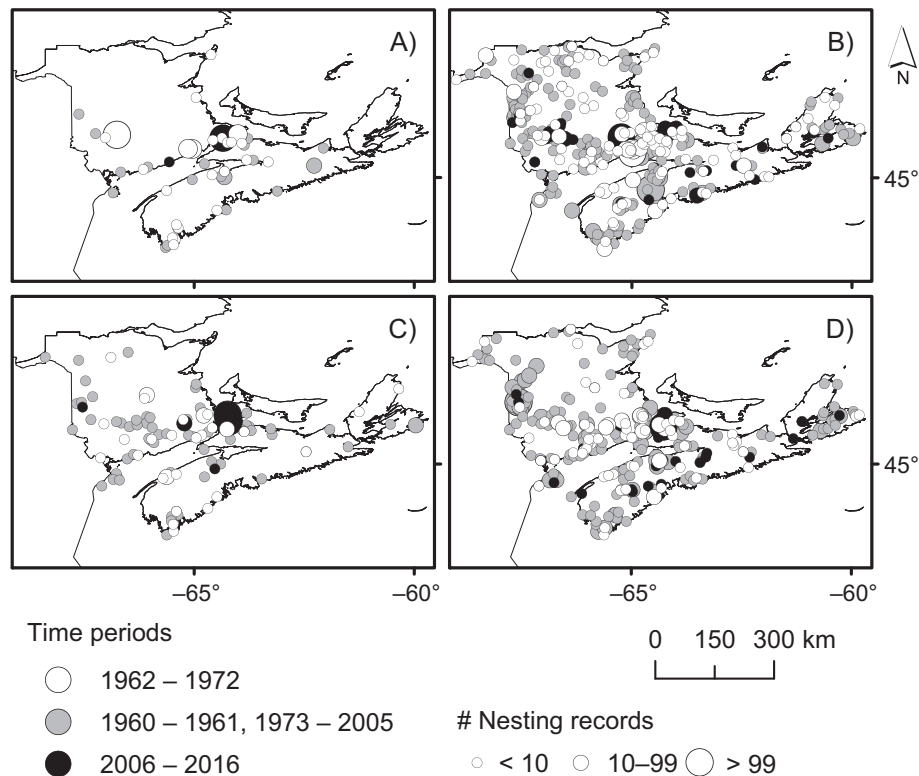
Fig. 1. Temporal and spatial distribution of nest records for Bank, Barn, Cliff, and Tree Swallows where at least one variable of breeding phenology and breeding performance could be identified. Breeding records within 5 km and during the same period of time are represented by a single point on this map.

index_e.html. When temperature and precipitation data were not available from the same weather station (314 of 6692 breeding records), we used data from the two closest stations within 50 km. We excluded 320 nest records from our analyses because temperature (86) and precipitation (234) data were not available.

Although many studies examine the relationship between spring temperatures and breeding phenology (e.g., Dunn and Winkler 1999, Hussell 2003), recent work has also demonstrated that winter temperature can affect breeding phenology and performance of insectivorous birds (Williams et al. 2015). This is likely due to the effects of temperature and/or precipitation on overwinter insect survival and development (Irwin and Lee 2000, Musolin and Saulich 2012, Templer et al. 2012). Our exploratory data analysis suggested that minimum temperature and/or median precipitation over short periods of time throughout the winter were most predictive of breeding

phenology for Barn and Tree Swallows. Therefore, we determined minimum temperature and median precipitation across six consecutive 14-d windows (e.g., 1–14 January, 15–28 January) from 1 January to 25 March for all breeding records from 1960 to 2016 with weather data, resulting in 12 weather variables. Then, to reduce the number of weather variables, we conducted a principal components analysis with the centered and scaled weather variables. We identified four principal components with eigenvalues ≥1.0 (Table 1) to include in our models below (Norman and Streiner 1994). In general, loadings for these principal components indicated that the first (PC1) was related to temperature, with higher values indicating colder temperatures, and the remaining three (PC2, PC3, and PC4) were related to precipitation at different times during the winter, with higher values indicating less precipitation.

Next, to determine the best-fitting models to explain the potential effects of winter temperature

Table 1. Results of a principal components analysis for temperature and precipitation variables.

Variables	PC1	PC2	PC3	PC4
T1	**−0.38**	0.20	−0.02	0.06
T2	**−0.42**	0.12	−0.01	−0.17
T3	**−0.42**	−0.08	0.10	−0.01
T4	**−0.39**	0.12	−0.10	−0.06
T5	**−0.38**	−0.23	0.09	0.07
T6	**−0.40**	0.11	0.11	−0.09
P1	−0.17	**−0.54**	−0.16	0.21
P2	−0.08	−0.19	**−0.62**	0.07
P3	−0.05	0.15	**−0.53**	0.46
P4	0.03	0.05	−0.44	**−0.80**
P5	−0.02	**−0.66**	0.17	−0.22
P6	−0.09	**0.28**	0.18	−0.01
Eigenvalue	3.77	1.35	1.15	1.04
Variance	0.31	0.11	0.10	0.09
Cumulative variance	0.31	0.43	0.52	0.61

Notes: The first four principal components (PC1-4) had eigenvalues >1.0 and were used to model the relationships between Barn and Tree Swallow breeding phenology and performance. Bolded values indicate the highest loading for each variable.

T1, 1 to 14 January; T2, 15 to 28 January; T3, 29 January to 11 February; T4, 12 to 25 February; T5, 26 February to 11 March; T6, 12 to 25 March.

and precipitation on Barn and Tree Swallows breeding phenology and performance, we used a linear regression (clutch initiation date) or generalized linear model with a poisson distribution (clutch size, brood size, and nestling survival). Our full models included all four principal components identified above, year, latitude, and longitude, and, for models with different measures of breeding performance as the response variable (clutch size, brood size, and nestling survival), we included clutch initiation date to account for seasonal declines in breeding performance (Møller 1994, Wardrop and Ydenberg 2003, Dawson 2008). Finally, we included an interaction between data source (a categorical variable that identified the data as from the MNRS or a long-term study) and year to account for changes in breeding performance that could be attributed to the different sources of data. This interaction was only included in our initial models for Barn Swallow brood size and nestling survival (Appendix S1: Tables S1, S2). Graphical inspection of the results suggested that the inclusion of this term was due to smaller broods and lower nestling survival in one year (2016) of the three-year period when long-term data were available (Appendix S1:

Fig. S1). Since this result contrasted with our comparisons of the long-term data from 1962–1972 and 2006–2016 (Appendix S1: Table S2) and appeared to be driven by a single year, our results for these two response variables below only include data from the MNRS.

Finally, we centered and scaled all continuous explanatory variables (i.e., year, latitude, longitude, and clutch initiation date) in our models (Grueber et al. 2011), and then modeled all possible combinations of the variables included in the full model, as well as a null model without covariates. The best-fitting model was determined using Akaike's information criterion with the small sample size correction, AIC_c, and by examining the AIC_c weight, w_i (Burnham and Anderson 2002). Since many of the top models ($\Delta AIC_c \leq 2.0$) were similar, we averaged all models with a $\Delta AIC_c \leq 2.0$ to determine our parameter estimates and the relative importance of each variable. We were interested in the variables that had the greatest effect on our response, and therefore, we used the zero method for model averaging (Nakagawa and Freckleton 2011). We restrict our interpretation of these models to explanatory variables with a significant effect on the response (i.e., those variables with 95% confidence intervals that do not span zero). All analyses were performed in R version 3.4.2 (R Core Team 2017) using MuMIn version 1.40.0.

RESULTS

Changes in breeding phenology and performance

Bank Swallows initiated clutches at similar times in 2006–2016 compared to 1962–1972, whereas Barn, Cliff, and Tree Swallows initiated clutches 9.9, 8.1, and 10.4 d earlier in 2006–2016, respectively (Table 1).

Breeding performance was lower for Bank Swallows and higher for Barn and Tree Swallows in 2006–2016 compared to 1962–1972, and largely unchanged for Cliff Swallows (Table 2). These results are detailed below by each component of breeding performance.

Clutch sizes for Bank and Tree Swallows differed significantly between 1962–1972 and 2006–2016, with a decrease of 0.5 eggs/clutch for Bank Swallows and an increase of 0.5 eggs/clutch for Tree Swallows in the more recent period compared to the earlier period. Clutch sizes did not

Table 2. Comparisons of the breeding phenology and performance of Bank, Barn, Cliff, and Tree Swallows between two time periods, 1962–1972 and 2006–2016 using linear and generalized linear models.

Species	Time period	Clutch initiation date†	Clutch size	Brood size‡	Nestling survival‡	Hatching success	Nest success
Bank	1962–1972	39.0 ± 7.3 (25)	4.7 ± 0.7* (107)	4.4 ± 0.8*** (117)	4.1 ± 1.0*** (81)	95.6%*** (275)	78.8%*** (137)
	2006–2016	40.6 ± 2.9 (143)	4.2 ± 1.0 (291)	3.3 ± 1.0 (215)	2.9 ± 1.0 (165)	69.5% (325)	59.9% (284)
Barn	1962–1972	38.7 ± 6.6*** (88)	4.6 ± 1.0 (350)	4.4 ± 0.9 (270)	4.2 ± 1.1 (86)	91.7%*** (630)	60.3%** (156)
	2006–2016	28.8 ± 4.2 (190)	4.6 ± 1.0 (427)	4.3 ± 1.1 (304)	4.1 ± 1.1 (274)	79.4% (467)	72.7% (395)
Cliff	1962–1972	40.9 ± 3.2*** (28)	3.7 ± 0.9 (114)	3.1 ± 1.0 (47)	–	89.4%*** (180)	44.4% (45)
	2006–2016	32.8 ± 4.3 (133)	3.5 ± 0.9 (294)	3.1 ± 1.0 (132)		62.8% (290)	41.2% (221)
Tree	1962–1972	30.4 ± 6.0*** (68)	5.0 ± 1.2** (186)	4.6 ± 1.1** (160)	4.3 ± 1.4* (64)	93.4%** (286)	77.9% (95)
	2006–2016	20.0 ± 4.9 (449)	5.5 ± 1.0 (973)	5.2 ± 1.1 (777)	4.9 ± 1.2 (531)	86.3% (955)	74.6% (721)

Notes: Mean values are presented with SD and sample size in brackets below. Asterisks were used to indicate significant differences between time periods (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

† May 1 = day 1.

‡ Only data from successful nests are included in calculations of brood size and nestling survival.

differ significantly for Barn and Cliff Swallows between these time periods.

Hatching success for all species differed between 1962–1972 and 2006–2016, with decreases in hatching success in the later period for Bank (26.1%), Barn (12.3%), Cliff (26.6%), and Tree Swallows (7.1%) compared to the earlier period. For successful nests, brood size also differed significantly between 1962–1972 and 2006–2016, with a decrease of 1.1 nestlings/clutch for Bank Swallows and an increase of 0.6 nestlings/clutch for Tree Swallows in the later period compared to the earlier period. Broods sizes did not differ significantly for Barn and Cliff Swallows between periods.

Nest success also differed significantly between the two periods for Bank and Barn Swallows, with an 18.9% decrease in nests that had at least one surviving young for Bank Swallows and a 12.4% increase in nests with at least one surviving young for Barn Swallows in 2006–2016 compared to the earlier time period. Nest success did not differ significantly for the remaining species between these periods. Finally, for successful nests, nestling survival differed between 1962–1972 and 2006–2016, with a decrease of 1.2 nestlings/clutch for Bank Swallows and an increase of 0.6 nestlings/clutch for Tree Swallows in the later period compared to the earlier period. Survival did not differ significantly for Barn Swallows between these periods, and we were unable to analyze the data for Cliff Swallows due to the small sample size in 1962–1972 ($n = 9$).

Effects of climate on Barn and Tree Swallow phenology and performance

All of our top models for Barn and Tree Swallow breeding phenology included precipitation for both species, and, for Tree Swallows, temperature (Tables 3, 4). Model-average coefficients indicate that both species bred earlier after winters with less precipitation, and, for Tree Swallows, after warmer winters (Tables 5, 6).

Although temperature and precipitation were included in several top models for Barn and Tree Swallows breeding performance (Tables 3, 4), neither clutch size or brood size for both species, nor nestling survival for Barn Swallows were affected by temperature or precipitation (Tables 5, 6). However, for Tree Swallows, model-averaged coefficients indicate that nestling survival was higher after colder winters. Also, Tree Swallows nestling survival was both positively and negatively related to wintering precipitation during different periods during the winter.

In addition to the relationships with weather, we also found a negative relationship between clutch initiation date and year for both swallows (Table 5), with swallows breeding earlier in recent years. Also, for Barn Swallows, there were positive relationships between nestling survival and year, indicating an increase in nestling survival. This corroborates our previous analysis comparing changes in clutch initiation dates for both species and nest success for Barn Swallows between 1962–1972 and 2006–2016. Clutch initiation dates were negatively related to clutch size

Table 3. Model selection table for the best-fitting models for the relationships between temperature and Barn Swallow breeding phenology and performance.

Response variable	Model†‡	df	AIC_c	ΔAIC_c	w_i	Log likelihood
Clutch initiation date	Latitude + Longitude + PC2 + Year	6	1906.81	0.00	0.09	−947.27
	Latitude + Longitude + PC1 + PC2 + Year	7	1907.50	0.69	0.06	−946.56
	Latitude + PC2 + Year	5	1907.64	0.83	0.06	−948.72
	PC1 + PC2 + Year	5	1907.89	1.08	0.05	−948.85
	Latitude + PC1 + PC2 + Year	6	1908.36	1.55	0.04	−948.04
	Longitude + PC1 + PC2 + Year	6	1908.40	1.59	0.04	−948.06
	Latitude + Longitude + PC2 + PC4 + Year	7	1908.68	1.87	0.04	−947.16
Clutch size	CID	2	1811.05	0.00	0.04	−903.51
	CID + Longitude	3	1812.16	1.11	0.02	−903.05
	CID + PC4	3	1812.40	1.35	0.02	−903.18
	CID + Source	3	1812.51	1.46	0.02	−903.23
	CID + PC4 + Source	4	1812.58	1.52	0.02	−902.25
	CID + Latitude	3	1812.72	1.67	0.02	−903.34
	CID + PC3	3	1812.93	1.88	0.01	−903.44
	CID + PC1	3	1813.04	1.99	0.01	−903.50
Brood size	Latitude	2	1223.55	0.00	0.04	−609.75
	Latitude + Year	3	1224.02	0.47	0.03	−608.97
	Latitude + PC1 + Year	4	1224.68	1.13	0.02	−608.27
	Null	1	1224.85	1.30	0.02	−611.42
	CID + Latitude	3	1224.95	1.40	0.02	−609.43
	Latitude + PC3	3	1225.07	1.52	0.02	−609.49
	Latitude + PC3 + Year	4	1225.24	1.69	0.02	−608.55
	Latitude + PC4	3	1225.50	1.95	0.02	−609.71
	Latitude + PC1	3	1225.53	1.99	0.02	−609.73
Nestling survival	PC3 + Year	3	948.58	0.00	0.04	−471.23
	Year	2	948.62	0.04	0.04	−472.28
	PC2 + PC3 + Year	4	949.41	0.83	0.03	−470.61
	PC2 + Year	3	949.60	1.02	0.03	−471.74
	Latitude + PC1 + PC3 + Year	5	949.74	1.16	0.02	−469.73
	Latitude + PC1 + PC2 + PC3 + Year	6	949.85	1.27	0.02	−468.72
	Latitude + PC3 + Year	4	949.96	1.38	0.02	−470.88
	Latitude + PC1 + Year	4	950.18	1.60	0.02	−470.99
	Latitude + Year	3	950.18	1.60	0.02	−472.03
	PC4 + Year	3	950.30	1.72	0.02	−472.09
	PC3 + PC4 + Year	4	950.40	1.82	0.02	−471.10
	Longitude + PC3 + Year	4	950.40	1.83	0.02	−471.11
	PC1 + Year	3	950.57	1.99	0.02	−472.23
	PC1 + PC3 + Year	4	950.57	1.99	0.02	−471.19

Note: Only models within $\Delta AIC_c \leq 2.0$ of the top model are displayed.
† PC1-4 represents principal components 1–4 identified in Table 1.
‡ Source was a categorical variable representing data that were collected as part of the Maritime Nest Records Scheme or long-term monitoring projects.

for both species, and, for Tree Swallows, brood size and nestling survival, indicating higher performance with earlier breeding.

Discussion

The goal of our study was to determine whether changes in breeding performance over time, potentially as a result of changes in breeding phenology and climate change, could explain population declines for four swallows. We found changes in at least one measure of breeding performance for all species, but only Bank Swallows had consistently lower breeding performance in all components, particularly fewer nests fledgling young and lower nestling survival, that

Table 4. Model selection table for the best-fitting models for the relationships between temperature and Tree Swallow breeding phenology and performance.

Response variable	Model[†] [‡]	df	AIC_c	ΔAIC_c	w_i	Log likelihood
Clutch initiation date	PC1 + PC3 + Source + Year	6	6653.77	0.00	0.08	−3320.85
	Latitude + PC1 + PC3 + Source + Source:Year + Year	8	6654.15	0.38	0.06	−3319.01
	PC1 + PC3 + Source + Source:Year + Year	7	6654.31	0.54	0.06	−3320.10
	PC1 + PC3 + PC4 + Source + Year	7	6654.46	0.69	0.05	−3320.18
	Latitude + Source + PC1 + PC3 + Year	7	6654.46	0.69	0.05	−3320.18
	PC1 + PC3 + PC4 + Source + Source:Year + Year	8	6654.68	0.91	0.05	−3319.28
	Longitude + PC1 + PC3 + Source + Year	7	6655.01	1.23	0.04	−3320.45
	Latitude + PC1 + PC3 + PC4 + Source + Source:Year + Year	9	6655.08	1.31	0.04	−3318.46
	Latitude + PC1 + PC3 + PC4 + Source + Year	8	6655.57	1.80	0.03	−3319.72
	Longitude + PC1 + PC3 + PC4 + Source + Year	8	6655.71	1.94	0.03	−3319.79
	Latitude + Longitude + PC1 + PC3 + Source + Year	8	6655.73	1.95	0.03	−3319.80
Clutch size	CID	2	7026.48	0.00	0.07	−3511.24
	CID + PC2	3	7028.21	1.73	0.03	−3511.10
	CID + Source	3	7028.26	1.78	0.03	−3511.12
	CID + PC1	3	7028.28	1.80	0.03	−3511.13
	CID + Year	3	7028.28	1.80	0.03	−3511.13
	CID + Longitude	3	7028.31	1.83	0.03	−3511.15
	CID + PC4	3	7028.33	1.86	0.03	−3511.16
	CID + Latitude	3	7028.35	1.87	0.03	−3511.17
Brood size	CID + Source + PC1 + PC2	5	7682.25	0.00	0.04	−3836.11
	CID + Source + PC2	4	7683.00	0.75	0.02	−3837.49
	CID + Source + PC2 + PC4	5	7683.07	0.82	0.02	−3836.52
	CID + Source + PC1 + PC2 + PC4	6	7683.22	0.98	0.02	−3835.59
	CID + Longitude + Source + PC2	5	7683.55	1.30	0.02	−3836.76
	CID + Longitude + Source + PC1 + PC2	6	7683.66	1.41	0.02	−3835.81
	CID + Longitude + Source + PC2 + PC4	6	7683.85	1.60	0.02	−3835.90
	CID + Source + PC4	4	7683.90	1.65	0.02	−3837.94
	CID + Source	3	7684.02	1.77	0.01	−3839.00
	CID + Latitude + Source + PC1 + PC2	6	7684.09	1.85	0.01	−3836.02
	CID + Source + PC1 + PC2 + Year	6	7684.20	1.96	0.01	−3836.08
	CID + Source + PC1 + PC2 + PC3	6	7684.23	1.98	0.01	−3836.09
Nestling survival	CID + Source + PC1 + PC2	7	6522.74	0.00	0.09	−3254.33
	CID + Source + PC2	6	6522.78	0.05	0.09	−3255.36
	CID + Source + PC2 + PC4	7	6524.27	1.53	0.04	−3255.09
	CID + Source + PC1 + PC2 + PC4	5	6524.30	1.56	0.04	−3257.13
	CID + Longitude + Source + PC2	7	6524.41	1.68	0.04	−3255.17
	CID + Longitude + Source + PC1 + PC2	8	6524.49	1.76	0.04	−3254.20
	CID + Longitude + Source + PC2 + PC4	6	6524.52	1.78	0.04	−3256.23
	CID + Source + PC4	8	6524.69	1.95	0.03	−3254.29
	CID + Source	9	6524.71	1.98	0.03	−3253.29

Note: Only models within $\Delta AIC_c \leq 2.0$ of the top model are displayed.

† PC1-4 represents principal components 1–4 identified in Table 1.

‡ Source was a categorical variable representing data that were collected as part of the Maritime Nest Records Scheme or long-term monitoring projects.

could contribute to population declines. We also found that there was no change in the timing of Bank Swallow breeding in 2006–2016 compared to 1962–1972; in contrast, Barn, Cliff, and Tree Swallows were breeding 8–10 d earlier. Finally, for Barn and Tree Swallows, earlier breeding phenology was related to warmer winter temperatures, and, for Tree Swallows, higher nestling survival was associated with colder winter temperatures and changes in winter precipitation.

Only the Bank Swallow showed a consistent decrease in breeding performance across all five

Table 5. Model coefficients, SE, and 95% confidence intervals (CI) for the best-fitting models explaining the relationships between temperature, precipitation, and breeding phenology or performance for Barn Swallows.

Response†	Explanatory variables‡,§	Estimate	SE	Lower 95% CI	Upper 95% CI	Relative importance (N¶)
Clutch initiation date	(Intercept)	363.24	48.46	267.97	458.52	
	Latitude	0.89	0.69	0.12	2.23	0.76 (5)
	Longitude	0.29	0.34	−0.12	1.10	0.60 (4)
	PC1	0.23	0.29	−0.09	0.96	0.52 (4)
	PC2	**−1.54**	**0.30**	**−2.14**	**−0.94**	**1.00 (7)**
	PC4	−0.01	0.11	−0.79	0.49	0.09 (1)
	Year	**−0.18**	**0.02**	**−0.22**	**−0.14**	**1.00 (7)**
Clutch size	(Intercept)	1.45	0.69	0.10	2.81	
	CID	**−0.00**	**0.00**	**−0.01**	**−0.00**	**1.00 (8)**
	Latitude	0.00	0.01	−0.04	0.07	0.10 (1)
	Longitude	0.00	0.01	−0.05	0.02	0.14 (1)
	PC1	0.00	0.00	−0.02	0.03	0.09 (1)
	PC3	0.00	0.01	−0.03	0.05	0.09 (1)
	PC4	−0.01	0.02	−0.08	0.02	0.23 (2)
	Source	0.01	0.04	−0.06	0.17	0.22 (2)
Nestling survival	(Intercept)	−12.38	4.69	−21.62	−3.15	
	Latitude	−0.03	0.07	−0.28	0.07	0.32 (5)
	Longitude	0.00	0.01	−0.05	0.09	0.05 (1)
	PC1	0.01	0.03	−0.04	0.14	0.30 (5)
	PC2	0.01	0.03	−0.03	0.12	0.23 (3)
	PC3	0.04	0.04	−0.02	0.14	0.57 (8)
	PC4	0.00	0.02	−0.07	0.12	0.11 (2)
	Year	**0.01**	**0.00**	**0.00**	**0.01**	**1.00 (14)**

Note: Bolded explanatory values indicated those with an effect on the response.

† Model coefficients for Barn Swallow brood size are not provided because 95% confidence intervals for all explanatory variables spanned zero.

‡ PC1-4 represents principal components 1–4 identified in Table 1.

§ Source was a categorical variable representing data that were collected as part of the Maritime Nest Records Scheme or long-term monitoring projects.

¶ Number of averaged models.

measures between 1962–1972 and 2006–2016. We estimated that this decline in reproductive performance would result in an estimated 46% reduction in fledglings/pair. While we do not know the mechanism behind this reduction in breeding performance, the Bank Swallow was the only swallow that did not advanced their clutch initiation dates in recent years. Therefore, like other migratory birds that exhibit little or no change in spring phenology, it is possible that a mismatch between food supply and breeding phenology is driving population declines (Møller et al. 2008). Another possible cause of the reductions in breeding performance is carry-over effects from winter to breeding for this species (T.L.I., G. Mastromonaco, F. Angelier, K.A. Hobson, and M.L.L., *unpublished data*). Carry-over effects from poor wintering conditions to breeding have also been linked to population declines for some migratory birds (Finch et al. 2014), but

other studies have found that breeding conditions have a greater effect on populations than carry-over effects from non-breeding conditions (Ockendon et al. 2013, Rushing et al. 2016).

Aside from decreased hatching success, we did not find a consistent decline in breeding performance over time for the remaining three species. Breeding performance either increased slightly (Barn and Tree Swallows) or there was no change (Cliff Swallows), possibly due to advances in breeding phenology over time. These results are consistent with studies on a European population of Barn Swallows and the Willow Tit *Poecile montanus* that had higher breeding performance with earlier breeding phenology (Møller 2008, Vatka et al. 2011). Although we did not directly measure food availability across this time period, it is possible that by breeding earlier, swallows in our study may have aligned breeding with periods of abundant food

Table 6. Model coefficients, SE, and 95% confidence intervals (CI) for the best-fitting models explaining the relationships between temperature, precipitation, and breeding phenology or performance for Tree Swallows.

Response	Explanatory variables[†],[‡]	Estimate	SE	Lower 95% CI	Upper 95% CI	Relative importance (N[§])
Clutch initiation date	(Intercept)	314.58	36.85	242.29	386.87	
	Latitude	−0.23	0.40	−1.45	0.34	1.00 (11)
	Longitude	0.04	0.13	−0.25	0.67	1.00 (11)
	PC1	**1.33**	**0.14**	**1.05**	**1.62**	**0.41 (5)**
	PC3	**−0.43**	**0.16**	**−0.75**	**−0.11**	**0.40 (4)**
	PC4	−0.06	0.12	−0.44	0.12	0.39 (5)
	Source	38.35	61.74	−82.72	159.43	1.00 (11)
	Source:Year	−0.02	0.03	−0.11	0.02	1.00 (11)
	Year	**−0.14**	**0.02**	**−0.17**	**−0.11**	**0.19 (3)**
Clutch size	(Intercept)	1.81	0.70	0.44	3.17	
	CID	**−0.01**	**0.00**	**−0.01**	**−0.01**	**1.00 (8)**
	Latitude	0.00	0.01	−0.03	0.04	0.11 (1)
	Longitude	0.00	0.00	−0.02	0.03	0.11 (1)
	PC1	0.00	0.00	−0.01	0.02	0.11 (1)
	PC2	0.00	0.00	−0.01	0.02	0.10 (1)
	PC4	0.00	0.00	−0.02	0.02	0.10 (1)
	Source	0.00	0.01	−0.06	0.04	0.11 (1)
	Year	0.00	0.00	0.00	0.00	0.10 (1)
Brood size	(Intercept)	1.92	0.98	0.00	3.83	
	CID	**−0.01**	**0.00**	**−0.01**	**−0.01**	**1.00 (12)**
	Latitude	0.00	0.01	−0.05	0.07	1.00 (12)
	Longitude	0.00	0.01	−0.01	0.05	0.51 (6)
	PC1	−0.01	0.01	−0.03	0.00	0.34 (4)
	PC2	0.02	0.01	−0.00	0.04	0.23 (3)
	PC3	0.00	0.00	−0.02	0.03	0.06 (1)
	PC4	0.00	0.01	−0.01	0.04	0.06 (1)
	Source	**0.08**	**0.03**	**0.01**	**0.14**	**0.87 (10)**
	Year	0.00	0.00	−0.00	0.00	0.06 (1)
Nestling survival	(Intercept)	4.80	2.72	−0.53	10.13	
	CID	**−0.01**	**0.00**	**−0.02**	**−0.01**	**1.00 (9)**
	Latitude	−0.07	0.05	−0.16	0.00	0.82 (7)
	Longitude	0.00	0.01	−0.04	0.05	0.52 (5)
	PC1	**0.04**	**0.02**	**0.01**	**0.08**	**1.00 (9)**
	PC2	**−0.04**	**0.01**	**−0.07**	**−0.02**	**0.17 (2)**
	PC3	0.00	0.01	−0.02	0.04	0.16 (2)
	PC4	**0.04**	**0.01**	**0.01**	**0.07**	**0.08 (1)**
	Source	−0.77	3.19	−9.89	6.94	1.00 (9)
	Source:Year	0.00	0.00	−0.00	0.01	1.00 (9)
	Year	−0.00	0.00	−0.00	0.00	0.08 (1)

Note: Bolded explanatory values indicated those with an effect on the response.
 † PC1-4 represents principal components 1–4 identified in Table 1.
 ‡ Source was a categorical variable representing data that were collected as part of the Maritime Nest Records Scheme or long-term monitoring projects.
 § Number of averaged models.

(Møller et al. 2008, but see Dunn et al. 2011). In addition, recent research in this region indicates that food availability does not limit breeding success for Barn, Cliff, and Tree Swallows, suggesting that insect abundance is high throughout the breeding season (Imlay et al. 2017).

One other possible explanation for our results is changes in the survival of different age classes of Bank, Barn, and Tree Swallows. In general, swallows with previous breeding experience breed earlier and have higher performance than younger swallows (Hussell and Quinney 1987,

Wardrop and Ydenberg 2003), although senescence may reduce performance for very old individuals (Møller and de Lope 1999). Therefore, lower survival rates for older Bank Swallows and younger Barn and Tree Swallows could result in the changes we observed (i.e., lower performance for Bank Swallows and higher performance for Barn and Tree Swallows, respectively). However, without long-term data on age class structure in populations prior to the onset of population declines, we are unable to examine this possibility.

In this region, climate change has resulted in warmer winter temperatures (especially minimum temperatures) and reductions in snowfall and snow depth (Mekis and Vincent 2011, Vincent et al. 2012, 2015), which are related to advances in breeding phenology for Barn and Tree Swallows. Similar results between temperature and breeding phenology have been reported for a variety of other migratory birds (Sanz 2003, Townsend et al. 2013), including North American populations of Tree Swallows (Dunn and Winkler 1999), but to our knowledge, this is the first study also demonstrating the importance of winter precipitation on breeding phenology. Winter temperature and precipitation were not related to clutch size and brood size for Barn and Tree Swallows, nor nestling survival for Barn Swallows, suggesting that conditions during breeding, like cold snaps and breeding habitat, likely have a stronger effect on performance than winter weather (Ambrosini et al. 2002, Ghilain and Bélisle 2008, Winkler et al. 2013). However, for Tree Swallows, nestling survival was lower after warmer winters, less precipitation during early January and March, and more precipitation during late February.

Since neither species is present on the breeding grounds during the winter, it seems likely that winter temperature and precipitation is affecting Barn and Tree Swallow breeding phenology and performance through insect availability (Williams et al. 2015). Snow pack is an important factor affecting overwinter insect survival (Templer et al. 2012); reductions in snow pack associated with warmer temperatures and/or reduced precipitation (like we currently observe in the Maritimes; Mekis and Vincent 2011, Vincent et al. 2012, 2015) may result in an earlier, but less abundant and diverse insect population (Finn and Poff 2008). While we are uncertain about the cause of contrasting trends for precipitation during different times of the winter, we speculate that it may be driven by the effects of winter precipitation on the survival and/or development of different types of insects during periods when they are most vulnerable (Todd 1996, Irwin and Lee 2000, Musolin and Saulich 2012). Ultimately, regardless of the annual variation in temperature and precipitation and associated effects on annual breeding performance, for Barn and Tree Swallows breeding performance was higher in 2006–2016, compared to 1962–1972, indicating that at this time, climate change is not negatively affecting breeding performance across a broader time period.

It is possible that the relationships we observed between winter weather on the breeding grounds and breeding phenology and performance are due to similar conditions between breeding and non-breeding location. In this case, the effects on breeding phenology and performance are the result of carry-over effects from winter to breeding. This explanation has more support for Maritime breeding Tree Swallows that winter in southern Florida and Cuba (Burke 2014) and are potentially within a short enough distance for weather to be correlated. However, Maritime breeding Barn Swallows winter in central South America (Hobson et al. 2015, Hobson and Kardynal 2016); the large distance between wintering and breeding locations this species offers less support for this explanation.

Conclusions

The cause of broad-scale population declines for aerial insectivores in North America is currently unknown. Breeding performance declined substantially for Bank Swallows and is likely contributing to population declines; however, for the other three swallows, performance is unchanged or higher. Interestingly, the only species experiencing lower breeding performance (Bank Swallow) did not advance its breeding phenology, whereas the other species did, by 8–10 d, likely in response to warmer temperatures (Dunn and Winkler 1999, Sanz 2003, Townsend et al. 2013) and/or less precipitation. An inability to advance breeding phenology for Bank Swallows might contribute to their lower breeding performance. Declines in aerial insectivores have

been attributed to a broad-scale common driver affecting multiple species (Nebel et al. 2010, Smith et al. 2015, but see Michel et al. 2016). However, our results suggest that population declines for these three of species cannot be explained by reductions in breeding performance. Furthermore, for Barn and Tree Swallows, climate change does not appear to be driving population declines through reduced breeding performance at this time. Together, this suggests that future work should consider the potential effects of conditions during migration and winter on population declines through their effects of swallow survival. For example, adult survival in Afro-Palearctic populations of Bank and Barn Swallows is closely related to precipitation during the winter (Cowley and Siriwardena 2005, Robinson et al. 2008, Norman and Peach 2013).

Citizen scientist data from programs like the MNRS present valuable opportunities for examining trends in breeding phenology and performance for a variety of species and over longer periods of time than most research projects. For our study, the MNRS data spanned a period of 57 yr, both before and after these species began experiencing steep declines (e.g., mid-1980s; Nebel et al. 2010, Smith et al. 2015). We recommend that data from the MNRS and other related programs be used in similar projects aimed at understanding changes in breeding phenology, performance, and population trends.

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Supporting Information

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