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First egg dates of Tree Swallows (*Tachycineta bicolor*) nesting in boxes in west Michigan advanced with increasing spring temperatures between 1993 and 2018

Las fechas del primer huevo de Golondrinas de árbol (*Tachycineta bicolor*) que anidan en cajas en el oeste de Michigan, fueron adelantadas con el aumento de temperaturas en primavera entre 1993 y 2018

Michael P. Lombardo [1], *Nathaniel Wagner* [1], *Jared M. Laughlin* [1], *Sango Otieno* [2], *Levi Rosendall* [2], *Clara Voetberg* [2] and *Alejandro Hoban* [2]

ABSTRACT. Many bird species have advanced their first egg dates in response to recent milder winters and increases in spring temperatures. Tree Swallows (*Tachycineta bicolor*) begin egg laying earlier in warmer springs at most, but not all, study sites. We examined whether Tree Swallows that nested in boxes in west Michigan responded to an increase in spring temperatures from 1993 to 2018 by advancing their first egg dates. May, but not April, mean daily temperatures got significantly warmer from 1993 to 2018. We found that the first egg dates, but not mean first egg dates, of both second year (SY) and after second year (ASY) females got earlier between 1993 and 2018. The first egg dates of SY females did not get earlier in response to warmer April or May temperatures but got earlier when there were more days in May with measurable rain. The first egg dates of ASY females got earlier with warmer April and May temperatures. Overall, the relationships between weather conditions and first egg dates of both SY and ASY females were complex and varied yearly. The climatic conditions that influence Tree Swallow first egg dates are complex because stochastic rain and wind conditions interact with air temperatures to affect the availability of the aerial insect prey of swallows thereby influencing the ability of females to begin egg laying.

RESUMEN. Muchas especies de aves han adelantado las fechas de su primer huevo, en respuesta a inviernos recientes más suaves, y al incremento de temperaturas en primavera. Las Golondrinas de árbol (*Tachycineta bicolor*) empiezan a poner huevos más temprano en primaveras más cálidas en la mayoría, pero no en todos los sitios de estudio. Examinamos si las Golondrinas de árbol que anidaban en cajas en el oeste de Michigan respondieron a un incremento en las temperaturas en primavera, desde 1993 hasta 2018, adelantando las fechas de su primer huevo. Las temperaturas medias diarias de Mayo, no así las de Abril, se volvieron significativamente más cálidas de 1993 a 2018. Encontramos que las fechas del primer huevo, mas no la media de las fechas del primer huevo, tanto de hembras del segundo año (SY) como de hembras de después del segundo año (ASY), fueron más temprano entre 1993 y 2018. Las fechas del primer huevo de las hembras SY no fueron más temprano en respuesta a temperaturas más cálidas en Abril o Mayo, pero sí lo fueron cuando hubieron más días en Mayo con lluvia medible. Las fechas del primer huevo de las hembras ASY fueron más temprano con temperaturas más cálidas en Abril y Mayo. En general, las relaciones entre las condiciones climáticas y las fechas del primer huevo de hembras SY y ASY fueron complejas y variaron anualmente. Las condiciones climáticas que influyen en las fechas del primer huevo de las Golondrinas de árbol son complejas porque la lluvia estocástica y las condiciones del viento interactúan con las temperaturas del aire, afectando la disponibilidad de insectos aéreos que son presas de las golondrinas, y por tanto influyendo en la habilidad de las hembras para comenzar a poner huevos.

Key Words: *climate change; first egg date; nest box; Tachycineta bicolor; Tree Swallow*

INTRODUCTION

Within species, birds that begin egg laying earlier in the breeding season tend to produce more offspring that subsequently become breeders than those that begin egg laying later (Dhondt and Hublé 1968, Newton and Marquiss 1984, Spear and Nur 1994, Grand and Flint 1996, Saino et al. 2012, Lombardo et al. 2020). Therefore, the timing of egg laying in birds has important consequences for fitness because it influences the ability of parent birds to pass their genes to the next generation (Fisher 1958). Many bird species have advanced their egg-laying dates in response to increasing spring temperatures and milder winters (Crick et al. 1997, Sanz 2002, 2003, Both et al. 2004, Visser et al. 2009). For example, in North America, Eastern Kingbirds (*Tyrannus tyrannus*; (Murphy et al. 2022), Tree Swallows (*Tachycineta bicolor*; Dunn and Winkler 1999, Rioux Paquette et al. 2014, Bourret et al. 2015, Irons et al. 2017, Shipley et al. 2020), Eastern Bluebirds (*Sialia sialis*; Torti and Dunn 2005), Black-throated Blue Warblers (*Setophaga caerulescens*; Townsend et al. 2013), and Red-winged Blackbirds (*Agelaius phoeniceus*; Torti and Dunn 2005), amongst other species have begun laying earlier in warmer springs (Dunn and Winkler 2010). However, mid-winter temperatures may be more important in some species. For example, the timing of egg laying in European Starlings (*Sturnus vulgaris*) breeding in southern British Columbia was influenced more by mid-winter than early spring temperatures that affect the life cycles of their soil-inhabiting invertebrate prey (Williams et al. 2015, Leonard and Williams 2023).

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[1]Biology Department, Grand Valley State University, [2]Statistics Department, Grand Valley State University

Increasing spring temperatures have been associated with earlier first egg dates across the breeding range of Tree Swallows. For example, Dunn and Winkler (1999) noted that Tree Swallow laying dates advanced by 5–9 d, depending on location, across North America between 1959 and 1991. In southern Québec, laying dates advanced by 1.7 d from 2005 to 2011 in one analysis (Rioux Paquette et al. 2014) and 4.2 d from 2004 to 2013 in another (Bourret et al. 2015) and was associated with an increase of nearly 3 °C. Near Ithaca, New York laying dates advanced by 13 d from 1972 to 2015 and were associated with a 1.9 °C increase in temperatures in May and June from 1989 to 2015 (Shipley et al. 2020). However, advances in egg-laying date across the range of Tree Swallows are not uniform. For example, although first egg dates were negatively correlated with spring temperatures they did not advance between 1969 and 2001 at Long Point in southern Ontario (Hussell 2003). At two Alaskan study sites monitored from 2000 to 2015, first egg dates advanced at a site near Fairbanks but not at the other, 433 km to the southeast (Irons et al. 2017). Similarly, Sockman and Courter (2018) found that although spring temperatures were not associated with the timing of egg laying, increasing precipitation delayed first egg dates of Tree Swallows breeding in Ohio. Collectively, these observations suggest that the ways that Tree Swallow first egg dates respond to warming spring temperatures vary across their range.

Tree Swallows are considered income breeders because their timing of egg laying is associated with their recent foraging success rather than long-term stored somatic resources (e.g., calcium, fat) as in capital breeders (Winkler and Allen 1995, 1996, Pahl et al. 1997). Prevailing air temperatures, precipitation, and other weather variables affect the availability of their aerial insect prey (Taylor 1963, Lifjeld et al. 2002, Winkler et al. 2013). Therefore, warmer spring temperatures should theoretically create better conditions for aerial insects (Taylor 1963) and consequently, better breeding conditions for Tree Swallows. However, an earlier start of laying may not necessarily be advantageous for them because it may produce a mismatch between the earlier emergence and peak abundance of insects needed to feed their nestlings (Imlay and Leonard 2019) and increased chances of encountering inclement weather (Berzins et al. 2020, Shipley et al. 2020).

Advanced laying dates coupled with subsequent population declines have been observed in Tree, Barn (*Hirundo rustica*), and Cliff Swallows (*Petrochelidon pyrrhonota*; Imlay and Leonard 2019). Although it is possible that climatic conditions on overwintering grounds or during migration could affect the timing of breeding, warmer spring weather conditions on breeding grounds appear to have the greatest effect on the timing of breeding in migratory birds (Ockendon et al. 2013). Likewise, weather conditions on Tree Swallow breeding grounds, rather than overwintering grounds, appear to have the greater effect on adult survival and fledging success (Weegman et al. 2017). For example, cool temperatures coupled with rain and strong winds typically result in reduced fledging success, especially if they occur several days before expected fledging, because they reduce the availability of the aerial insects that parents feed their nestlings (Winkler et al. 2013, Berzins et al. 2020, Wheelwright et al. 2022).

We predicted that first egg dates of Tree Swallows breeding from 1993 to 2018 in nest boxes in west Michigan would be earlier in years with warmer spring temperatures in ways consistent with numerous other studies of Tree Swallows (Dunn and Winkler 1999, Winkler et al. 2002, Hussell 2003, Fast 2007, Bourret et al. 2015, Irons et al. 2017, Sockman and Courter 2018, Shipley et al. 2020). Most female Tree Swallows breeding in nest boxes are older, more experienced after-second-year (ASY) females. A smaller proportion are younger, less experienced, second-year (SY) females that are easily identified by their mostly brown dorsal plumage (Winkler et al. 2020). We examined separately the relationships between spring temperatures on first egg dates for SY and ASY females because ASY females typically return from migration and begin laying earlier in the breeding season than SY females (Winkler et al. 2020). Except for Bourret et al. (2015), studies of the relationship between spring temperatures and first egg dates have not examined separately first egg dates of ASY and SY females. We also predicted that first egg dates would be earlier in years with positive North Atlantic Oscillation Index (NAOI) values because they are associated with warmer temperatures and wetter conditions in eastern continental United States (https://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml). The NAO, an oscillation around the long-term mean of the difference in sea-level pressure between the subtropical center of high surface pressure and the subarctic center of low pressure, affects ecological conditions in the North Hemisphere throughout the year although the greatest interannual variability occurs during winter months (Hurrell 1995). Positive NAOI values have been associated with long-term changes in the timing of breeding in several species of Northern Hemisphere birds in northern Europe (Forchhammer et al. 1998, Sanz 2002, 2003) and North America (Weatherhead 2005), including Tree Swallows (Fast 2007, McArthur et al. 2017).

METHODS

Field methods

We studied first egg dates of Tree Swallows nesting in wooden nest boxes affixed to metal poles from 1993 to 2018 on the Grand Valley State University campus (GVSU), Allendale, Michigan (42° 57′ N, 85° 53′ W). The number of boxes available for breeding varied yearly from 81 to 120. From 1993 to 2009, nest boxes were arranged in grids in an old field. Johnson and Lombardo (2000) provided a description of the ecological characteristics of the study site for this period. All nest boxes were rearranged around stormwater retention ponds constructed on the study site during 2009 (n = 3 ponds) and 2011 (n = 4 ponds). Starting in 2013 we attached 48 cm diameter aluminum pizza pans below each nest box to help prevent the high rates of predation that occurred in 2000, 2001, 2006, 2007, and 2012 from raccoons (*Procyon lotor*) and feral cats (*Felis catus*). There was no evidence of predation at nest boxes between 2013 and 2018. As a proxy for habitat quality, we calculated yearly nest box occupancy as the proportion of nest boxes within which we found 1 or more eggs each year. Using nest box occupancy as a proxy for yearly habitat quality assumes that nest box occupancy reflects the yearly assessments of habitat quality by swallows choosing to breed at our study site.

We started monitoring breeding activity ~1 May each year. At each nest box, we monitored the progress of nest building and recorded the date of clutch initiation (i.e., the date that the first egg in a clutch was laid). We used non-toxic ink to mark each egg in numerical sequence on the morning it was laid. Evaluating first egg date data requires a caveat: unless we had banding data that indicated otherwise, we assumed that the first appearance of an egg in a nest box at our study site was that female's first nesting attempt because it was impossible to know whether any nest was a particular female's first egg laying attempt without sacrificing the bird and counting her postovulatory follicles (Kennedy et al. 1989).

We used traps mounted inside of nest boxes to capture breeding females (Yunick 1990). Females were captured at various stages during the breeding season, although most were captured while they were tending nestlings. Females were banded with U.S. Geological Service aluminum bands for individual identification.

We used a breeding female's plumage characteristics to classify it as either (a) SY female if it had a mostly (i.e., > 50%) brown dorsal plumage, (b) after-hatching year (AHY) female if its dorsal plumage was ~50% brown and ~50% iridescent blue-green, or (c) ASY female if it had mostly iridescent blue-green dorsal plumage (Cohen 1980, Hussell 1983, Winkler et al. 2011). We analyzed first egg data 321 times at the nests of SY females and 1082 times at the nests of ASY females; AHY females (n = 43) made up only 3.0% of egg-laying females of known plumage category for which we had data; their first egg dates are not included in our analyses. The plumage category of another 189 egg-laying females was not detected because we did not capture them; their first egg dates are not included in our analyses.

We used weather data collected during April and May at a weather station on the GVSU campus to investigate the possible effects that weather conditions had on first egg dates. We collected April weather data because ASY females typically return to our study site starting in late March and early April and choose mates and nest boxes for breeding. April weather conditions are likely to affect the physical condition of females prior to the onset of egg-laying in May. We collected May weather data because most egg-laying begins in May (see below) and because Tree Swallows are income breeders and their timing of egg laying is based on recent foraging success (Winkler and Allen 1995, 1996, Pahl et al. 1997). Wind speed data were available only from 2003 to 2005 and 2007–2018 for April and 2003–2018 for May so we did not include wind speed data in our analyses. No weather data for May 2002 were available because of weather station failure. We used the following weather variables in our analyses: mean daily temperatures (°C), mean daily rainfall (cm), total monthly rainfall (cm), and the number of days per month with measurable rain. We examined these weather variables because they had the potential to affect the abundance of the aerial insect prey of Tree Swallows and thus the amount of energy and nutrients available to female Tree Swallows for egg formation. The availability of aerial insects may influence the timing of clutch initiation by female Tree Swallows (Lifjeld et al. 2002, Dunn et al. 2011, Winkler et al. 2013). We did not collect data on aerial insect abundance. The effects of air temperatures and rainfall on egg mass varied yearly at our study site (Lombardo et al. 2021) and, therefore, may have also affected first egg dates.

Statistical analyses

We examined the data for normality using a Kolmogorov-Smirnov test with SPSS 24 (IBM 2016) and used, where appropriate, parametric or nonparametric analyses with GraphPad Prism (GraphPad 2005), SAS 9.4 (SAS Institute 2016), and SPSS. We set 1 January = date 1 for our statistical analyses but hereafter use calendar dates to ease the interpretation of our results in the context of doing ornithological field work.

We used multiple linear regression analyses with PROC MIXED in SAS to examine the relationship between percent nest box occupancy and year. Year was treated as a factorial variable in these analyses. We used multiple linear regression analyses in PROC GLM and PROC REG in SAS to analyze the relationships between mean daily April and May temperatures with each other and with year and linear regression and correlation analyses to examine the relationships between the other weather variables and year.

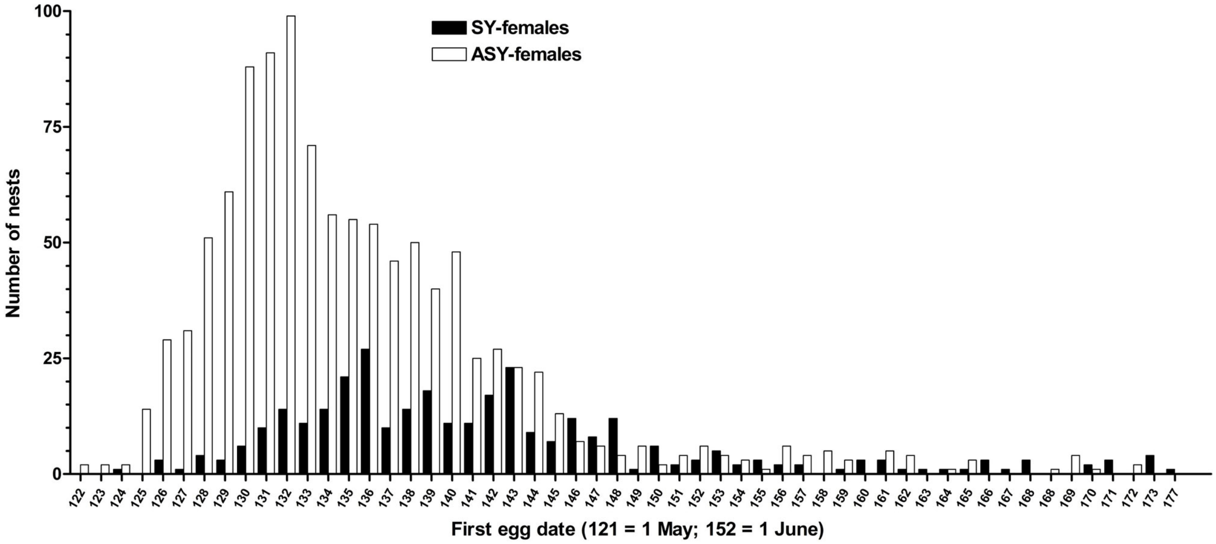
We compared the first egg dates of SY and ASY females using an independent samples *t*-test. We calculated the effect size (Cohen's d) of this two-sample comparison using an online effect size calculator at https://www.socscistatistics.com/effectsize/default3.aspx. By convention, an effect size of d = 0.8 is considered large, d = 0.5 medium, and d = 0.2 small (Cohen 1992). We used a Kruskal-Wallis test to compare the median first egg dates of SY and ASY females.

We used PROC MIXED to examine the interactions between first egg dates, female plumage category, and year. This analysis treated year as a factorial variable.

We used multiple linear regression analyses with PROC MIXED in SAS to examine the relationships between first egg dates and the following factors: year, mean daily April and May temperatures, the number of days with measurable rain in April and May, the total amount of April and May rainfall, NAOI, and percent nest box occupancy separately for SY and ASY females. Year was treated as a quantitative variable in PROC MIXED. We used PROC MIXED because it uses mixed linear models and takes into account repeated measures, as determined by band number from the same female, and unbalanced data (SAS Institute 2016). In each model, first egg date was the dependent variable and the abiotic factors listed above were the independent variables. We used the Akaike Information Criterion (AIC; Akaike 1974) to compare two models, one that included percent nest box occupancy and one that did not. We compared these models because percent nest box occupancy covaried with year (see below). By convention, when comparing models for their relative usefulness in describing the relationships between the dependent and independent variables, the model with the smallest AIC is the preferred model because it is the candidate model that is closest to the "true" model (Akaike 1974). Moreover, if the difference between the AICs of candidate models is less than two, the models are statistically indistinguishable and the principle of parsimony requires the modeler to choose the simplest model (i.e., the model with fewest independent variables; Portet 2020). Finally, we calculated separately for SY and ASY females the Variance Inflation Factors (VIF) for each of the independent variables in our PROC MIXED models to detect any multicollinearity (i.e., the correlations between multiple independent variables in a multiple regression model) between variables that might bias our interpretations of the results; by convention, VIF values of greater than 10 suggest multicollinearity between variables (Neter et al. 1989).

Unless otherwise noted, data are presented as mean ± SD. All statistical tests were two-tailed. Differences between measures were considered statistically significant if $P \leq 0.05$. When appropriate, we

Fig. 1. Distribution of first egg dates of second-year (SY) and after-second-year (ASY) female Tree Swallows (*Tachycineta bicolor*) nesting in boxes in west Michigan from 1993 to 2018.



calculated Holm-Bonferroni sequential corrections for multiple tests (Gaetano 2018, *unpublished manuscript*, https://www.researchgate.net/publication/236969037_Holm-Bonferroni_Sequential_Correction_An_EXCEL_Calculator) and report $P_{adjusted}$ values.

RESULTS

General summary

For 1403 nests monitored from 1993 to 2018, the great majority of first egg dates (1305/1403, 93%) occurred before 1 June each year (Fig. 1). Forty-five times SY females and 53 times ASY females began egg laying on or after 1 June. When all nests were considered, the mean first egg date of all females was 16 May ± 8.48 days and ranged from 1 May in 2002 at a nest where we did not capture the laying female and 26 June in 1993 at a SY female nest. For all females at all nests, the median first egg date was 15 May, and the modal first egg date was 12 May.

Based on banding data, females bred at our study site 1.51 ± 0.94 times. Most banded females (778/885, 89%) females bred only once or twice.

Percent nest box occupancy patterns from 1993 to 2018

Percent nest box occupancy increased significantly from 1993 to 2018 (PROC MIXED, estimate = 1.12 ± 0.07, $t = 14.9$, df = 342, $P < 0.001$; df = 342 (i.e., sample size [n = 1018] – 675 unique bird bands – 1). Percent nest box occupancy ranged from 24.5% in 2008 after a year of devastating predation in 2007 when young fledged from only one nest to 94.1% in 2017. Mean percent nest box occupancy was 63.61 ± 20.5%.

Weather patterns from 1993 to 2018

Mean daily April temperatures (8.02 ± 1.85 °C) were, as expected, significantly cooler than mean daily May temperatures (14.55 ± 2.28 °C; paired-$t = 10.90$, df = 24, $P < 0.001$). Mean daily April and May temperatures were not significantly correlated ($r = -0.03$, $n = 25$, $P = 0.89$).

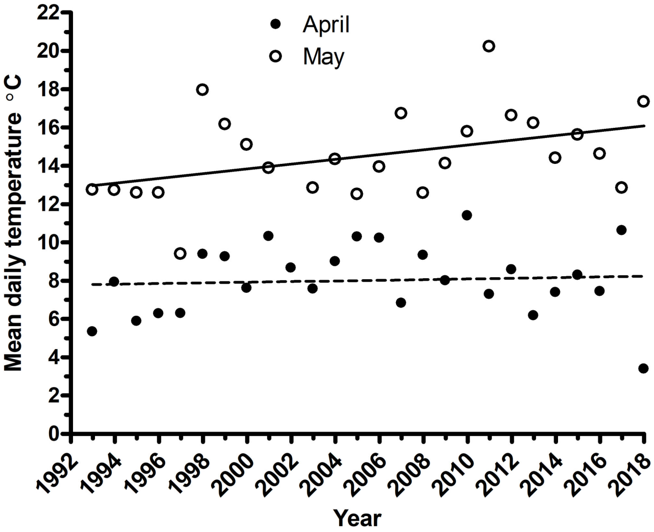
Based on the results of an ANCOVA analysis, we are 95% confident that mean daily May temperatures were 5.37 °–7.65 ° C higher than mean daily April temperatures for every additional year in the model ($F = 68.04$, df = 2,48, $P < 0.0001$, $r^2 = 0.74$, Root MSE=2.023). Mean daily temperatures in April did not change significantly from 1993 to 2018 but mean daily temperatures in May increased by 3.1 °C from 1993 to 2018 (Fig. 2). We used ANCOVA to test for the equality of the slopes and Y-intercepts of the regression lines of temperature regressed on year for April and May. Interestingly, the slopes of the regression lines for April and May were not statistically different (estimate = 0.11 ± 0.07 [SE], $t = 1.45$, df = 1, $P = 0.15$) but the Y-intercepts were (estimate = 7.07 ± 0.64 [SE], $t = 11.00$, df = 1, $P < 0.001$). April 2018 had the coolest mean daily temperatures (3.39 °C); April 2010 had the warmest (11.39 °C; Fig. 2). May 1997 had the coolest mean daily temperatures (9.39 °C); May 2011 had the warmest (20.22 °C; Fig. 2).

There were no significant differences between April and May in mean total rain or mean days with rain (both $P \geq 0.48$). April 2005 had the least total rainfall (2.77 cm); April 2017 had the most (27.10 cm). May 1998 had the least total rainfall (1.79 cm); May 2017 had the most (27.10 cm). Neither total April rainfall nor the number of days in April with measurable rain were significantly correlated with year (both $P \geq 0.18$). Neither total May rainfall nor the number of days in May with measurable rain were significantly correlated with year (both $P \geq 0.44$). NAOI did significantly change from 1993 to 2018 ($r = 0.11$, $n = 26$, $P = 0.59$).

First egg dates of SY and ASY females differed

First egg dates of both SY and ASY females were normally distributed (Kolmogorov-Smirnov test; both $P \geq 0.09$). Mean first egg dates of SY females were, on average, 7 d later in May than those of ASY females; the effect size was medium ($d = 0.73$; Table 1). Median first egg dates of SY females were, on average, 6 d later in May than those of ASY females (Table 1). The modal first egg date of SY females was 16 May. The modal first egg date of ASY females was 12 May. The earliest first egg date of SY females was

Fig. 2. Mean daily April and May temperatures (°C) and year. April, dashed regression line; $y = 0.02x + 7.79$ (95% CI = -0.33-0.44, $F = 0.12$, df = 1,24, $P = 0.73$, $n = 26$, $r^2 = 0.005$,). May, solid regression line; $y = 0.12x + 12.85$ (95% CI = 0.03-0.70, $F = 5.0$, df = 1,23, $P = 0.03$, $n = 25$, $r^2 = 0.18$).



4 May 2000, the latest 26 June 1993. The earliest first egg date of ASY females was 2 May 2002 and 2010, the latest 21 June 1999 (Fig. 1).

First egg dates were related to year ($F = 8.29$, df = 25, 1124, $P < 0.001$), female plumage category ($F = 145.51$, df = 1, 99, $P < 0.001$), and the interaction between year and female plumage category ($F = 1.90$, df = 25, 1124, $P = 0.005$) in a PROC MIXED model that examined the interactions between first egg dates, female plumage category, and year and treated year as a factorial variable. This finding led us to examine the yearly relationships between female plumage class and first egg dates by setting 1997 and 2017 as reference years (i.e., the years with the coolest and warmest mean daily May temperatures, respectively).

The first egg dates of SY females significantly differed across years when compared to 1997 ($F = 3.83$, df = 25, 146, $P < 0.001$) and 2011 ($F = 3.83$, df = 25, 146, $P < 0.001$). However, only first egg dates in 1993, 2001, 2005, 2009, 2011, and 2012 remained significantly different (all $P_{adjusted} < 0.04$) from first egg dates in 1997, and only first egg dates in 1996, 1997, and 2003 remained significantly different from first egg dates in 2011 (all $P_{adjusted} = 0.003$) after Holm-Bonferroni sequential correction for multiple comparisons.

The first egg dates of ASY females significantly differed across years when compared to either 1997 ($F = 11.51$, df = 25, 879, $P < 0.001$) or 2011 ($F = 11.51$, df = 25,879, $P < 0.001$). However, first egg dates of all years except 2007 remained significantly different (all $P_{adjusted} < 0.05$) from the first egg dates in 1997, and first egg dates in 1996, 1997, 1998, and 2003 remained significantly different (all $P_{adjusted} = 0.007$) when compared to first egg dates in 2011 after Holm-Bonferroni sequential correction for multiple comparisons.

Table 1. Mean and median first eggs dates of second year (SY) and after-second-year (ASY) female Tree Swallows (*Tachycineta bicolor*) nesting in nest boxes in west Michigan between 1993 and 2018. Mean egg dates represented as mean ± SD (n).

First egg dates	SY females	ASY females	Statistical comparison	df	P
Mean	22 May ± 10.06 days (321)	15 May ± 7.65 days (1082)	$t = 10.71$†	435.51	< 0.001
Median	20 May	14 May	$X^2 = 107.14$‡	1	< 0.001

† Students *t*-test with unequal variances.
‡ Kruskal-Wallis median test.

A mixed linear model that took into account the first egg dates of females that bred multiple times at our study site found an average difference between SY and ASY females in first egg date was 6.76 ± 0.64 days ($t = -10.58$, error df = 824, $P < 0.001$, 95% CI = -8.01 – -5.51). After controlling for multiple comparisons, mean first egg dates of SY females were significantly later than those of ASY females in 1998, 1999, 2003, 2004, 2014, 2015, 2017, and 2018 (Table 2). We examined separately in subsequent analyses the relationships between SY and ASY female first egg dates and the independent variables because of the statistically significant differences we detected between the first egg dates of SY and ASY females.

Relationships between first egg dates of SY and ASY females and year, weather variables, and percent occupied nest boxes

Mean first egg dates of SY and ASY females did not change significantly from 1993 to 2018 (SY females; $y = 310.28–0.08x$, $F = 0.61$, df = 1, 24, $P = 0.44$: ASY females; $y = 301.25–0.08x$, $F = 1.02$, df = 1,24, $P = 0.32$). The PROC MIXED multiple regression model that examined the relationship between first egg dates and year, weather variables, and percent occupied nest boxes revealed that first egg dates for SY females got earlier from 1993 to 2018 ($P = 0.04$) and with more days of rain in May ($P = 0.05$); none of the other independent variables had a significant effect on SY female first egg dates (Table 3). The PROC MIXED multiple regression model revealed that first egg dates for ASY females got earlier from 1993 to 2018 ($P = 0.07$) and with warmer mean daily April temperatures ($P = 0.006$), warmer mean daily May temperatures ($P = 0.003$), and when a greater percentage of nest boxes were occupied ($P = 0.01$); none of the other variables had a significant effect on ASY female first egg dates (Table 3). The first egg dates of both SY and ASY females tended to get later with more total rain in May (Table 3). Finally, the VIFs for the independent variables for both SY (all VIF ≤ 5.18) and ASY females (all VIF ≤ 4.51) were less than 10 indicating that correlations between the multiple independent variables did not bias the results of our multiple regression model by influencing the least square estimates (Neter et al. 1989).

We reran the PROC MIXED models excluding percent nest box occupancy because we wanted to examine the effect of year on first egg dates without including percent nest box occupancy in the models because year and percent nest box occupancy covaried; percent nest box occupancy increased from 1993 to 2018 (see above). The new model did not substantially affect the estimates of the independent variables of the SY female model but a comparison of the AICs of the two models (Table 3) led us to

Table 2. Comparing yearly mean first egg dates of second year (SY) and after-second-year (ASY) female Tree Swallows (*Tachycineta bicolor*) nesting in boxes in west Michigan from 1993 to 2018. Estimate represents the difference in days between ASY and SY female mean first egg dates ± SE. For example, in 1993 SY female mean first egg date was 2.17 ± 2.22 days later than ASY female mean first egg date. Second Year and ASY female mean first egg dates were compared with *t*-tests. Statistically significant differences after correcting for multiple comparisons (i.e., 0.05/26, P ≤ 0.0019) are indicated by bold font.

					95% C. I.	
Year	Estimate ± SE	*t*	df	P	Lower	Higher
1993	2.17 ± 2.22	0.98	11	0.35	-2.72	7.05
1994	3.97 ± 2.95	1.35	37	0.19	-2.01	9.95
1995	4.55 ± 1.51	3.03	39	0.004	1.51	7.60
1996	2.82 ± 1.37	2.06	33	0.05	0.04	5.61
1997	4.00 ± 1.50	2.66	54	0.01	0.98	7.01
1998	9.26 ± 2.26	4.10	50	**< 0.001**	4.72	13.80
1999	7.95 ± 1.88	4.24	57	**< 0.001**	4.19	11.70
2000	4.69 ± 2.56	1.84	64	0.07	-0.41	9.79
2001	-0.36 ± 2.07	-0.18	50	0.86	-4.51	3.79
2001	7.97 ± 2.35	3.39	21	.003	3.08	12.86
2003	9.37 ± 1.74	5.39	44	**< 0.001**	5.86	12.87
2004	5.08 ± 0.94	5.40	70	**< 0.001**	3.20	6.696
2005	2.82 ± 1.30	2.17	86	0.03	0.24	5.39
2006	4.18 ± 2.00	2.08	79	0.04	0.19	8.17
2007	1.88 ± 1.82	1.04	30	0.31	-1.82	5.59
2008	6.61 ± 2.19	3.02	20	**0.007**	2.04	11.18
2009	2.19 ± 1.03	2.13	47	0.04	0.12	4.26
2010	4.55 ± 3.76	1.21	23	0.24	-3.22	12.32
2011	0.50 ± 2.22	0.49	37	0.63	-1.57	2.57
2012	4.00 ± 2.76	1.45	19	0.16	-1.78	9.78
2013	2.43 ± 1.84	1.32	25	0.20	-1.65	6.21
2014	5.97 ± 1.29	4.62	50	**< 0.001**	3.37	8.57
2015	12.32 ± 2.25	5.48	59	**< 0.001**	7.82	16.82
2016	5.18 ± 1.80	2.87	64	0.006	1.58	8.78
2017	4.31 ± 1.30	3.32	82	**0.001**	1.73	6.89
2018	5.24 ± 1.61	3.25	75	**0.0017**	2.03	8.46

conclude that the model excluding percent boxes occupied is the model that is closer to the "true" model (Akaike 1974, Portet 2020). Rerunning the ASY female model excluding percent boxes occupied revealed a stronger effect of year on first egg dates (P = 0.008) and that none of the estimates of the other independent variables were substantially changed (Table 3). The ASY model excluding percent nest box occupancy is statistically indistinguishable from the previous model because the difference between the AICs of the two models is less than two (Portet 2020; Table 3). Following the principle of parsimony, we choose the model that excludes percent nest box occupancy as a closer representation of the "true" model because it is simpler (i.e., includes fewer variables; Akaike 1974, Portet 2020).

DISCUSSION

We examined the first egg dates of SY and ASY female Tree Swallows breeding in nest boxes in west Michigan: SY females began egg laying nearly 7 d later, on average, than did ASY females. Our observations are consistent with data in the extensive Tree Swallow literature showing that SY females typically return from migration later and begin laying later than ASY females (Winkler et al. 2020). First egg dates of ASY females got earlier with greater nest box occupancy. Bourret et al. (2015) found that among Tree Swallows breeding in southern Québec that both SY and ASY females laid their eggs earlier when nest box occupancy was higher. These results suggest that greater nest box occupancy may reflect greater habitat quality (e.g., food resources) allowing swallows to begin breeding earlier.

Numerous studies of songbirds in the Northern Hemisphere, including those of Tree Swallows, have shown that first egg dates have gotten earlier during the last several decades as climate change has produced warmer spring temperatures (U.S. Global Change Research Program 2017, Dunn 2019). Therefore, we predicted that Tree Swallow first egg dates at our study site would get earlier with increasing spring temperatures during the course of our study. Mean daily May temperatures at our study site increased by 3.1 °C from 1993 to 2018. However, our observations were only partly consistent with this prediction. First egg dates of SY females got significantly earlier from 1993 to 2018 and were estimated by PROC MIXED to be, on average, 6.02 days earlier in 2018 than in 1993, but not with warmer mean daily April or May temperatures. This result is not surprising because SY females typically arrive from migration later than ASY females (Winkler et al. 2020) and we observed few SY females at our study site prior to 1 May (Lombardo, *personal observation*). Thus, the first egg dates of SY females are not likely to have been affected by April temperatures at our study site. Second year female first egg dates got earlier with more days of measurable rain in May. This outcome is surprising because rain tends to decrease the availability of aerial insects (Cox et al. 2019, 2020). The first egg dates of ASY females got significantly earlier from 1993 to 2018 and were estimated by PROC MIXED to be, on average, 3 days earlier in 2018 than in 1993. The first egg dates of ASY female Tree Swallows advanced with warmer mean daily April and May temperatures. The physical condition of ASY females likely benefits from warmer April temperatures because warmer temperatures are associated with increased aerial insect abundance (Taylor 1963). Better physical condition entering the egg laying period may lead to earlier first egg dates in May. The addition of ponds in 2009 and 2010 may have influenced the availability of aerial insects with aquatic larval stages and made our study site more attractive to Tree Swallows arriving from spring migration but there was not an uptick in nest box occupancy or advancement in first egg dates associated with the addition of ponds. Berzins et al. (2020) found that spring pond density had positive effects on female Tree Swallow life time reproductive success in Saskatchewan and British Columbia, Canada.

Most researchers that have analyzed the relationship between Tree Swallow first egg dates and increasing spring temperatures over the last several decades have found an advancement of Tree Swallow first egg dates (Dunn and Winkler 1999, Rioux Paquette et al. 2014, Irons et al. 2017, Shipley et al. 2020) but, except for Bourret et al. (2015), have not separately analyzed SY and ASY female first egg dates. Similar to the SY females in our study population, Bourret et al. (2015) found that the first egg dates of SY females in southern Québec were about 5 d later than those of ASY females and were significantly earlier when spring temperatures warmed between 2004 and 2015. The first egg dates of ASY females in same study also advanced with warmer spring temperatures (Bourret et al. 2015).

Table 3. The relationship between first egg dates, years since 1992, weather variables, and percent boxes occupied. Effect estimates calculated using PROC MIXED in SAS 9.4 (SAS Institute 2016). Number of years since 1992 = 26. NAOI = North Atlantic Oscillation Index. Statistically significant P values (i.e., P ≤ 0.05) indicated in bold font. For second year (SY) females, error df = sample size – number of parameters (n = 10) in model. In this model, SY females were those SY females from whom we recorded only once their first egg dates (i.e., SY females that did not return one or more times as an after-second-year [ASY] female). For ASY females the first egg dates of 665 females were recorded one or more times. Therefore, the error df for the intercept = 665 – 1. For all other parameters, error df = 1000 – 665 – 1. AIC = Akaike Information Criterion (Akaike 1974).

		Percent boxes occupied included in model				Percent boxes occupied not included in model			
Female plumage category	Effect	Estimate ± SE	Error df	*t*	P	Estimate ± SE	Error df	*t*	P
Second Year (n = 273)	Intercept	150.96 ± 8.64	263	17.48	**< 0.001**	152.10 ± 7.98	264	19.06	**< 0.001**
	Years since 1992	-0.23 ± 0.11	263	-2.08	**0.04**	-0.23 ± 0.11	264	-2.06	**0.04**
	Mean daily April temp.	-0.79 ± 0.58	263	-1.37	0.17	-0.81 ± 0.58	264	-1.41	0.16
	Total April rain	-0.10± 0.17	263	-0.61	0.54	-0.09 ± 0.16	264	-0.54	0.60
	April days with rain	-0.12 ± 0.42	263	-0.28	0.78	-0.19 ± 0.37	264	-0.53	0.60
	Mean daily May temp.	0.56 ± 0.34	263	1.64	0.10	0.56 ± 0.34	264	1.62	0.11
	Total May rain	0.34 ± 0.19	263	1.78	0.08	0.34 ± 0.19	264	1.80	0.07
	May days with rain	-0.74 ± 0.38	263	-1.97	**0.05**	-0.68 ± 0.33	264	-2.07	**0.04**
	NAOI	-1.07 ± 0.80	263	-1.34	0.18	-1.05 ± 0.80	264	1.32	0.19
	Percent nest boxes occupied	0.02 ± 0.05	263	0.35	0.73				
		AIC = 2052.5				AIC = 2048.4			
After-Second-Year (n = 1000)	Intercept	149.09 ± 3.27	664	45.57	**< 0.001**	146.29 ± 3.08	664	47.53	**< 0.001**
	Years since 1992	-0.08 ± 0.05	326	-1.79	0.07	-0.12 ± 0.04	327	-2.68	**0.008**
	Mean daily April temp.	-0.62 ± 0.22	326	-2.77	**0.006**	-0.62 ± 0.22	327	-2.76	**0.006**
	Total April rain	0.10 ± 0.08	326	1.38	0.17	0.07 ± 0.07	327	0.96	0.33
	April days with rain	-0.18 ± 0.15	326	-1.22	0.22	-0.07 ± 0.14	327	0.46	0.65
	Mean daily May temp.	-0.38 ± 0.13	326	-2.99	**0.003**	-0.36 ± 0.13	327	-2.81	**0.005**
	Total May rain	0.11 ± 0.07	326	1.60	0.11	0.11 ± 0.07	327	1.64	0.10
	May days with rain	0.13 ± 0.14	326	0.91	0.36	-0.0001 ± 0.13	327	0.00	1.00
	NAOI	0.29 ± 0.32	326	0.90	0.37	0.26 ± 0.32	327	0.80	0.42
	Percent nest boxes occupied	-0.05 ± 0.02	326	-2.49	**0.01**				
		AIC = 6872.7				AIC = 6872.8			

There appear to be study population differences in the relationship between Tree Swallow first egg dates and spring temperatures. For example, Hussell (2003) found that first egg dates were earlier when spring temperatures were warmer but did significantly change between 1969 and 2001 at Long Point in southern Ontario. Moreover, first egg dates did not advance between 2000 and 2015 in Ohio (Sockman and Courter 2018).

Studies (e.g., Dunn and Winkler 1999, Rioux Paquette et al. 2014, Irons et al. 2017, Shipley et al. 2020) that did not separately analyze the relationships between spring temperatures, first egg dates, and female plumage category paint only a partial picture of the effect of increasing spring temperatures on the timing of first egg dates in Tree Swallows. Thus, observations of the timing of first egg dates in other Tree Swallow populations plus our observations that the relationships between first egg dates, female plumage category, and weather conditions varied yearly suggest that the factors that influence the first egg dates of Tree Swallows are complex and vary throughout their range.

First egg dates are influenced by temperature change on the global and site-specific scale for many aerial insectivorous species (Dunn 2019). As elsewhere in the temperate zone, spring weather conditions can be variable in west Michigan but they are probably less variable than those experienced by Tree Swallow breeding populations located further inland from the weather-modifying effects of large bodies of water (Frankson et al. 2022); our study site is located approximately 27 km east of Lake Michigan. Hussell (2003) noted that although Tree Swallow first egg dates at Long Point, Ontario were negatively correlated with spring temperatures they did not significantly change from 1969 to 2001. Long Point is a narrow peninsula extending southward into Lake Erie. Indeed, the weather-moderating effects of the Great Lakes and distance from the Atlantic Ocean may play a role in the increases observed in Tree Swallow populations monitored in the southern Great Lakes region (Michel et al. 2016) while their populations elsewhere in their range are declining, especially in eastern North America (Nebel et al. 2010, Smith et al. 2015, Imlay and Leonard 2019, Rosenberg et al. 2019).

Because breeding songbirds may have variable sensitivities to changing climatic conditions related to site-specific nesting locations and thus different climatic factors, increases in spring temperatures may not be the only factor influencing first egg dates. For example, some species are influenced more by precipitation (e.g., Eastern Phoebe [*Sayornis phoebe*], Ovenbird [*Seiurus aurocapilla*], and Hooded Warbler [*Setophaga citrina*]) whereas others (e.g., Cedar Waxwing [*Bombycilla cedrorum*], American Redstart [*Setophaga ruticilla*], and American Goldfinch [*Spinus tristis*]) are influenced more by temperature (McDermott and DeGroote 2016). Rainfall significantly affected the advancement of the first egg dates of SY but not ASY females in our study. Rainfall has been a factor associated with delaying first egg dates in Tree Swallow populations in Alaska (Irons et al. 2017) and Ohio (Sockman and Courter 2018). Windy conditions also decrease the availability of aerial insects (Freeman 1945). Irons et al. (2017) found that windy conditions delayed first egg dates of breeding Tree Swallows in Alaska. We did not evaluate the effect of windy conditions on first egg dates because of the paucity of data at our study site for that variable.

In general, songbirds in the Northern Hemisphere have responded to increasing spring temperatures by beginning egg-laying earlier. However, the phenological responses of Northern Hemisphere songbirds in response to increasing spring temperatures are not uniform and vary geographically and with microclimates (Sanz 2002, 2003, Both and te Marvelde 2007, Møller 2008, Burger et al. 2012, Townsend et al. 2013). For example, Sockman and Courter (2018) reported that the first egg dates of both Eastern Bluebirds and Tree Swallows were associated with latitude and microclimate variation in regions of Ohio.

Although climate indices like the NAOI are associated with continent-wide changes in climate and have been associated with variations in the population dynamics of aerial insectivores elsewhere in North America (Michel et al. 2021), we did not detect a statistically significant relationship between NAOI and first egg dates. This result is not surprising because our study site is located 1287 km west of the Atlantic Ocean. Moreover, the effects of the NAO on the phenology of spring migration and thus the timing of breeding of birds in the Northern Hemisphere are not yet fully understood. Yearly variation in the NAO may contribute only little to the variation in the phenology of spring migration and thus the timing of breeding (Haest et al. 2018).

Identifying the ecological factors influencing Tree Swallow first egg dates will help increase our understanding of how songbirds respond to climate change in general, and may, more specifically, help explain the decline of aerial insectivores in eastern North America (Nebel et al. 2010, Smith et al. 2015, Imlay and Leonard 2019, Rosenberg et al. 2019). Laying earlier in the season is generally considered to be adaptive because female Tree Swallows that begin egg laying earlier in the season produce more local recruits than do those that begin egg laying later (Winkler and Allen 1996, Winkler et al. 2004, Shutler et al. 2006, Dawson 2008, Lombardo et al. 2020). However, aerial insectivores, including Tree Swallows, may be especially susceptible to inclement weather (e.g., cold snaps) and climate change (Winkler et al. 2013, Berzins et al. 2020, Shipley et al. 2020, Wheelwright et al. 2022) because of their effects on the abundance of aerial insects. Therefore, a mismatch between the availability of ecological requirements (e.g., food resources) of breeding birds arriving on breeding grounds and egg-laying earlier has the potential to cause further declines in songbird populations (Saino et al. 2011, Visser and Gienapp 2019). This may be partly responsible for the declines observed in a variety of local Tree Swallow populations (Shutler et al. 2012). Consequently, we predict that advancing first egg dates in the face of unpredictable periods of inclement weather (e.g., cold snaps, rain) during the early part of the Tree Swallow breeding season may lead to further population declines (Berzins et al. 2020, Shipley et al. 2020). This is likely to have a greater negative effect on the lifetime reproductive success of ASY than of SY females because ASY females typically begin egg laying earlier in the season (Winkler et al. 2020). Consequently, recruitment in subsequent breeding seasons is predicted to decline because most local recruits are produced earlier rather than later in the breeding season (Winkler et al. 2004, Shutler et al. 2006, Dawson 2008, Lombardo et al. 2020). Moreover, migratory species like Tree Swallows may continue to suffer lower reproductive success if the climate continues to warm (Halupka et al. 2023).

In summary, just as multiple factors are likely responsible for Tree Swallow population declines in some locations in eastern North America (Imlay and Leonard 2019, Spiller and Dettmers 2019), the factors influencing the timing of first egg dates are also likely to be complex. For example, previous analyses that revealed that advancements of Tree Swallow first egg dates were associated with the increasing spring temperatures but did not examine the relationships between first egg dates and female plumage category may only partly predict how other Tree Swallow life history characteristics associated with first egg dates (e.g., the probability of local recruitment) might be shaped by climate change.

Author Contributions:

Lombardo: data collection, data analysis, writing and revising paper
Wagner: data collection, data analysis
Laughlin: data collection, data analysis
Otieno: data analysis, revising paper
Rosendall: data analysis, revising paper
Voetberg: data analysis, revising paper
Hoban: data analysis, revising paper

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Data Availability:

The data that support the findings of this study are openly available at https://doi.org/10.6084/m9.figshare.25315669.v1. Ethical approval for this research study was granted by Institutional Animal Care and Use Committee at Grand Valley State University.

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