

CLIMATE CHANGE, SPRING TEMPERATURES, AND TIMING OF BREEDING OF TREE SWALLOWS (*TACHYICINETA BICOLOR*) IN SOUTHERN ONTARIO

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ABSTRACT.—Several European studies have indicated advances in breeding dates of birds in the last 30 years, which authors attributed to climate change. In North America, Dunn and Winkler (1999) reported a continent-wide advance of five to nine days in breeding dates of Tree Swallows (*Tachycineta bicolor*) between 1959 and 1991. I present results of an intensive study of Tree Swallows breeding on and near Long Point, Ontario, at four sites monitored 1969–2001, 1977–1986, 1978–2001, and 1987–2001. Local air temperatures varied among sites, according to distance from Lake Erie, but there was no significant regional trend in April and May temperatures between 1969 and 2000. Median and 10th percentile dates of clutch initiation by females that were at least two years old varied among years by up to 20 days overall and 18 days within sites, and differed by 0–14 days between sites in the same year. There were no significant differences in average timing of laying among the 1970–1980, 1980–1990, and 1990–2000 periods. Nevertheless, there was a significant trend towards earlier laying in 1990–2000, which was attributable to exceptionally early laying and warm May weather in 1998–2001. Across all sites, median dates of clutch initiation were strongly correlated with average daily maximum temperatures in the first four, five-day periods in May, but clutches at one site were initiated three days earlier than predicted by temperatures alone. I estimate that climate warming of 5°C in May could result in an average advance of about seven days in the median date of laying of Tree Swallows at those sites. My results indicate that spring temperatures are strongly correlated with timing of laying, but show that spring temperatures have not increased in the Long Point region and timing of the breeding season has not advanced throughout North America. Received 5 September 2002, accepted 13 March 2003.

RÉSUMÉ.—Plusieurs études européennes ont révélé un devancement de la date de reproduction chez les oiseaux au cours des 30 dernières années. Les auteurs ont attribué ce phénomène aux changements climatiques. En Amérique du Nord, Dunn et Winkler (1999) ont reporté, à l'échelle du continent, un devancement de cinq à neuf jours de la date de reproduction chez l'Hirondelle bicolor (*Tachycineta bicolor*) entre 1959 et 1991. Je présente les résultats d'une étude approfondie de la reproduction chez l'Hirondelle bicolor dans quatre sites de la région de Long Point, Ontario. Le suivi de chacun de ces sites a été effectué de 1969 à 2001, 1977 à 1986, 1978 à 2001 et de 1987 à 2001. La température locale de l'air variait entre les sites et elle était fonction de la distance au Lac Érié. Par contre, il n'y avait pas de tendance régionale significative dans les températures des mois d'avril et mai entre 1969 et 2000. Les dates médianes et du dixième de centile d'initiation de couvées, par des femelles âgées d'au moins deux ans, variaient entre les années, et ce jusqu'à 20 jours pour l'ensemble des sites et 18 jours à l'intérieur d'un même site. Ces dates différaient également de 0 à 14 jours entre les sites pour une même année. Il n'y avait pas de différence significative dans la chronologie moyenne de ponte entre les périodes 1970-1980, 1980-1990 et 1990-2000. Néanmoins, il y avait une différence significative allant dans le sens d'une ponte plus précoce en 1998-2001. Pour tous les sites, les dates d'initiation de couvées étaient fortement corrélées avec les températures maximales moyennes dans les quatre premières périodes de cinq jours en mai. Mais, les couvées d'un site étaient initiées trois jours plus tôt que la date prédite à partir des températures seulement. J'ai estimé que le réchauffement climatique de 5°C en mai pourrait résulter dans un devancement moyen d'environ sept jours de la date médiane de ponte chez l'Hirondelle bicolor dans ces

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sites. Mes résultats indiquent que les températures printanières sont fortement corrélées avec la chronologie de ponte. Mais, ils montrent également que les températures printanières n'ont pas augmenté dans la région de Long Point et que la chronologie de la saison de reproduction n'a pas été devancée à travers toute l'Amérique du Nord.

IT HAS LONG been known that many factors influence timing of breeding in birds. In a brief review published more than 60 years ago, Margaret Morse Nice pointed out that although the timing of laying "must be a genetically controlled matter in each species, nevertheless it is influenced by environmental factors" (Nice 1937:97). She mentioned length of daylight, altitude, temperature, humidity, precipitation, food supply, and changes in nesting habitat as environmental variables that were known or suspected to directly affect breeding seasons. However, most early studies provided only anecdotal or qualitative evidence in support of those ideas, because the spatial or temporal extent of the data was insufficient for rigorous quantitative analyses.

By the 1970s, several long-term studies in Europe had shown that dates of egg-laying were negatively correlated with spring temperatures in Great (*Parus major*) and Blue tits (*P. caeruleus*) (Kluyver 1952, Perrins 1965, Lack 1966, Van Balen 1973, Slagsvold 1976). Recent work has indicated that, in warm springs, not only timing of breeding of the Pied Flycatcher (*Ficedula hypoleuca*), but also its dates of arrival and postfledging dispersal were earlier, and clutch size and breeding success were higher (Winkel and Hudde 1997, Sokolov 2000).

Concern about effects of climate change has resulted in renewed interest in the relationship between temperature and timing of breeding. An analysis of laying dates of 65 species of birds breeding in Britain showed that 20 species had significant trends towards earlier laying between 1971 and 1995, whereas only one laid significantly later (Crick et al. 1997). Subsequent analyses correlated those trends with spring temperatures and the North Atlantic Oscillation (Forchhammer et al. 1998, McCleery and Perrins 1998, Crick and Sparks 1999). In England, March and April temperatures showed a curvilinear trend since 1940, becoming cooler in the 1960s and 1970s, then warming sharply in the mid-1990s, and were related to laying dates among 17 species that showed significant weather effects in Britain (Crick and Sparks 1999).

In North America, geese nested progressively earlier in the Hudson Bay region from 1951 to 1986, which was attributed to a warming trend in the 1970s, following unusually cool weather from 1964 to 1970 (MacInnes et al. 1990). Another study reported an advance of 10.1 days in the mean date of first laying of Mexican Jays (*Aphelocoma ultramarina*) in southeastern Arizona from 1971 to 1998 (Brown et al. 1999).

An analysis of timing of laying of 3,450 clutches of Tree Swallows (*Tachycineta bicolor*) from most of the species' breeding range across the northern United States and Canada revealed an advance in laying date of up to nine days during 1959 to 1991, which the authors attributed to increasing surface air temperatures during that period (Dunn and Winkler 1999). That study was based on nest records submitted to several nest record card programs. Some of those data may have originated from intensive studies at specific sites, but many records were collected opportunistically. Moreover, data included records from the southern Great Lakes region, but few from north of the lakes in Ontario.

Here, I present results on timing of breeding from an intensive study involving over 3,000 clutch initiations of Tree Swallows breeding in nest boxes at and near Long Point, Ontario, on the north shore of Lake Erie. Data are available from one site on Long Point from 1969 to 2001, and from three other sites on the nearby mainland for various periods during 1977–2001. I looked for evidence of long-term changes in local spring temperatures and the initiation of egg-laying, and for relationships between spring temperatures and egg-laying.

STUDY AREA AND METHODS

I examined dates of clutch initiation by Tree Swallows nesting in nest boxes maintained by Long Point Bird Observatory at four sites near Port Rowan, Ontario, Canada (42°37'N, 80°27'W): Long Point (LP), 1 km from the eastern tip of the Long Point peninsula in Lake Erie; Sewage Lagoons (SL), Port Rowan's waste treatment ponds ~0.5 km west of the village; Backus Field (BF), 3.25 km north-northwest of Port

Rowan in the Backus Conservation Area; and Mud Creek (MC), 1 km east of BF.

Long Point, BF, and SL nest boxes were occupied by Tree Swallows since 1969, 1976, and 1977, respectively. The LP site is 33 km east of SL in dune grass habitat with many shallow ponds and scattered cottonwoods (*Populus deltoides*). At SL, nest boxes were on a wide grassy bank forming the perimeter of two ponds of 5.4 and 2.2 ha, separated by a 10 m wide embankment. At BF, nest boxes were on strips of uncultivated land planted with young trees among three cultivated fields, adjacent to a wooded area with large trees. By 1986, the habitat at BF was becoming unsuitable and in 1987 BF nest boxes were moved to MC, which was similar to and in the same creek system as BF. From 1987 to 1995, nest boxes at MC were in and along the sides of the creek valley and on uncultivated land adjacent to a hay field. In 1996, ~80% of nest boxes were moved out of the valley into the hay field, which was not subsequently cultivated. Backus Field and MC were the most sheltered of the sites, with the most varied habitats and lowest insect abundance. Sewage Lagoons was relatively uniform, and its ponds usually produced large numbers of flying insects. Long Point was very exposed to effects of severe weather but contained natural ponds that produced moderate to large numbers of insects (Hussell and Quinney 1987, D. J. T. Hussell unpubl. data). Mean daily temperatures in April and May averaged about 0.8 and 1.0°C lower, respectively, at LP than at the mainland sites; but the difference between daily maximum and minimum temperatures was lower at LP than at the mainland sites because of the moderating effect of Lake Erie.

Plywood nest boxes stood ~1.5 m above the ground (or sometimes above water at LP) on steel poles spaced ~24 m apart in lines or grids. With few exceptions (all in the earliest years at LP), nest boxes were of similar design, with a floor measuring 140 × 140 mm, and an opening 35 mm in diameter centered 155 mm above the floor. Some boxes were more closely spaced or had a reduced floor area, but those were excluded from the present analysis.

During the laying period nest boxes were checked daily, usually in late morning or afternoon, or rarely every second or third day. Eggs were numbered with indelible ink marks when first found. Eggs are laid in the early morning (Robertson et al. 1992, D. J. T. Hussell unpubl. data), so clutch initiation date was the date on which the first egg was found, if the nest had been checked daily. If not, clutch initiation date was calculated assuming that one egg was laid per day. Occasionally, the first two eggs appeared between daily checks, in which case clutch initiation was arbitrarily assigned to the previous day or the current day according to whether the previous day's nest check was before noon (mean solar time) or after noon, respectively.

After the eggs hatched, adults were trapped in their nest boxes, sexed by the presence of a brood patch (female) or cloacal protuberance (male), and banded if not previously banded. Females were aged as yearling (SY, birds in their second calendar year) or older (ASY, birds in their third or later calendar year) on the basis of plumage differences (Hussell 1983a). A few females could not be aged. Yearling and unaged females were excluded here because yearling females appear to differ from older ones in several reproductive variables (De Steven 1978, Stutchbury and Robertson 1988) and few of them nested at any of my sites. I also excluded clutch initiation dates of females that were not trapped (usually because their clutches were abandoned or lost to predators); of second clutches in the same nest box (which may or may not have been repeat clutches by females that had lost or abandoned an earlier clutch); of clutches that lost two or more eggs during egg-laying or had laying interruptions of >5 days, possibly indicating takeover by a different female (Leffelaar and Robertson 1985); and of clutches in nests where there was evidence that eggs were laid by more than one female (Quinney 1983). Because Tree Swallows are almost never double brooded (Hussell 1983b) and >90% of nest boxes were usually occupied by swallows early in the breeding season, those restrictions ensure that all or nearly all clutch initiation dates used here were of first nesting attempts by ASY females.

Daily maximum and minimum temperatures were measured at each site with an alcohol-mercury maximum-minimum thermometer, read and reset in the morning and evening. At SL, BF, and MC, the thermometer was in a simple screen (to protect it from direct sunlight) ~1 m above ground at the same place among nest boxes each year, except that the MC thermometer was moved to a new location in 1996, so that it was within the area of the relocated nest boxes. At LP, the thermometer was in a screen on the north-facing wall of a building ~50 m from the southeast corner of the nest box grid. Those temperatures were available starting in 1978 at SL and BF (1985 missing from both sites), 1987 at MC and 1989 at LP. Temperature measurements started on dates ranging from 24 April to 15 May and there were occasional days with missing data within the seasons, so missing data were estimated from temperatures recorded at weather stations for all dates 1969–2000 at Erie, Pennsylvania (~50 km south of LP on the south shore of Lake Erie), for 1989–1999 at Long Point lighthouse (1 km east of LP), and for 1978–1999 at Simcoe, Ontario (25 km northeast of MC). First, separate regressions were run with known Long Point and Simcoe daily maximum, minimum, and mean temperatures as dependent variables and 13 predictor variables consisting of 1st- to 4th-order date terms, Erie daily maximum, minimum, and mean temperatures, three interaction variables between date and the three

Erie temperature variables, and three interactions among pairs of the three Erie temperature variables. Those regression equations provided estimates of missing Long Point and Simcoe temperatures ($R^2 = 0.925$ to 0.969 ; $n = 1,457$ for Long Point, $n = 2,174$ or $2,175$ for Simcoe). Following a similar procedure, the measured or estimated Long Point and Simcoe temperatures were then used to estimate missing LP, SL, BF, and MC maximum and minimum temperatures. Eighteen predictor variables were used, consisting of Long Point and Simcoe maximum, minimum, and mean temperatures and the square of those variables; three interactions between pairs of the Long Point maximum, minimum and mean temperatures; and three interactions between pairs of Simcoe maximum, minimum, and mean temperatures. To predict MC maximum and minimum temperatures, a dummy variable representing the 1987–1996 and 1997–2001 periods was added (because of the different thermometer and nest box positions in those two periods) and six interactions between the period dummy variable and Long Point and Simcoe maximum, minimum, and mean temperatures. After deletion of outliers (>2 standard deviations [SD] from the predicted value, probably because of errors reading thermometers by me or my assistants), regressions were run again and yielded R^2 values ranging from 0.862 to 0.970 ($n = 551$ and 544 for LP, $1,076$ and $1,091$ for SL, 465 and 466 for BF, and 774 and 784 for MC, for maximum and minimum temperatures, respectively). Those regression results were used to estimate missing values and replace outliers.

Medians and 10th percentiles of clutch initiation dates were analyzed for each site and year. The median provides a measure of the middle of the breeding season, whereas the 10th percentile is close to the earliest date but, unlike the earliest date, is independent of sample size. I excluded site years with fewer than 10 clutch initiations of ASY females, which removed data from LP in 1973 and 1974, BF in 1976, and SL in 1977, leaving a total of 3,126 clutch initiations for analysis. Because site-year sample sizes varied from 10 to 85 (mean = 39.1, SD = 15.4, $n = 80$), all regression analyses were weighted in proportion to sample size.

Median and 10th percentile dates of clutch initiation were the days i and j , respectively, on which the 50th and 10th percentile initiations occurred. As variables in analyses, they were defined more precisely as follows. Median date of clutch initiation is defined as $i - 0.5 + (N / 2 - F_{i-1}) / f_i$, where N , F_{i-1} , f_i were the total number of clutch initiations, the cumulative number of initiations up to and including day $i - 1$, and number of initiations on day i , respectively (Zar 1999). Similarly, 10th percentile date of clutch initiation is $j - 0.5 + (N / 10 - F_{j-1}) / f_j$.

Because the calendar date of the vernal equinox varies (range ~ 0.97 days in 1969–2001) and is currently becoming progressively earlier, there is a small

bias toward an earlier calendar date of all spring phenomena (Sagarin 2001). That bias was corrected by subtracting the difference between the actual and the mean calendar date of the vernal equinox (for the years 1969–2001) from the median and 10th percentile dates of clutch initiation. Likewise, for estimating temperature trends and effects of temperatures on clutch initiations, temperatures were adjusted for variations in the vernal equinox. For example, for a year in which the vernal equinox was 0.2 days earlier than average, the mean temperature for any day k was calculated as $0.2 \times T_{k-1} + 0.8 \times T_k$, where T_k and T_{k-1} are mean temperatures on day k and on the preceding day, respectively. If the vernal equinox was 0.2 days later than average, the mean temperature on day k was $0.8 \times T_k + 0.2 \times T_{k+1}$.

Trends in timing of the median and 10th percentile dates of clutch initiations with year were modeled with polynomial regressions in year. I chose the order of polynomial that minimized Akaike's Information Criterion (AIC), while retaining all lower order terms, provided that there were at least five cases per independent variable. I tested whether timing of clutch initiations and pattern of change in timing differed among sites by including dummy variables for site and site-year interaction variables. Differences in timing between single years and between blocks of years estimated by the polynomial regressions were tested with methods described in Francis and Hussell (1999). To investigate changes in timing of breeding, I chose to test differences in estimated dates of clutch initiations between pairs of the years 1970, 1980, 1990, and 2000; and in estimated mean dates of clutch initiations between pairs of the periods 1970–1980, 1980–1990, and 1990–2000.

Average difference in timing between the 10th percentile and median dates of clutch initiation were estimated by fitting a covariance model in which the 10th percentile and median dates were the factors and polynomial terms in year were the covariates. I tested whether the pattern of change over time differed between the 10th percentile and median dates by including interaction terms between the factors and covariates in the preceding model.

Because of the large number of potential independent variables, it is not valid to attempt to test the effects of each day's temperatures on clutch initiation. Instead, effects of maximum and minimum site temperatures averaged over arbitrary five-day periods starting 1 April were modeled with a stepwise procedure, as follows. First, the five-day temperature period with the strongest relationships with median and 10th percentile dates of clutch initiation across all sites was found. That proved to be the average maximum temperature for 6–10 May in both cases. Then average maximum temperatures for adjacent five-day periods were added to the regression (i.e. the next periods tested were 1–5 May and 11–15 May) until no

additional periods added explanatory power to the regressions at $P < 0.05$. Then minimum temperatures for each five-day period were tested to determine whether those variables explained additional variation ($P < 0.05$). Next, dummy variables for site and site-temperature interaction variables were added (using only those temperature variables already in the model) in a backward stepwise regression (P to retain = 0.1), to determine whether there were any additional effects of site that were not explained by temperatures alone. Finally, any remaining effect of year was examined by testing the significance of polynomial year terms added to the model.

To determine whether there was any change in local temperature climate between 1969 and 2000, similar methods to those for clutch initiation (above) were used on means of maximum, minimum, and mean temperatures for Erie, Pennsylvania for the months of April and May.

RESULTS

CHANGES IN TEMPERATURE CLIMATE AT ERIE

April and May mean maximum daily temperatures increased from 1969 to 2000 by an average of 0.022 and 0.031°C per year; mean minimum daily temperatures by 0.024 and 0.038°C per year; and mean of mean daily temperatures increased by 0.027 and 0.040°C, respectively. However, none of the trends was significant ($P > 0.24$ in all cases). All changes in mean monthly temperatures at Erie from 1969 to 2000 were linear. Quadratic to 5th-order polynomial terms in year were tested and found to be not significant.

TIMING OF CLUTCH INITIATION

Median and 10th percentile dates cited below for specific years are raw calendar dates. Unless stated otherwise, all other results are based on precise dates adjusted for variation in the vernal equinox (see above).

Among all sites and years the start of egg-laying, represented by the 10th percentile of clutch initiations, ranged from 7 to 26 May (Table 1). Median dates averaged 3.5–4.1 days later than the 10th percentile and ranged from 10 to 28 May (Table 1).

Within years, calendar dates of 10th percentile and median dates of clutch initiations differed between sites by 0–14 days and 0–10 days, respectively (means 4.01 and 3.80 days; SD = 2.74 and 2.55, respectively; $n = 73$). Clutch ini-

tiations at LP averaged 3.7–5.9 days later than at the other sites (Table 1).

Patterns of change in 10th percentile and median dates of clutch initiations with year, as well as differences among sites, proved to be very similar (see below), so results of site and year effects are presented only for median dates.

Clutch initiations at Long Point.—Median dates of clutch initiation at LP varied from 14 May (2000) to 28 May (1978 and 1997; Table 1). Five of the six earliest median dates occurred after 1990 (1982, 1991, 1998, 1999, 2000, and 2001), whereas the latest were spread more evenly across the period (Fig. 1A).

A 4th power polynomial in year gave the best fit to the annual median dates of clutch initiation ($R^2 = 0.310$, $P = 0.041$, $n = 31$; Fig. 1A). The mean of the median dates did not differ significantly in any of the comparisons between pairs of decades (1970–1980, 1980–1990, and 1990–2000; $P > 0.515$ in all comparisons). The regression estimate of the median date for 2000 was 5.0 days earlier than for 1970 (marginally nonsignificant; $P = 0.084$); 5.1 days earlier than for 1980 ($P = 0.009$); and 5.9 days earlier than for 1990 ($P = 0.007$); and estimates for 1970, 1980, and 1990 did not differ from each other ($P > 0.549$ in all comparisons).

Clutch initiations at Sewage Lagoons.—Median dates of clutch initiation at SL varied from 10 May (1998, 1999, 2000, and 2001) to 27 May (1997; Table 1). The five earliest median dates were after 1990 (1993, 1998, 1999, 2000, and 2001) and the latest was in the same decade (1997; Fig. 1B).

A cubic regression in year gave the best fit to annual median dates of clutch initiation according to AIC_c , although marginally not significant ($R^2 = 0.301$, $P = 0.062$, $n = 24$; Fig. 1B). Mean of the median dates did not differ significantly between decades 1980–1990 and 1990–2000 ($P = 0.964$). The regression estimate of the median date for 2000 was 6.6 days earlier than for 1980 ($P = 0.019$) and 6.0 days earlier than for 1990 ($P = 0.026$), but median dates did not differ between 1980 and 1990 ($P = 0.802$).

Clutch initiations at Backus Field and Mud Creek.—Dates of clutch initiation at BF and MC were similar to each other and to those at SL (Table 1, Fig. 1C).

At MC, linear regressions in year provided the best fit to median dates of clutch initiation and showed that they were nonsignificantly 4.2 days ($P = 0.134$) earlier in 2000 than in 1990.

TABLE 1. Median and 10th percentile dates of clutch initiations of Tree Swallows.

Site	Years	n	Date of clutch initiation (May) ¹	
			10th percentile	Median
Long Point	1969–1972, 1975–2001	31	18.9 (10–26)	22.4 (14–28)
Sewage Lagoons	1978–2001	24	13.0 (7–22)	16.5 (10–27)
Backus Field	1977–1986	10	14.9 (12–22)	18.7 (14–23)
Mud Creek	1987–2001	15	13.0 (8–21)	17.1 (11–25)

¹Dates shown are weighted means (weights = site-year sample sizes), corrected for variation in the vernal equinox (see text), and range of calendar dates (in parentheses).

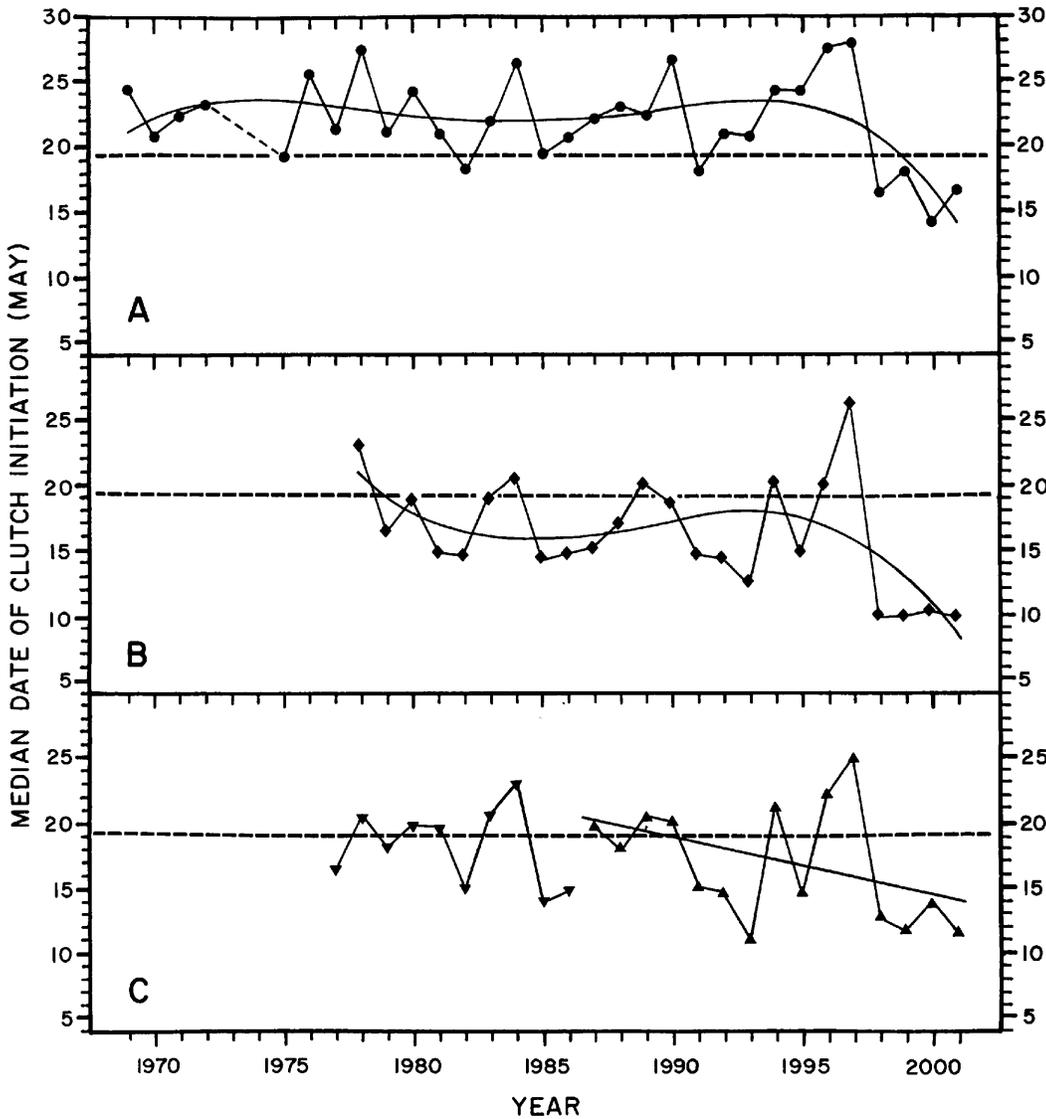


FIG. 1. Median dates of clutch initiation of ASY female Tree Swallows at (A) Long Point (LP), 1969–2001; (B) Port Rowan Sewage Lagoons (SL), 1978–2001; (C) Backus Field (BF), 1977–1986, and Mud Creek (MC), 1987–2001. Horizontal broken line shows unweighted mean of median dates for the three sites monitored in 1978–2001. Curves (in A and B) and straight line (in C) show regression estimates of the trends (see text).

At BF, there were insufficient data to analyze trends in timing of breeding at that site, but the data were used in the following combined analyses of all sites.

Clutch initiations at all sites.—A 4th-power polynomial regression with dummy variables for site and site-year interaction terms indicated that the pattern of change with time of median dates of clutch initiation did not differ among sites. However, median dates were earlier at the mainland sites than at LP by 5.5 days at SL, 4.0 days at BF, and 4.2 days at MC ($P < 0.022$ in each case).

Considering all sites together, the pattern of change in the median date of clutch initiation was similar to that at LP alone. The mean of the median date did not differ significantly in any of the comparisons among pairs of decades (1970–1980, 1980–1990, and 1990–2000, $P > 0.252$ in all comparisons). The regression estimate of median date of clutch initiation for 2000 was 4.7 days earlier than for 1970 ($P = 0.065$), 5.3 days earlier than for 1980 ($P < 0.001$), and 5.5 days earlier than for 1990 ($P = 0.001$), and estimates of the median dates for 1970, 1980, and 1990 did not differ ($P > 0.711$ in all comparisons).

An analysis of covariance, with site and date of clutch initiation category (10th percentile and median) as factors and polynomial terms in year as covariates, showed that there were no significant differences in the pattern of change over time or among sites in those two measures of timing of breeding ($P > 0.05$). The 10th percentile date of clutch initiations averaged 3.6 days earlier than the median across all sites ($P < 0.001$); and SL, BF, and MC averaged 5.5, 4.8, and 4.3 days earlier than LP in median and 10th percentile dates of clutch initiation, respectively ($P < 0.001$).

VARIATION IN MAY TEMPERATURES AT LONG POINT, SEWAGE LAGOONS, BACKUS FIELD, AND MUD CREEK

Mean maximum daily temperatures during 1–20 May varied among years and between sites by 10.8°C, from 13.0 to 23.8°C (maximum temperatures in that time period have the strongest relationship to clutch initiation; see below; Fig. 2). With one exception (1984), LP always had the lowest temperatures of the four sites, and SL was always intermediate between LP and the other two mainland sites. Annual temperatures

differed by up to 8.8°C within sites and were positively correlated among sites. Nevertheless, differences among sites in the same year ranged from <0.6°C to nearly 4.8°C (mean = 3.25, SD = 1.00, $n = 24$ years with data from three sites). Therefore, in the following analyses, each site year was treated as providing an independent observation of the effect of temperature on timing of clutch initiation.

EFFECTS OF TEMPERATURE ON TIMING OF CLUTCH INITIATION

Considering all sites together, maximum daily temperatures in the first four, five-day periods in May gave the best prediction of the median date of clutch initiation. Neither mean minimum temperatures or site-temperature interaction variables explained additional variation in median date ($P > 0.100$); but addition of dummy variables for site indicated that median dates were significantly earlier at SL by an average of 3.2 days ($P < 0.001$) than predicted by temperature alone. Median date of clutch initiation was then estimated as $\hat{Y}_{ij} = 20.280 - 0.538X_{1ij} - 0.408X_{2ij} - 0.312X_{3ij} - 0.206X_{4ij} - 3.194S_{SL}$ ($R^2 = 0.848$, $P < 0.001$; Table 2), where \hat{Y}_{ij} is the estimated median date of clutch initiation; and X_{1ij} , X_{2ij} , X_{3ij} , and X_{4ij} are differences from normal mean maximum temperatures (°C) for 1–5, 6–10, 11–15, and 16–20 May, respectively, at site i in year j ; and S_{SL} is a dummy variable for site whose value was 1 or 0 when site i was SL or another site, respectively. (Normal temperatures were means of LP, SL, and MC temperatures for 1969–2000.) Standardized regression coefficients indicated that temperatures in the first two five-day periods in May had the largest influence on the prediction of the median date, followed by the SL site and temperatures in the second two five-day periods, in that order (Table 2).

Successive inclusion of 1st- to 4th-order year terms in the preceding model did not add significantly to explained variation in median date of clutch initiation ($P > 0.05$), but addition of 1st- to 5th-order terms was significant ($P = 0.020$), possibly indicating that a small proportion of the longer term variation in the median dates was not explained by the temperature and site variables in the model. Moreover, a considerably higher proportion of variance in median dates was explained by temperatures and site alone ($R^2 = 0.848$) than by a 5th-power polynomial in

TABLE 2. Influence of maximum daily temperatures and site on median dates of clutch initiation.

Period (May)	Variable	Regression coefficient	Standardized coefficient	<i>P</i>
	Intercept	20.280		
1-5	T_1	-0.538	-0.384	<0.001
6-10	T_2	-0.408	-0.309	<0.001
11-15	T_3	-0.312	-0.209	0.002
16-20	T_4	-0.206	-0.141	0.012
	S_{SL}	-3.194	-0.297	<0.001

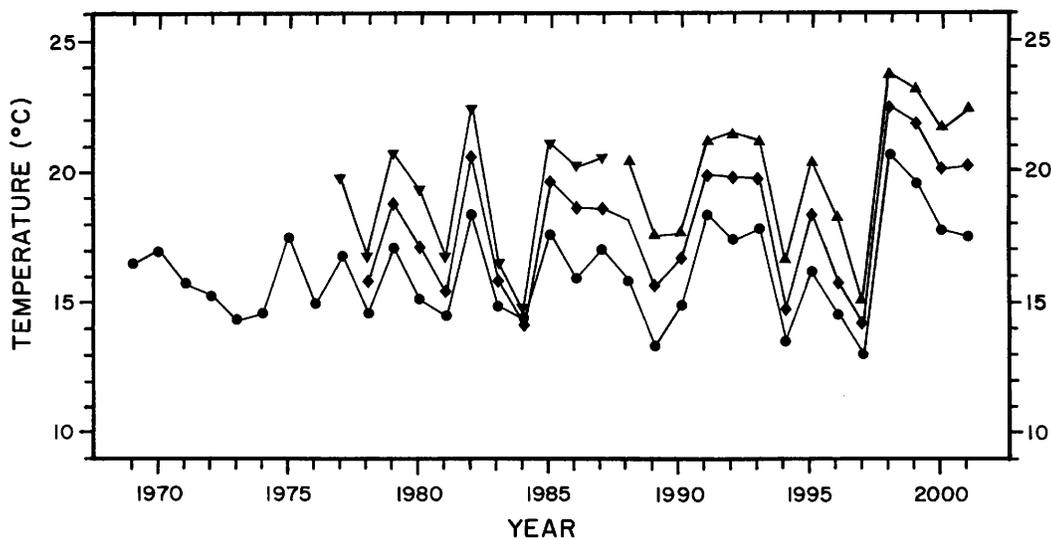


FIG. 2. Mean maximum daily temperatures, 1-20 May, at LP, 1969-2001 (circles); SL, 1978-2001 (diamonds); BF, 1977-1986 (triangles, apex down); and MC, 1987-2001 (triangles, apex up).

year and site alone ($R^2 = 0.528$), again showing that early May temperatures account for much of the year-to-year variation in timing of breeding as well as for the overall pattern of change.

A separate analysis of the 10th percentile dates of clutch initiation gave similar results, except that only temperatures in the first three five-day periods in May and the SL site had significant effects on the predicted date ($R^2 = 0.822$, $P < 0.001$; Table 3). Likewise, addition of 1st- to 5th-order polynomial terms in year did not add significantly to explained variation, indicating that early May temperatures predict a substantial proportion of year-to-year variation in the start of egg-laying as well as longer term trends.

DISCUSSION

April and May daily maximum, minimum, and mean temperatures at Erie, Pennsylvania,

increased by $<1.25^\circ\text{C}$ over the 31-year period 1969-2000 but did not show significant trends. There were large annual fluctuations in temperature, representing deviations from the trends. That was typical of the Lake Erie region generally: spring temperatures in that region showed zero or small positive changes during the second half of the twentieth century (Zhang et al. 2000; Climate Prediction Center, National Oceanic and Atmospheric Administration [NOAA], see Acknowledgments).

Despite within-site annual variation of as much as 18 days in median and 17 days in 10th percentile dates of clutch initiation (Table 1), there were no differences in average dates of clutch initiation by Tree Swallows among the decades, 1970-1980, 1980-1990, and 1990-2000. Nevertheless, there was a shift to earlier clutch initiations within the last decade (1990-2000). Across all sites, the median dates of clutch ini-

TABLE 3. Influence of maximum daily temperatures and site on 10th percentile dates of clutch initiation.

Period (May)	Variable	Regression coefficient	Standardized coefficient	<i>P</i>
	Intercept	16.701		
1–5	T_1	-0.656	-0.451	<0.001
6–10	T_2	-0.516	-0.377	<0.001
11–15	T_3	-0.251	-0.163	0.016
	S_{SL}	-2.937	-0.263	<0.001

tiation averaged 5.5 days earlier in 2000 than at the end of the previous decade. That clearly resulted from four unusually early years in 1998, 1999, 2000, and 2001 (Fig. 1). Clutch initiations during 1990–2000 did not average earlier than in previous decades partly because there were also some exceptionally late years in that decade, notably 1996 and 1997. Whether the early clutch initiations of the last four years represent the beginning of a trend to earlier breeding remains to be determined by future observations. However, early May temperatures were lower and Tree Swallows began laying later in 2002 than in any year in my study, indicating that the warm springs of 1998–2001 probably represent an exceptional run of years rather than the beginning of a longer term trend (D. J. T. Hussell unpubl. data). Overall, I conclude that there is no evidence of a trend in dates of clutch initiation of Tree Swallows at Long Point during the years from 1969 to 2001, and that is consistent with the lack of change in spring temperatures in that region over the same years.

Photoperiod is probably the primary cue to gonadal development and timing of breeding in Tree Swallows, as in many other north-temperate birds (Immelman 1971); but, because it does not vary between years, its effects cannot be detected in observational field studies such as this one. Other environmental factors—such as temperature, food abundance, and habitat—may modify the photoperiod response. Provided that those factors vary in the populations under study, their direct and indirect effects may be detected as correlations with timing of breeding.

Here, dates of clutch initiations were correlated with temperatures in the prelaying and early laying periods in the first 20 days of May (Tables 2 and 3). Those results do not necessarily indicate that temperature is the proximate cause of variation in clutch initiations. Instead, factors related to temperature, such as

the general advance of plant growth or insect abundance, could be the proximate cues used by swallows to trigger laying. That maximum daily temperatures were more strongly related to clutch initiations than were minimum temperatures suggests that the progress of the growing season may be important but does not necessarily mean that minimum temperatures are unimportant, because maximum and minimum temperatures tend to be correlated with each other.

Despite strong relationships between laying dates and early and mid-May temperatures, the latter variables did not fully explain differences in clutch initiation dates among sites. Clutch initiations at LP were later than at other sites, presumably because of the stronger cooling influence of the waters of Lake Erie, but median clutch initiations at SL averaged 3.2 days earlier than at the other sites, after controlling for temperature effects. That discrepancy could arise if positions of thermometers at each site do not accurately reflect temperature regimes experienced by swallows at that site. Alternatively, it could represent a real difference among sites in one or more additional variables not included in the model. A likely candidate for such a variable is insect abundance during the prelaying period, because insects were almost always more abundant at SL than at the other sites (Hussell and Quinney 1987, Quinney et al. 1986, D. J. T. Hussell unpubl. data), despite cooler daily maximum temperatures in May at SL than at the other two mainland sites (Fig. 2).

My regression analysis of effects of temperature on clutch initiation dates indicates that an average increase in daily maximum temperature of 1°C in each of the first four, five-day periods in May was linked to an average advance of 1.46 days in the median date of clutch initiation. A predicted average increase of 5°C because of climate warming should therefore result in an average advance of 7.32 days in median dates

of clutch initiation. Although it is not strictly valid to extrapolate such predictions outside the range of the observations on which they were based, those results suggest that climate warming of 5°C in May might result in swallows laying eggs as much as one week earlier in some years than the earliest dates observed in 1969–2001. Median dates of clutch initiation differed by as much as 18 days in the past 33 years and mean daily maximum temperatures during 1–20 May varied by up to 10.8°C among years and sites. Therefore a change in average temperature of 5°C is well within the observed response capacity of Tree Swallows. Studies of timing of clutch initiation in relation to temperature at sites near the southern limits of the breeding range of the species in the United States might indicate how swallows respond to higher temperatures.

My results agree with those of Dunn and Winkler (1999) that spring temperatures are an important determinant of egg-laying time in Tree Swallows. They showed that the mean of April and May temperatures was negatively correlated with laying date. I was able to narrow down the critical time period at my sites to the first 20 days of May, with the first 10 days having the strongest effects.

In contrast to my results, Dunn and Winkler (1999) found a significant continent-wide increase in surface temperatures and an advance in laying date of five or nine days (depending on the method of analysis) during 1959–1991. They indicated that the greatest advancement in laying occurred in the 1960s (2.9 days) and the 1980s (3.3 days), whereas there was little change (0.5 days) in the 1970s. I have no data relevant to the 1960s, but average laying dates did not differ between the 1970s and 1980s at my sites, nor were there significant changes during those decades. Those results are consistent with the absence of change in spring temperatures at my sites and in the Great Lakes region generally, but not with Dunn and Winkler's (1999) conclusion that Tree Swallows are breeding earlier across the northern United States and Canada. Although they reported that rates of change to earlier laying were greater in western and southern locations than in northern and eastern ones, they did not estimate regional variation in rates of change in laying dates. Subsequent analyses have shown that the strongest rate of advancement in laying occurred in the prairie provinces of Canada, (P. O. Dunn

pers. comm.). My results indicate that in one region of eastern North America there was no advancement in laying date.

The latter result is consistent with regional variation in the rates of spring temperature changes in North America. In Canada, from 1950 to 1998, significant increases occurred in the west from British Columbia to Saskatchewan, with the largest increases (>3°C) in Alberta and Saskatchewan (Zhang et al. 2000). By contrast, southern Ontario, southern Quebec, and the Atlantic Provinces were stable or showed small (<1°C), nonsignificant increases (Zhang et al. 2000). Also, satellite data indicate that the growing season has increased most in northwestern Canada since 1981 (Myneni et al. 1997). In the United States in the second half of the twentieth century, spring temperatures increased in the northwest (north and west of a line from Minnesota to southern California), decreased over most of the southeast, and were relatively stable in a wide band from the southern Great Lakes to Texas (Cayan et al. 2001, Easterling et al. 1997; NOAA's Climate Prediction Center, U.S. Temperature and Precipitation Trends, see Acknowledgments). Given the strong negative relationship between spring temperatures and laying date of Tree Swallows (and other species), we should not expect to find advances in breeding seasons over the last 50 years in those parts of eastern North America where temperatures were stable or decreasing during that period.

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For more information on NOAA Climate Prediction Center's U.S. Temperature and Precipitation Trends, please see www.cpc.ncep.noaa.gov/mamtrend.gif or www.cpc.ncep.noaa.gov/trndtext.htm.

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