

Natal experience and pre-breeding environmental conditions affect lay date plasticity in Savannah Sparrows

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Citation: Burant, J. B., E. W. Heisey, N. T. Wheelwright, A. E. M. Newman, S. Whelan, D. J. Mennill, S. M. Doucet, G. W. Mitchell, B. K. Woodworth, and D. R. Norris. 2022. Natal experience and pre-breeding environmental conditions affect lay date plasticity in Savannah Sparrows. *Ecology* 103(2):e03575. 10.1002/ecy.3575

Abstract. Phenotypic plasticity allows organisms to adjust the timing of life-history events in response to environmental and demographic conditions. Shifts by individuals in the timing of breeding with respect to variation in age and temperature are well documented in nature, and these changes are known to scale to affect population dynamics. However, relatively little is known about how organisms alter phenology in response to other demographic and environmental factors. We investigated how pre-breeding temperature, breeding population density, age, and rainfall in the first month of life influenced the timing and plasticity of lay date in a population of Savannah Sparrows (*Passerculus sandwichensis*) monitored over 33 yr (1987–2019). Females that experienced warmer pre-breeding temperatures tended to lay eggs earlier, as did older females, but breeding population density had no effect on lay date. Natal precipitation interacted with age to influence lay date plasticity, with females that experienced high precipitation levels as nestlings advancing lay dates more strongly over the course of their lives. We also found evidence for varied pace of life; females that experienced high natal precipitation had shorter lifespans and reduced fecundity, but more nesting attempts over their lifetimes. Rainfall during the nestling period increased through time, while population density and fecundity declined, suggesting that increased precipitation on the breeding grounds may be detrimental to breeding females and ultimately the viability of the population as a whole. Our results suggest that females adjust their laying date in response to pre-breeding temperature, and as they age, while presenting new evidence that environmental conditions during the natal period can affect phenological plasticity and generate downstream, population-level effects.

Key words: among-individual differences; annual cycle; *Passerculus sandwichensis*; population density; precipitation; reproduction; temperature.

INTRODUCTION

For many species, the timing of breeding presents an important phenological trade-off (Kokko 1999). Individuals must weigh the risks of breeding too early under adverse weather conditions against a number of possible benefits. Potential risks of early breeding include the misalignment of reproduction with peaks in food

availability (“mismatch hypothesis”; Both et al. 2006, Charmantier et al. 2008), and reduced offspring production due to poorer body condition earlier in the season (Drent and Daan 1980, Rowe et al. 1994). In contrast, early breeding can mean valuable additional time for multiple reproductive attempts (Friesen et al. 2001) or to initiate additional breeding attempts if the first fails (Pakanen et al. 2014), and to rebuild muscle mass prior to autumn migration (Mitchell et al. 2012b). Earlier breeding can also allow more time for offspring to develop and accumulate energy reserves prior to seasonal shifts in resource availability (Mitchell et al. 2011, Whelan et al. 2016, Freeman et al. 2020), and initiate

Manuscript received 19 March 2021; revised 12 July 2021; accepted 24 August 2021. Corresponding Editor: Ian MacGregor-Fors.

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migration earlier (Mitchell et al. 2012a), resulting in improved offspring survivorship (Harris 1969, Parsons et al. 1976, Mitchell et al. 2011).

A number of environmental factors, including temperature (Nager and van Noordwijk 1995, Dunn 2004, Barrientos et al. 2007, Visser et al. 2009, Watts et al. 2018), precipitation (Mares et al. 2017; but see Barrientos et al. 2007), and large-scale climatic oscillations such as El Niño and the North Atlantic Oscillation (Wilson et al. 2007, Dunn and Winkler 2010) have been shown to influence timing of breeding in birds. A wide variety of taxa have been found to adjust their breeding phenology in response to changes in these environmental conditions (Dunn 2004, Parmesan 2006, Froy et al. 2019). Many species have advanced the timing of breeding in concert with shifts in global climatic conditions (Jonzen et al. 2006, Parmesan 2006, Both and te Marvelde 2007, Vatka et al. 2011, Helm et al. 2019), although the ability to respond to environmental change may be limited in many long-distance migrants (Both et al. 2010). Importantly, environmental effects on individual reproductive timing, and their consequences for reproductive success and recruitment, can ultimately alter overall population trajectories (e.g., Kentie et al. 2018). Phenotypic plasticity, the capacity of a given genotype to express different phenotypes against a varied environmental background, is one mechanism through which organisms can adjust their phenology in response to annual variation or long-term change in environmental conditions (Charmantier and Gienapp 2014, Sauve et al. 2019).

In addition to environmental conditions, a number of intrinsic and demographic factors have also been shown to influence the timing of breeding. In many species, young and inexperienced females breed later in the season than older and more experienced females (Whelan et al. 2016, Sauve et al. 2019). Population density can also affect phenology (Clutton-Brock et al. 1987, Wilson et al. 2007, Bourret et al. 2015), for example, through intraspecific competition and resource availability. The effects of natal conditions on reproductive phenology have not been extensively studied, although Song Sparrows (*Melospiza melodia*) born in low density cohorts showed greater plasticity in lay dates (Wilson et al. 2007). This introduces the intriguing possibility that other conditions experienced early in life can influence the timing of subsequent life-history events.

Phenotypic plasticity in response to extrinsic and intrinsic factors can be parsed into within- and among-individual (between-individual) effects (Dingemanse and Wolf 2013). Within-individual effects represent the degree of plasticity expressed in response to variation in environmental conditions over an individuals' lifetime (e.g., facultative behavioral responses), whereas among-individual effects represents the plastic response of the population (e.g., as a result of different genetic backgrounds or environmental experiences; van de Pol and Wright 2009, Dall et al. 2012, Charmantier and Gienapp 2014). It is possible that a population-level response to

variation in environmental conditions could be driven (almost) entirely by within-individual plasticity (Nussey et al. 2007, van de Pol and Wright 2009). However, such responses may also be driven by the differential survival of individuals with different phenotypes (van de Pol and Wright 2009, Fox et al. 2019, Froy et al. 2019). If among-individual differences drive population-level change in a particular trait of interest, it is more likely that directional selection for the trait (e.g., pressure to adjust to changing climatic conditions) would lead to a particular phenotypic composition in a population (Monaghan 2008). If differences between phenotypes are genetically based (which may not be the case for many important traits in our study system; Wheelwright et al. 2014), among-individual effects may equate to an adaptive evolutionary response (Gienapp et al. 2008, Fox et al. 2019). Several studies have suggested that the effect of within-individual plasticity on the distribution of traits is equivalent in magnitude to the overall population-level response (Charmantier and Gienapp 2014, Froy et al. 2019), and that selective pressures would need to be much greater and consistent in direction to result in an evolutionary response (Charmantier et al. 2008, Merilä and Hendry 2014).

We examined factors influencing the plasticity of clutch initiation date in an individually marked population of Savannah Sparrows (*Passerculus sandwichensis*) studied over three decades on Kent Island, New Brunswick, Canada. Savannah Sparrows are ground-nesting, short-distance migrants (Dixon 1978). Individuals on Kent Island display high site fidelity (Wheelwright and Mauck 1998), making it possible to track reproductive attempts of many females over the course of their lifetime and obtain the repeated records required to address questions related to plasticity in lay date. We examined multiple hypotheses to explain variation in lay date in Savannah Sparrows (Table 1). We aimed to assess whether female Savannah Sparrows show within- and among-individual differences in lay date plasticity in response to annual fluctuations in average temperature during the pre-breeding period, adult breeding population density, and individual age (i.e., as a result of senescence or increased experience). We also investigated whether plasticity in female lay dates was influenced by precipitation conditions experienced during their natal year.

METHODS

Study site and field sampling

Savannah Sparrows are migratory songbirds that breed in grasslands across much of North America and winter across the southern United States, Mexico, and parts of Central America (Wheelwright and Rising 2020). The data used in this analysis were collected as part of a long-term demographic study of Savannah Sparrows breeding on Kent Island, New Brunswick, Canada (44.58° N, 66.76° W), an island approximately

TABLE 1. Hypotheses regarding the effects of pre-breeding and breeding environmental and demographic conditions on lay date in Savannah Sparrows (*Passerculus sandwichensis*).

Hypothesized effect	Hypothesized mechanism	Prediction	Predictor variable(s)
Pre-breeding temperature influences lay date.	Early nesting maximizes nesting attempts.	Warm pre-breeding temperature results in early lay dates.	within-female temperature, among-female temperature
Age influences lay date.	Experience confers fitness advantages.	Older females nest earlier.	within-female age, among-female age
Density influences lay date.	Density affects intraspecific competition.	High density results in later lay date.	within-female density, among-female density
Lay date adjustment with age is modulated by natal precipitation.	Developmental conditions drive phenotypic differences.	High natal precipitation results in later lay date in the first breeding season.	within-female age × natal precipitation
Lay date adjustment with age is modulated by temperature.	Experience allows females to identify optimal pre-breeding conditions.	Females respond better to pre-breeding temperatures as they age.	within-female age × temperature
Lay date adjustment with age is modulated by density.	Experience influences the competitiveness of females.	Females experiencing low lifetime densities lay earlier as they age.	within-female age × among-female density
Plastic response to temperature differs.	Genetic or environmental differences among females affect response.	Degree of plasticity varies among individuals.	temperature × female ID (I × E)
Plastic response varies with age.	Genetic or environmental differences among females affect response.	There is variation in lay date adjustment with age.	age × female ID (I × Age)

Note: I, individual; E, environment; ID, identity.

100 ha in size that lies southeast of Grand Manan Island in the Bay of Fundy (Fig. 1A). Our study site consisted of an ~10-ha grassy plot in the central portion of the island, which was subdivided with gridlines 50 m apart. A number of features of this population make it well suited to asking questions about phenotypic plasticity. Savannah Sparrows on Kent Island exhibit high natal and breeding site philopatry, relatively short dispersal distances between natal and breeding sites (Wheelwright and Mauck 1998), and limited dispersal off-island (B. K. Woodworth, D. R. Norris, J. B. Burant, A. E. M. Newman, *unpublished data*). High site fidelity allowed for repeated sampling of the same individuals across multiple years. In addition, since the breeding population on Kent Island has been studied on an annual basis nearly continuously since 1987 (excluding 2005–2007), the data set met the relatively large sample size requirements to explore questions about plasticity (van de Pol and Wright 2009, Charmantier and Gienapp 2014).

Annual monitoring between late May and the end of July consisted of capture and banding of all unbanded individuals in the study area, resighting newly and previously banded individuals, observation of established breeding territories, nest-finding and monitoring, and banding of all nestlings. All individuals in the study site were fitted with a unique combination of a numbered aluminum leg band from United States Fish and Wildlife Service (USFWS) or Canadian Wildlife Service (CWS) and three randomly determined colored leg-bands. Based on measured dispersal distances within our study area (Wheelwright and Mauck 1998), unbanded adults on the

study site found in late May were presumed to be immigrants from elsewhere on Kent Island or neighboring islands. These immigrants were also captured, banded, and measured (tarsus length, unflattened wing chord, bill length, bill depth, and body mass) before the end of the annual monitoring period. Age of on-site nestlings was known to be exact based on hatching day, while unbanded immigrants were assumed to be in their first breeding summer at the time of capture (based on strong philopatry). At the time of capture, sex was determined (for adults) by the presence of a brood patch in females and a distended cloaca in males (females are also shorter winged and lighter than males), and was later confirmed with behavioral observations (only males sing, only females incubate; Wheelwright and Rising 2020). Consistent and comprehensive annual monitoring made it possible to estimate annual density as the number of adults breeding on the study grid (Woodworth et al. 2017a).

Nests were primarily found in the late stages of egg-laying or during incubation and were monitored every other day to record clutch size, hatch date, fledge date, number of fledglings, and nest fate. Mean incubation period for Savannah Sparrows is 11.8 d (Dixon 1978), with a range of 11–13 d, and begins when the penultimate egg is laid. Therefore, date of incubation initiation was estimated with minimal error by subtracting 12 d from the date of first hatching, and lay date was estimated by subtracting one less than the clutch size from the incubation initiation date. Hatch date or lay date could not be estimated for nests that failed prior to hatching, unless the nest was found before the clutch

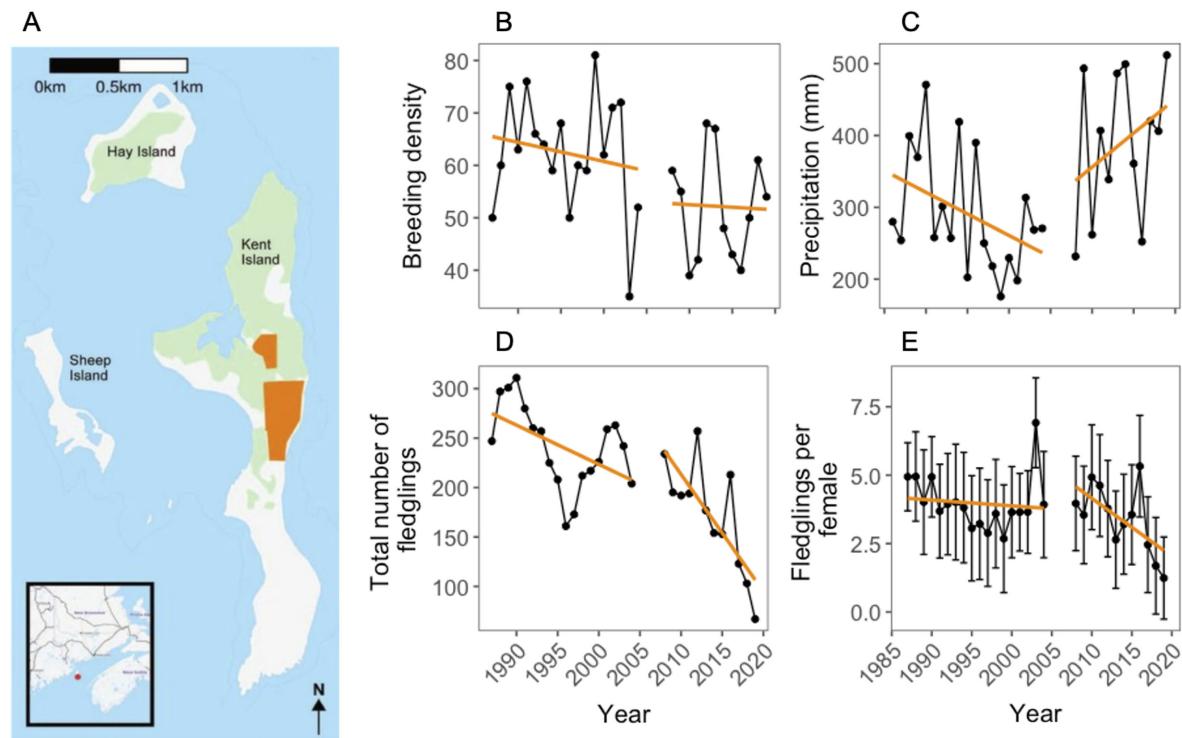


FIG. 1. Map of study site, demographic trends, and environmental conditions. (A) Map of the long-term Savannah Sparrow study site on Kent Island, New Brunswick, Canada (44.58° N, 66.76° W), along with neighboring Sheep and Hay Islands, located in the Bay of Fundy (inset). Green areas indicate forest; white and orange areas indicate open field/meadow. Savannah Sparrows breed throughout the orange and white areas but are only monitored within the study site (shown in orange). (B) Annual breeding population density. (C) Total precipitation (mm) during the breeding period (15 April–31 July). (D) Total number of fledglings banded within the study area per year. (E) Number of fledglings per breeding female (mean \pm SD). Orange lines indicate the linear trend for the two contiguous series of data collection (1987–2004 and 2008–2019).

was completed. If the nest was found with an incomplete clutch, lay date was estimated by subtracting the initial clutch size from the date the incomplete clutch was found; this method was used to determine lay dates for 18 of 915 nests that failed prior to hatching. Nest depredation rates on Kent Island are high (~50% of nests are depredated; Dixon 1978), causing some females to attempt as many as five nests in a single breeding season. We only included first broods per female per year in this study because we were only interested in plastic responses and the timing of subsequent reproductive attempts is strongly correlated with the timing and success of first broods (Wheelwright and Rising 2020).

The capture and handling of Savannah Sparrows on Kent Island was in compliance with the Animal Care Committee at the University of Guelph (animal use protocol number 3576) and a banding permit from the Canadian Wildlife Service (permit number 10789).

Temperature and precipitation data

Following Woodworth et al. (2017b), we obtained climate data from an Environment and Climate Change Canada weather station at the airport in Saint John,

New Brunswick, Canada (45.32° N, 65.89° W), approximately 110 km northeast of Kent Island (data available online).¹⁰ Kent Island temperatures are closely modulated by the cold waters of the Bay of Fundy, causing temperature to be substantially cooler on Kent Island than on Grand Manan Island or the mainland. Thus, while temperatures may be higher in Saint John, it was assumed that the overall climatic trends would be largely equivalent in the Bay of Fundy region (Woodworth et al. 2017b). Daily mean temperatures ($^{\circ}$ C) were extracted for the pre-breeding period through the end of peak first brood initiation (15 April–1 July) for each of the 30 yr for which nesting data were available (1987–2004, 2008–2019). Temperature data were used to conduct a climate sensitivity analysis and to investigate long-term trends. Daily totals of precipitation (mm) for the same 30-yr period were obtained for the pre-breeding period through the end of the breeding period (15 April–31 July) to investigate broader precipitation trends. We also subset these data for the peak nestling/fledgling period (1 June–31 July) and used the sum of the daily precipitation values over this period as a measure of precipitation

¹⁰ www.climate.weather.gc.ca

conditions experienced during nestling development (hereafter natal precipitation).

Climate sensitivity analysis

To determine the temporal pre-breeding window during which temperature best predicted lay date, we first conducted a climate sensitivity analysis (van de Pol et al. 2016). This was a sliding window approach, which averaged mean daily temperatures across windows that vary in length and initiation date. Models of these hypothetical windows were compared, along with a null model (lay date $\sim (1|\text{female ID}) + (1|\text{year})$), using ΔAIC_c values (Burnham and Anderson 2002) to determine the most influential pre-breeding window. The average temperature during the identified window with the lowest ΔAIC_c value was used in subsequent analyses (referred to as pre-breeding temperature). We limited our analysis to the pre-breeding period, which we estimated to last from the approximate arrival of males on Kent Island (early arrival date 15 April; Woodworth et al. 2016) to 12 d (corresponding to the average incubation period; Dixon 1978) before the mean hatch date (13 June). The climate sensitivity models were run over this 48-d period. No specific constraint on window size was set, as we wanted to determine the entire range over which pre-breeding temperature could influence lay date. The climate sensitivity analysis estimated that the most influential pre-breeding temperature window for lay date was the period from 3 May to 26 May and demonstrated that this window was a substantial improvement from a randomly selected one (Appendix S1: Fig. S1).

Statistical analysis

All analyses were conducted in the R statistical environment (v. 3.6.1; R Core Team 2019). The data and code used for the analysis are publicly available on the Figshare open access repository (Burant et al. 2021). Linear regressions (LM; Gaussian) were conducted to determine long-term trends in pre-breeding temperature and natal precipitation, while generalized linear models (GLM; Poisson distribution, identity link) were used for breeding density and fledglings per cohort. Average per capita fecundity was calculated by dividing fledglings per cohort by density and tested using a linear model. We characterized annual adult breeding population density as the maximum number of paired breeding males and females in the central part of the study area (Fig. 1A) during a given breeding season. There is a gap in the data set from 2005 to 2007, during which few birds were banded and no nests were monitored. Thus, the same linear regressions were repeated to compare the first (1987–2004) and second (2008–2019) periods of contiguous data collection.

We fitted linear mixed models (LMMs) using restricted maximum likelihood in the *lme4* package (Bates et al. 2015), with random effects for female ID

and year. We included several fixed effects in models of female clutch initiation dates based on a priori hypotheses listed in Table 1, including natal precipitation (see definition in *Methods: Temperature and precipitation data*; continuous), breeding population density (integer), and female age (integer). In subsequent analyses, females were split into high (172–378 mm) and low (81–171 mm) natal precipitation groups based on the median value (171 mm). We used a multiple regression to test whether females in the high and low rainfall groups differed in their advancement in laying date with age. Within-subject centering was used to test for within- and among-individual effects of pre-breeding temperature, female age, and breeding density (van de Pol and Wright 2009, Whelan et al. 2016). Among-individual effects were calculated as the mean value that females experienced across their lifetime, while within-individual effects were calculated as the individuals' value for a given breeding year minus their mean value over their lifetime.

Climate sensitivity analysis.—The climate sensitivity analysis was conducted using the *climwin* package (van de Pol et al. 2016). We used all available data for clutch initiation dates ($n = 915$ first nests), including data from females with only a single nest observation ($n = 414$ of 612 females). We compared ΔAIC_c values from our selected model to a series of randomly generated windows using the *randwin* function.

Individual variation in plasticity.—To test for individual variation in plasticity, we used a subset of clutch initiation dates from females with two or more breeding years ($n = 501$ nest attempts, 198 females). Our fixed-effects structure included all variables hypothesized to influence laying date and three two-way interaction terms between within-individual effects and additional factors predicted to influence lay date (Table 1). Random-effects structure was evaluated by comparing LMMs with random effects of increasing complexity while maintaining a constant fixed effect structure via likelihood ratio tests. To test for individual variation in plasticity in response to temperature (individual \times environment [$I \times E$]), we included a random slope term for pre-breeding temperature in the female identity (ID) random effect. In a separate model, we tested for variation in lay date as females aged by including a random slope term for age in the female ID random effect ($I \times \text{Age}$). These tests supported the inclusion of a random intercept term for female ID (pairwise comparison, $\chi^2 = 24.91$, $df = 1$, $P < 0.0001$), but did not support the inclusion of random slope terms for pre-breeding temperature ($\chi^2 = 0.51$, $df = 2$, $P = 0.78$) or mean-centered age ($\chi^2 = 0.46$, $df = 2$, $P = 0.79$).

Intrinsic and extrinsic drivers of lay date.—Since we did not find evidence for significant $I \times E$ or $I \times \text{Age}$, we included all clutch initiation dates before proceeding to

test for intrinsic and extrinsic drivers of clutch initiation dates, which allowed us to increase statistical power (suggested by Martin et al. 2011). Our initial model included all main effects and interaction terms hypothesized to influence laying date. Using Kenward-Roger approximation of degrees of freedom (Bolker et al. 2009), we implemented a stepwise model selection process to remove non-significant fixed effects and interaction terms (Bolker et al. 2009), with P values estimated using *lmerTest* (Kuznetsova et al. 2017). All continuous fixed effects were mean centered prior to analysis in order to standardize measurements across individuals.

Effects of natal conditions on fitness proxies.—We used independent one-tailed t tests to compare longevity, fecundity, and number of lifetime nesting attempts among females that experienced high or low natal precipitation (see definitions under *Methods: Statistical analysis*).

RESULTS

Long-term demographic trends

Breeding population density of Savannah Sparrows on Kent Island has declined over time (GLM, $\beta = -0.51 \pm 0.14$ individuals per year (mean \pm SE), $Z_{1,28} = -3.69$, $P < 0.001$, $R^2 = 0.19$; Fig. 1B), with a corresponding long-term decline in total number of fledglings per cohort (GLM, $\beta = -4.46 \pm 2.26$ fledglings per year, $Z_{1,28} = -17.03$, $P < 0.0001$, $R^2 = 0.55$; Fig. 1D). This appeared to be largely driven by a decline between 2008 and 2019 (GLM, $\beta = -13.13 \pm 1.06$

fledglings per year, $Z_{1,10} = -12.34$, $P < 0.0001$, $R^2 = 0.60$), while a less severe decline occurred between 1987 and 2004 (GLM, $\beta = -3.73 \pm 0.71$ fledglings per year, $Z_{1,16} = -5.29$, $P < 0.0001$, $R^2 = 0.25$). Per capita fecundity was relatively constant between 1987 and 2004 (LM, $\beta = -0.02 \pm 0.05$ fledglings per female per year, $F_{1,16} = 0.22$, $P = 0.65$, $R^2 = 0.01$), but declined markedly between 2008 and 2019 (LM, $\beta = -0.21 \pm 0.09$ fledglings per female per year, $F_{1,10} = 5.98$, $P = 0.03$, $R^2 = 0.37$; Fig. 1E). However, there was no overall decline in per capita fecundity over the entire study period (LM, $\beta = -0.04 \pm 0.02$ fledglings per female per year, $F_{1,28} = 3.86$, $P = 0.06$, $R^2 = 0.12$), suggesting that the decline in total number of fledglings was related to changes in density rather than individual reproductive performance (Fig. 1E).

Pre-breeding temperature and natal precipitation

Annual laying dates were found to be earlier in years with warmer pre-breeding temperatures and later in years with colder pre-breeding temperatures (LM, $\beta = -1.86 \pm 0.39$ d/ $^{\circ}$ C, $F_{1,28} = 22.4$, $P < 0.0001$, $R^2 = 0.44$; Fig. 2A). Both annual mean lay date (LM, $\beta = 0.01 \pm 0.06$ d/yr, $F_{1,28} = 0.035$, $P = 0.79$, $R^2 < 0.01$) and annual mean daily temperature during the pre-breeding window (LM, $\beta = 0.002 \pm 0.02$ $^{\circ}$ C/yr, $F_{1,28} = 0.02$, $P = 0.90$, $R^2 < 0.01$) showed no evidence of a linear change through time. Breeding season precipitation increased over the study period (LM, $\beta = 3.54 \pm 1.79$ mm/yr, $F_{1,28} = 4.9$, $P = 0.057$, $R^2 = 0.12$), particularly in the last decade (Fig. 1C). Precipitation during the peak-nesting period also showed a long-term increase

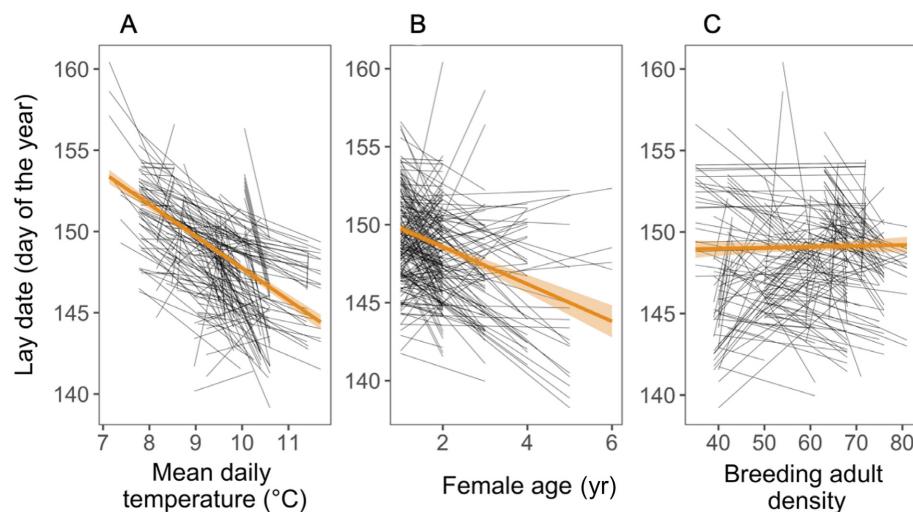


FIG. 2. Influence of environmental and demographic drivers on the timing of first clutch lay dates. We investigated individual and population-level changes in lay date in response to changes in (A) annual mean daily pre-breeding temperature ($^{\circ}$ C), (B) female age, and (C) breeding population density. Thin black lines indicate the within-individual change in lay date in response to changes in each predictor variable (temperature, age, density). Thick orange lines indicate the population level effect (among-individual effect) and indicate the average change in lay date in response to the predictor variables. Sample sizes: unique females = 612; first broods = 915.

(LM, $\beta = 2.82 \pm 1.16$ mm/yr, $F_{1,28} = 5.93$, $P = 0.02$, $R^2 = 0.17$), and all years from 2013 onward were high natal precipitation years.

Intrinsic and extrinsic drivers of laying date

In the final model (see *Methods: Statistical analysis*), we found evidence for significant within- and among-individual effects of pre-breeding temperature and among-individual effects of age on lay date (Appendix S1: Table S1). Within individuals, females responded to higher pre-breeding temperatures by laying their eggs earlier (Fig. 2A). Among individuals, females that experienced high pre-breeding temperatures throughout their lifetime laid eggs earlier than females that experienced colder pre-breeding conditions over their lifetime. Individuals also advanced their lay dates as they aged, with older females laying significantly earlier than younger females (Fig. 2B). However, within- and among-female changes in density were not found to influence lay date (Fig. 2C).

Relative to females that experienced low natal precipitation (multiple regression, $\beta = -0.72 \pm 0.22$ d/yr, $t = -3.20$, $P = 0.001$), those that experienced high natal precipitation advanced lay dates more with increasing age and experience (marginal effect of high natal precipitation, $\beta = -2.02 \pm 0.38$ d/yr, $t = -3.46$, $P < 0.001$, $R^2 = 0.06$; Fig. 3). Females in the high natal precipitation group were more variable in their lay dates in their first breeding year (17 May–14 June; Fig. 3) than

females in the low natal precipitation group (23 May–15 June), although the mean lay dates for each group only differed by one day (high natal precipitation, 31 May ± 5.80 d; low natal precipitation, 30 May ± 4.94 d).

Effects of natal conditions on fitness proxies

We found evidence that natal precipitation influenced both longevity and reproductive output. Females that experienced high natal precipitation had shorter lifespans ($t = 2.67$, $df = 889$, $P = 0.004$) and produced significantly fewer young over their lifetime ($t = 3.92$, $df = 2,017$, $P < 0.0001$) than individuals that experienced low natal precipitation. Females in the high precipitation group also produced fewer fledglings per nesting attempt ($t = 4.64$, $df = 2,074$, $P < 0.0001$), but had more nesting attempts over their lifetimes ($t = 2.69$, $df = 2,067$, $P = 0.003$) and were, therefore, able to match the annual reproductive output (fledglings per year) of the low natal precipitation group.

DISCUSSION

Our 33-yr data set provides evidence that Savannah Sparrows adjust breeding phenology in response to variation in environmental and demographic conditions on the breeding grounds, as well as conditions experienced as nestlings. Temperature conditions on the breeding grounds during the period between adult arrival and clutch initiation (pre-breeding temperature) influenced

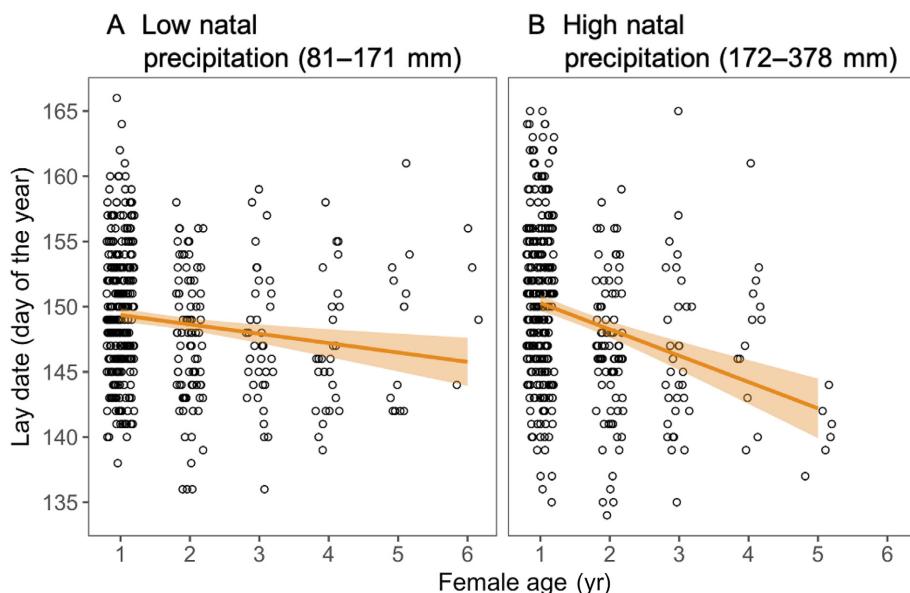


FIG. 3. Carry-over effect of total precipitation during the natal breeding period on lay date advances with age. Cumulative natal precipitation (mm) was calculated for each year of the study, with females split into low (81–171 mm) and high (172–378 mm; see *Methods: Temperature and precipitation data* and *Methods: Statistical analysis*). (A) Low natal precipitation. (B) High natal precipitation. Orange lines indicate the linear relationship between age and lay date for each precipitation group. Sample sizes: low precipitation = 477 first broods; high precipitation = 438 first broods.

both among- and within-individual plasticity in lay date, with females laying earlier in response to warm pre-breeding temperatures. However, because females that experienced different pre-breeding temperature ranges showed similar shifts in lay dates in response to temperature (i.e., equivalent slopes), the population-level trend was largely explained by within-individual shifts in lay date in response to changes in pre-breeding temperature. Similarly, our results show both among- and within-individual variation in lay date with age, such that older females initiate their clutches earlier than young females. We also demonstrate shortened lifespans and reduced fecundity in females that experienced poor natal conditions (i.e., high precipitation during the natal period), along with stronger phenological adjustment of lay dates, likely resulting in a greater number of life-time nesting attempts and providing some evidence for differences in pace of life in Savannah Sparrows.

Our results support the large body of evidence pointing to the impacts of temperature on shifts in breeding phenology (Barrientos et al. 2007, Visser et al. 2009, Mares et al. 2017, Watts et al. 2018, Froy et al. 2019). The primary finding of most of these studies has been a long-term phenological advance (earlier breeding) with warming temperatures (Both et al. 2006), with lay date advancements of as much as ~ 7 d/ $^{\circ}\text{C}$ in some species (Dunn 2004). In contrast, while pre-breeding temperatures on Kent Island vary widely on across years, there has been no long-term increase in pre-breeding temperatures at the study site and, therefore, no corresponding long-term advance of lay date in Savannah Sparrows. The lack of temperature increase is curious, particularly given evidence that sea surface temperatures in the Bay of Fundy are warming faster than 99.9% of the global oceans (Pershing et al. 2015), and temperatures on continental islands, such as Kent Island, are likely to be regulated by sea surface temperature. The absence of directional warming may also be attributed to increased fog formation in the Bay of Fundy and specific local effects of the Labrador Current. It is worth reiterating that our climatic data are sourced from the mainland, at a site approximately 5 km inland, which may be experiencing different trends than those out in the bay. That said, if a warming trend on Kent Island emerges, then individual-level plasticity in Savannah Sparrows may allow compensatory advances in laying. Whether this will be beneficial or create a mismatch with peak food abundance during the nestling period is unknown. However, a recent study in a nearby continental population of Savannah Sparrows showed that females did not shift the timing of nesting in response to phenological shifts in habitat availability (McGowan et al. 2021). We do know that Savannah Sparrows appear to advance their lay date less than other species that have been studied (Both and Visser 2001, Dunn 2004, Husby et al. 2010). For example, Great Tits (*Parus major*) in the Netherlands and United Kingdom advanced their lay dates by 3.3 d/ $^{\circ}\text{C}$ and 5.2 d/ $^{\circ}\text{C}$, respectively (Husby et al. 2010),

while Savannah Sparrows on Kent Island are estimated to advance laying by approximately 1.9 d/ $^{\circ}\text{C}$. This is interesting given the relatively high inter-annual variability in pre-breeding temperatures in our system and suggests that either (1) the response to any potential future warming (and concomitant effects) may be limited, at least initially, which could have downstream consequences for population persistence, or (2) female Savannah Sparrows have a broader thermal breeding tolerance relative to other species and that there will be few downstream effects.

Consistent with the results of a previous study of this population (Wheelwright and Schultz 1994), we found that the timing of breeding in Savannah Sparrows on Kent Island varies with individual age. Accumulated lifetime experience has been widely documented to confer fitness advantages in many bird species (Wheelwright and Schultz 1994, Wilson et al. 2007, Whelan et al. 2016, Sauve et al. 2019). Therefore, advances in lay date with age at both the individual and population level in Savannah Sparrows are not surprising and provide further evidence that experience may confer improved foraging efficiency and may allow females to more accurately respond to pre-breeding conditions, resulting in optimal laying date. Likewise, previous work has suggested that older females spend the non-breeding period in regions closer to the breeding grounds (Woodworth et al. 2016), which may advance spring arrival dates to Kent Island and facilitate early nesting.

Low food availability in developmental stages of an organism's life can have negative downstream repercussions for a number of morphological and physiological traits influencing fitness, including individual lifespan (Metcalfe and Monaghan 2001, Monaghan 2008, Freeman et al. 2020). Savannah Sparrows are less active in the rain (all authors, *personal observation*), suggesting that increased precipitation in an individual's natal year may have detrimental effects on parental feeding of nestlings and lead to difficulty in foraging by newly fledged young, resulting in a poor nutritional state (Öberg et al. 2015). To compensate for poor natal conditions, organisms often undergo rapid growth and development (Metcalfe and Monaghan 2001). The costs of compensatory growth can be great, for both the short-term prior to adulthood and the long-term as individuals age (Metcalfe and Monaghan 2001). In this way, natal conditions can carry over to influence future individual performance. Consistent with findings in other species (Monaghan 2008), we show that females that experienced high natal precipitation had significantly shorter lifespans. This compensatory response to poor natal conditions may also be what drives the more dramatic phenological response with age in high natal precipitation females. To compensate for anticipated shorter lifespans, it is possible that females who experience high natal precipitation advance their lay date more dramatically in order to maximize nesting attempts, resulting in a faster pace of life compared to females

experiencing lower natal precipitation (Dammhahn et al. 2018). Additionally, females that experienced high natal precipitation fledged fewer individuals per nest but had more nesting attempts over the course of their lives. While low natal precipitation females still produced more offspring over the course of their lives than high natal precipitation females due to increased longevity, it is likely that the more dramatic phenological response and increased number of nesting attempts in high natal precipitation females allowed these individuals to, at least partially, compensate for poor natal conditions.

Importantly, given that high natal precipitation females have lower fecundity, a significant increase in precipitation during the breeding period over the 33-yr study suggests the potential for further declines in the Kent Island Savannah Sparrow population through reduced population-level reproductive output. It is possible that the decline in population density documented on Kent Island (Woodworth et al. 2017a) resulted from reduced reproductive output at the population level in response to increasing precipitation, which has been demonstrated in Tree Swallows (*Tachycineta bicolor*) breeding on the island (Taylor et al. 2018). This is particularly concerning given that every year since 2013 was a higher-than-average precipitation year, and that breeding ground precipitation has been increasing since 2008. Importantly, this increasing trend in precipitation may complicate interpretation of our results, since females born in these years may still be reproductively active in future breeding seasons (i.e., the data may be right censored). In addition to the possible carry-over effect of natal precipitation on future reproduction, rainfall during each breeding period could also have immediate impacts on breeding adults. For example, heavy precipitation, especially early in the breeding season, may limit reproductive output through metabolic stress (de Bruijn and Romero 2013).

Understanding the mechanisms by which birds plastically adjust their phenology is of increasing importance in light of ongoing environmental shifts and climate change. This is particularly relevant given that individual responses to environmental change are ultimately linked to population dynamics, and appropriate phenological adjustments may be central to population persistence. Our results highlight the importance of understanding developmental conditions and illustrate how natal conditions may influence a broad spectrum of life history traits. We also confirm the importance of pre-breeding temperature and age for breeding phenology in migratory passerines and suggest a novel mechanism by which birds may adjust their phenology. It may also be pertinent to explore other factors influencing natal condition, such as temperature, population genetics, and density. Future studies should aim to examine the effects of these natal conditions, as well as possible effects of precipitation on phenology, fecundity, and density in wild populations, as they may influence

phenological shifts and individual fitness more than currently recognized.

ACKNOWLEDGMENTS

We thank the many researchers, undergraduate students, and field assistants who have assisted with the collection of the long-term Savannah Sparrow data set. Bowdoin Scientific Station on Kent Island kindly provided accommodations and continued access to the study site. This study was supported through grants and scholarships from the Natural Science and Engineering Research Council of Canada (D. R. Norris, A. E. M. Newman, D. J. Mennill, S. M. Doucet, B. K. Woodworth, G. W. Mitchell), the U.S. National Science Foundation (N. T. Wheelwright), the Canada Foundation for Innovation (D. R. Norris), the University of Guelph (D. R. Norris, J. B. Burant, B. K. Woodworth, G. W. Mitchell), and the Ontario Government (J. B. Burant). We would like to thank the two reviewers for their valuable feedback, which greatly improved the clarity of our work. This represents Bowdoin Scientific Station contribution no. 284. Authorship Statement: J. B. Burant and E. W. Heisey contributed equally to this work. J. B. Burant, E. W. Heisey, S. Whelan, and D. R. Norris were involved in initial discussions and study design. S. Whelan performed a preliminary analysis; E. W. Heisey conducted the final analysis of the complete data set and wrote the first draft. J. B. Burant and D. R. Norris revised later versions of the manuscript. N. T. Wheelwright initiated and maintained the long-term Savannah Sparrow study on Kent Island from 1987 to 2004; D. R. Norris and A. E. M. Newman have continued the study since 2008, in collaboration with D. J. Mennill and S. M. Doucet since 2013. G. W. Mitchell (2008–2010), B. K. Woodworth (2014–2016), J. B. Burant (2018–2019), and E. W. Heisey (2019) also contributed to collection of the long-term demographic data. All authors revised and approved the manuscript for publication. The authors declare no competing interests.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3575/supplinfo>

OPEN RESEARCH

Data and code for the analysis will be made publicly available on the Figshare repository at: <https://doi.org/10.6084/m9.figshare.14104829> (Burant et al. 2021). The analysis implemented existing tools and no novel code or packages were generated.