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Cite this article: Gow EA *et al*. 2019 A range-wide domino effect and resetting of the annual cycle in a migratory songbird. *Proc. R. Soc. B* **286**: 20181916. http://dx.doi.org/10.1098/rspb.2018.1916

Received: 26 August 2018
Accepted: 9 December 2018

Subject Category:
Ecology

Subject Areas:
behaviour, ecology

Keywords:
carry-over effects, life history, migration, *Tachycineta bicolor*, timing of breeding, tree swallow

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A range-wide domino effect and resetting of the annual cycle in a migratory songbird

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Latitudinal differences in timing of breeding are well documented but how such differences carry over to influence timing of events in the annual cycle of migratory birds is not well understood. We examined geographical variation in timing of events throughout the year using light-level geolocator tracking data from 133 migratory tree swallows (*Tachycineta bicolor*) originating from 12 North American breeding populations. A swallow's breeding latitude influenced timing of breeding, which then carried over to affect breeding ground departure. This resulted in subsequent effects on the arrival and departure schedules at autumn stopover locations and timing of arrival at non-breeding locations. This 'domino effect' between timing events was no longer apparent by the time individuals departed for spring migration. Our range-wide analysis demonstrates the lasting impact breeding latitude can have on migration schedules but also highlights how such timing relationships can reset when individuals reside at non-breeding sites for extended periods of time.

1. Introduction

An organism's annual cycle typically is divided into a series of events that are timed to maximize fitness. Determining timing of these events and how

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[†]Deceased 10 April 2015.

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4335911.

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they may be linked across stages of the annual cycle is fundamental for understanding how the environment shapes a species' ecology and evolution [1]. Timing of events within an annual cycle can also vary widely among populations of the same species and these differences can have consequences for life-history traits [2–5]. In addition, many species are advancing their breeding initiation dates in response to warmer temperatures, which in some cases may result in a phenological mismatch [6–8]. Understanding what drives the timing of events at the continental scale has important implications for understanding constraints on life-history variation and effective conservation.

Timing of breeding can influence individual reproductive success within a population and plays a key role in shaping phenotypic differences in reproductive traits among populations [9–11]. Among the most well-established geographical life-history pattern is a difference in timing of breeding in relation to latitude [2,5,12]. In the Northern Hemisphere, individuals breeding further north tend to breed later in the season than southern breeding individuals. As a potential consequence, northern breeding individuals may experience a shorter time period for reproduction and face stronger time constraints within the annual cycle [13]. However, whether and how differences in timing of breeding among populations carry over to influence subsequent timing events of the annual cycle is poorly understood.

In migratory animals, two previous studies have provided some evidence that the latitude at which individuals breed may influence timing and duration of events in subsequent periods of the annual cycle. Collared flycatchers (*Ficedula albicollis*) originating from two breeding latitudes, differed in their timing of breeding which then carried over to influence autumn migration departure date, the length of the non-breeding residence period, timing of spring migration and subsequent breeding initiation [14]. In bar-tailed godwits (*Limosa lapponica*) tracked from a single non-breeding site in New Zealand, breeding latitude was the primary factor driving timing of departure from the non-breeding grounds, duration of time spent at stopover sites and subsequent breeding arrival [15]. However, because both studies were based on data from a limited geographical area, it is unclear how strong or weak such a 'domino effect' [16] would be if individuals were sampled from populations across their breeding range and over a wider latitudinal span. A domino effect occurs when the timing at one phase of the annual cycle may carry over to affect the timing of any subsequent phase [16]. It is also possible that events may not be so tightly linked, particularly in species that track resources with strong phenological patterns, such as fruits, where large-scale movements within the annual cycle may be driven more by changes in resource abundance [17–20] than events related to timing of breeding. Examining the presence or strength of a domino effect across multiple populations also requires information on within-and among-population variation in the timing of events because individuals within a population may vary in their timing and individuals from specific populations may consistently be early or late.

In this study, we used light-level geolocators to track the daily movements and timing of events over an entire year for tree swallows (*Tachycineta bicolor*) originating from 12 geographically distinct breeding populations within their North American breeding range. Individual tracks were recovered from populations spanning over 25° of latitude, allowing us to present one of the most in-depth analyses of whether such domino effects occur, whether such effects are mediated by other factors such as geographical location and distance travelled among sites, and where domino effects may begin to break down during the annual cycle, if at all.

2. Material and methods

(a) Study species and data collection

Tree swallows breed in tree cavities, as well as nest-boxes, throughout Canada and the north/central United States (figure 1*a*). They occupy open habitats and forage for flying insects, often near water [21]. During the non-breeding season, tree swallows consume a variety of flying insects and berries from *Myrica* spp. Their non-breeding range extends from the southern USA to northern Panama (figure 1*a*). Unlike many other migratory birds [22,23], breeding populations of tree swallows are segregated on their non-breeding grounds by longitude rather than latitude [24].

Between 2010 and 2014, we equipped 561 adult tree swallows with an archival light-level geolocator (hereafter referred to as 'geolocators') at 12 breeding sites spanning latitudinal and longitudinal gradients across the tree swallows' breeding range (figure 1*a*). Overall, 161 geolocators were retrieved and 133 were free from malfunctions and used in this analysis (for further details about deployment, geolocators specifications and recovery see [24]). All birds were tracked once for one year. The coordinates for each site, number of recovered geolocators and details of geolocator analyses are in the electronic supplementary material.

(b) Statistical analyses

We constructed a series of models to examine events in the annual cycle. Although tree swallows are single-brooded, they may attempt a second nest following predation of the first. Using breeding data from the year of geolocator deployment, we obtained first egg date (date on which the first egg of the first clutch of the season was laid) and fledge date (date young left the nest of the last nest) from each swallow with a recovered geolocator. We extracted the following variables from each tree swallow with a geolocator: breeding site departure date, arrival and departure dates at the first autumn stopover site, arrival and departure dates from the non-breeding site and breeding site arrival date (electronic supplementary material, table S1). To account for factors that may influence a given timing event, models contained predictor variables relating to the previous time period, distance from the past stationary location, breeding latitude (continuous variable using breeding latitudes for each individual), current latitude (continuous variable for each individual), sex, as well as interactions among these predictor variables (electronic supplementary material, table S2). Geolocator error based on averaged location estimates from the breeding site was 46 ± 90 (s.d.) km (range: 1–431 km) in latitude and 52 ± 90 km (range: 3–459 km) in longitude. We considered birds to have departed from a site following a large (greater than or equal to 250 km) consistent latitudinal or longitudinal movement away from the stationary position for at least 2 days. The definitive prebasic moult (post-breeding moult) in tree swallows occurs from mid-July to October, with individuals undergoing the heaviest moult in the first month following breeding [25]. Unlike many other songbirds that moult on or near their breeding areas, tree swallows occupy communal roosting sites away from their breeding sites where they probably undergo moult [21]. We referred to this location as the first stopover site during autumn migration [21]. It is unknown whether all individual swallows finish their moult before moving to a second stopover site, although most of the moult is presumed to occur at the first stopover site [21,25]. Timing of arrival and departure from this site may be important for avoiding excessive energetic expenditure that may cascade

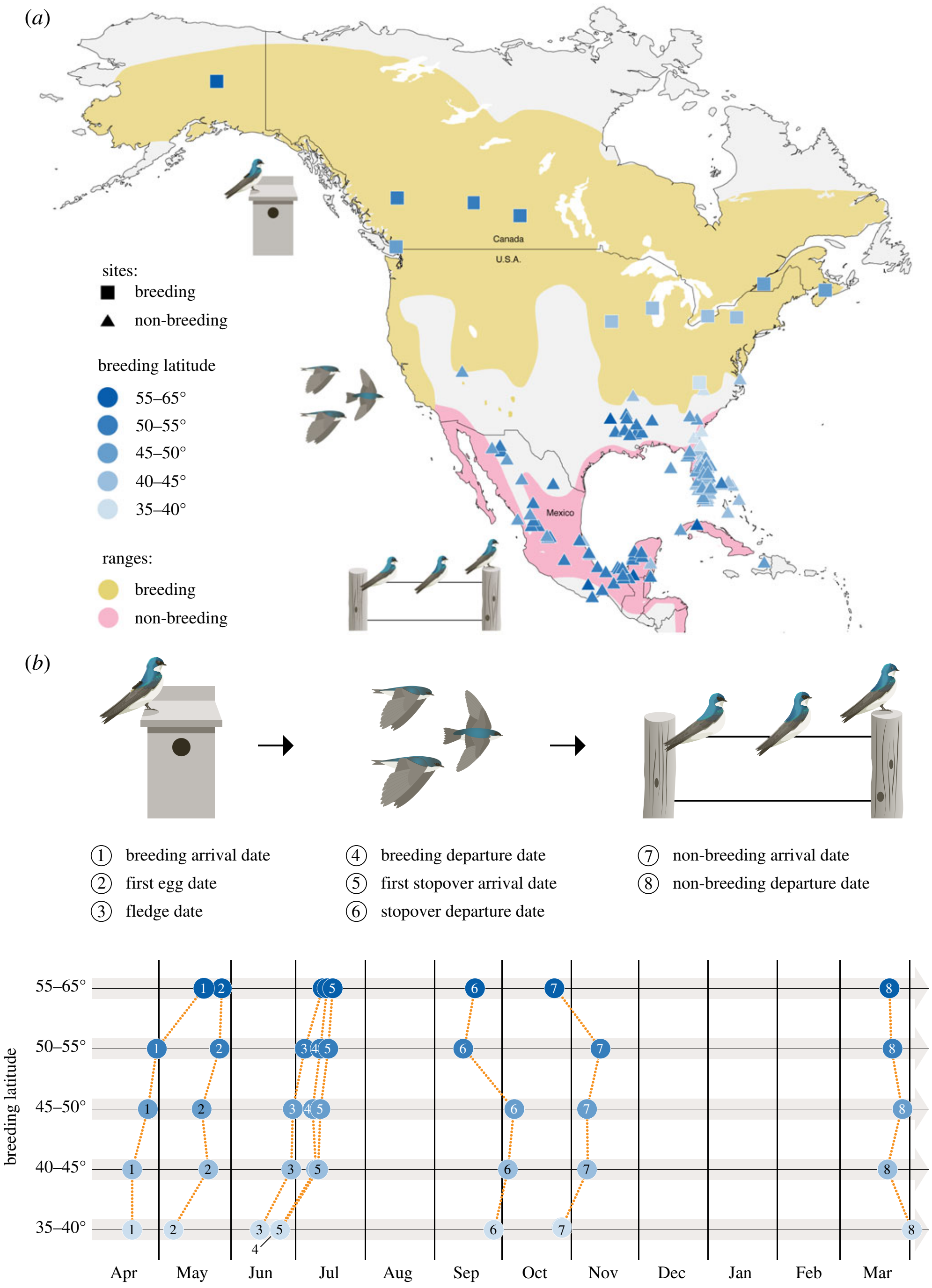

Figure 1. (*a*) Locations of 12 tree swallow (*Tachycineta bicolor*) breeding sites where geolocators were deployed and recovered (circles; $n = 133$ individuals), and non-breeding locations (triangles) are superimposed over the breeding (yellow) and non-breeding (pink) range (BirdLife International and NatureServe 2015). The breeding site coordinates and samples sizes within each latitude category (gradients of blue) are in the electronic supplementary material. (*b*) Timing of events within the annual cycle of tree swallows using light-logging geolocators originating from 12 breeding sites. The numbered circles represent the median timing of events by breeding latitude category (shown as the gradient of blue; *y*-axes). The orange dotted lines link events across different latitudes. The light blue arrows across each latitude show the direction of the annual cycle (*x*-axes). Figures designed by KAP Design.

into other periods of the annual cycle, especially if moult is incomplete prior to the onset of cold weather [25]. We considered a location to be a stopover site if an individual spent at least 21 days at the same location; this length of time was used to separate potential moulting sites from temporary stops on a migration route and to account for potential error in the accuracy of geolocator data.

We were unable to determine specifically when some swallows migrated to their first stopover site because it was probably very close to the breeding site and within the error associated with location estimates derived from geolocators. Because the relationships between fledging date and departure from the breeding site and subsequent arrival at the first stopover site were strongly positively correlated at the individual level ($R^2 = 0.70$, $\beta = 0.79 \pm 0.05$ s.e., $p < 0.0001$, $n = 112$; and $R^2 = 0.75$, $\beta = 1.00 \pm 0.06$, $p < 0.0001$, $n = 112$, respectively), we interpolated timing of departure from the breeding site and subsequent arrival at the first stopover site for individuals where breeding site departure date was unknown ($n = 27$). To do this, we used the equation generated from a linear mixed effects model (LMM) to predict breeding departure with fledging date as the predictor and breeding site as the random effect ($y = 0.44x + 144$). For interpolating arrival at the first stopover site (response variable; $n = 27$), we included the same predictor and random variables as above and calculated arrival at the first stopover location ($y = 0.16x + 161$).

We defined the first non-breeding site to be one where an individual spent the most time [26], or spent at least 28 days after

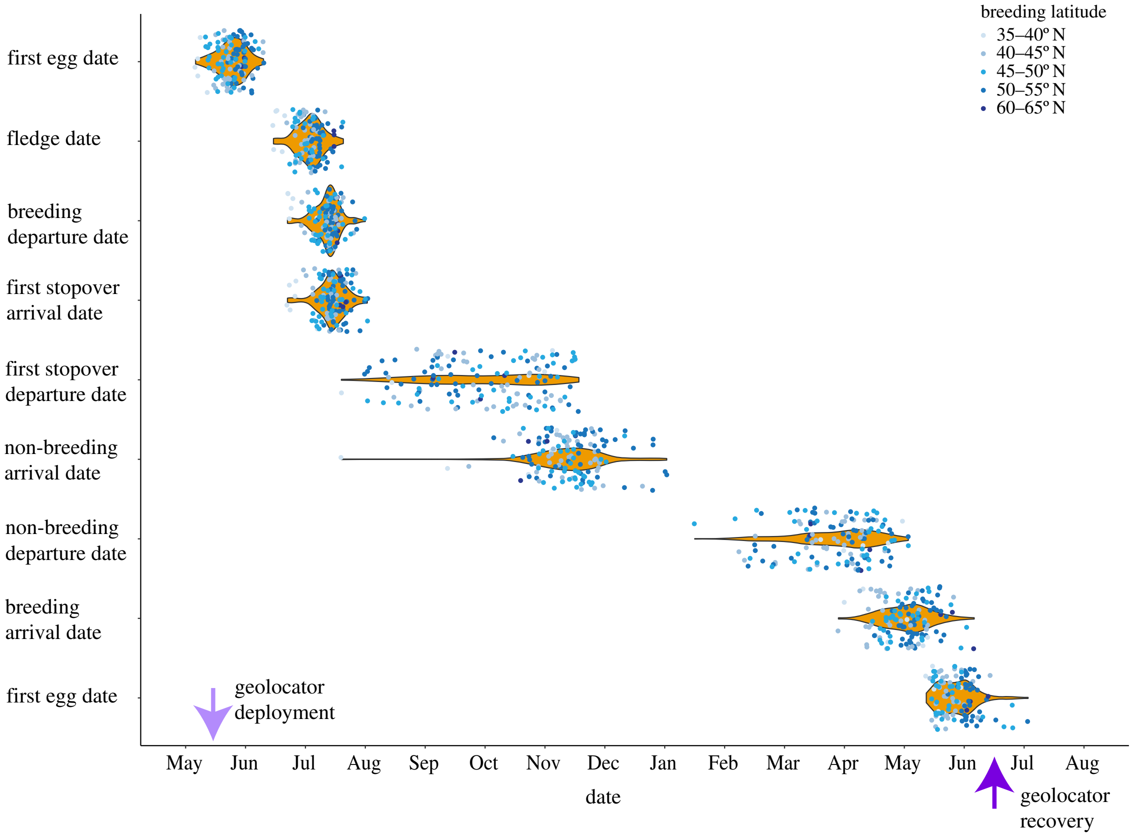

Figure 2. Timing of major events throughout the annual cycle of 133 tree swallows (*Tachycineta bicolor*) originating from 12 breeding sites. The shape and length of the violins are based on kernel density estimations of the distribution of the dates of each event within the annual cycle. Circles represent individual tree swallows with colour coding based on the breeding latitude category. (Online version in colour.)

departing from a stopover site, so as not to be confused with temporary movements for weather or local resource changes [26,27]. Although most tree swallows have more than one non-breeding location [28], we surmised that the initial non-breeding site would best represent when tree swallows entered a ‘non-breeding’ phase (separate from a stopover or moulting phase) of their annual cycle. To estimate non-breeding site departure date, we used the location of the final non-breeding site. We determined locations of the stopovers and non-breeding sites by calculating the mean location of all daily locations from each stationary time period. If the location occurred over the ocean, which was common in birds residing near coastal areas, we repositioned the mean location to the nearest point on land (stopover sites, $n = 10$ mean locations; non-breeding sites, $n = 38$ mean locations). Direct distances between sites were calculated between mean locations as determined using the definitions and methods above. Because individual breeding latitude and the distance between breeding site and the non-breeding site were strongly positively correlated ($R^2 = 0.82$, $p < 0.0001$), we only used breeding latitude as one predictor in our models.

We examined factors that influenced timing events within the annual cycle by first constructing LMMs for each timing event of interest (breeding arrival date, first egg date, fledge date, breeding departure date, arrival at first stopover, stopover departure, non-breeding arrival date and non-breeding departure date). For each timing event response variable, we established *a priori* candidate models consisting of our predictor variables of interest, possible interactions or a subset of possible interactions (see the electronic supplementary material, table S2 for models and variables). We then compared competing models using Akaike information criterion adjusted for small sample sizes (AIC_c) [29]. We considered models less than or equal to 2 $\Delta\text{AIC}_\text{c}$ units of the top model as competitive [30], and those between 2 and 4 $\Delta\text{AIC}_\text{c}$ to be ‘plausible’. To derive parameter estimates, we used a weighted model averaging over all models within less than or equal to 4 $\Delta\text{AIC}_\text{c}$ units [30]. We assessed variable importance using the 85% confidence interval (CI) [31] of the model-averaged estimates. Because predictor variables varied in their scale (i.e. latitude, distance and Julian dates), we standardized each predictor variable to a mean of zero and a variance of one (i.e. *z*-scores). The LMMs used maximum-likelihood estimation with a Gaussian distribution and all models included a random intercept of the breeding site. Because our dataset involved individuals from multiple breeding sites, we also constructed additional LMMs that separate within- versus between-population (breeding site) effects using within-subject centering for each timing event predictor variable [32] (further details in the electronic supplementary material).

All statistical analyses were conducted in R v. 3.3.2 [33]. LMMs were conducted using the R package lme4 [34] and lmerTest [35]. Model likelihoods and model averages were calculated using the MuMIn package [36]. Variance is expressed as ± s.d. for dispersion around the mean, and ± s.e. for error associated with model estimates. All analyses were based on individual values of latitude for individual swallows, but we used the predicted quartiles from our models for categorical interpretation and representation of our findings (see figures 1–3). We measured the influence of outliers in our analyses using Cook’s distance. Although some models contained outliers, we opted to keep those individuals in our analyses as their timings were biologically relevant.

3. Results

(a) Timing of arrival at the breeding site, first egg date and fledge date

Across all breeding sites, arrival date spanned 68 days (range: 23 March–30 May: mean: April 26 ± 12 days; $n = 125$; figures 1*b* and 2; electronic supplementary material, figure S1)

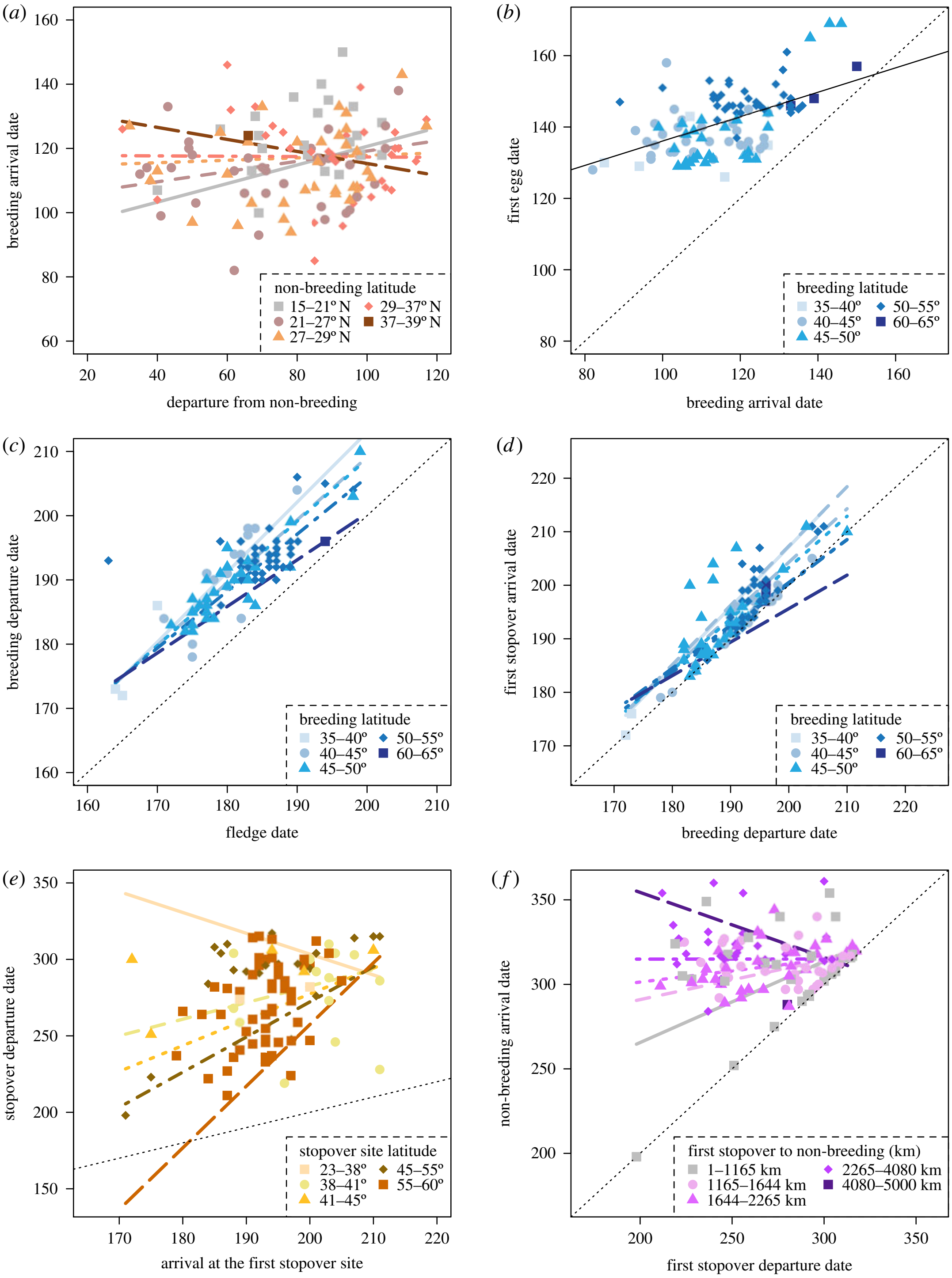

Figure 3. Relationships between timing of various events throughout the annual cycle in tree swallows (*Tachycineta bicolor*). (*a*) Departure from the non-breeding site interacts with non-breeding latitude to predict breeding site arrival date. (*b*) Breeding site arrival and breeding latitude positively predict the first egg date of tree swallows. (*c*) The fledge date and breeding latitude interact to predict breeding site departure date. (*d*) Breeding site departure date interacts with breeding latitude to positively affect first stopover site arrival date. (*e*) Arrival at the first stopover site and stopover latitude interact to influence stopover departure date. (*f*) First stopover departure date and the distance between the first stopover site and the non-breeding site interact to affect non-breeding arrival date. (*b–f*) The black dashed lines indicate the 1 : 1 line of the variables on the *x*-axis and *y*-axis. (*a,c–f*). The coloured lines represent the predicted quartiles (minimum, lower, median, upper and maximum) of the interaction and their associated range in values. (*a–f*) The colour-coded points represent individual tree swallows based on the predicted quartile categories. Dates are expressed as number of days past 1 January.

and the top supported models explaining variation in arrival date included breeding latitude, sex, non-breeding departure date, non-breeding latitude, the interaction between the latter two variables and the interaction between breeding latitude and non-breeding departure date (electronic supplementary material, tables S1 and S3). The interaction between non-breeding departure date and non-breeding latitude suggested that the positive slope between non-breeding departure and arrival on the breeding site weakened when swallows used more northern non-breeding sites (figure 3*a*). Breeding site arrival date was positively related to breeding latitude. Males arrived, on average, 4.5 ± 2.4 days earlier than females (mean male: April 25 ± 12, $n = 56$; female: April 28 ± 12, $n = 69$). Non-breeding latitude, non-breeding departure date and the interaction between breeding latitude and non-breeding departure date appeared in models with ΔAIC_c less than 4, but their confidence intervals overlapped zero (electronic supplementary material, table S1).

In the year of geolocator recovery, first egg dates ranged from 5 May to 25 June (mean: May 23 ± 8 days; $n = 108$; figure 2; electronic supplementary material, figure S1) and the top supported models included breeding latitude, date of arrival at the breeding site, their interaction and sex (electronic supplementary material, tables S1 and S3). Combining data from all breeding locations birds that returned to the breeding site early (figure 3*b*) and those that bred at lower latitudes had earlier first egg dates than late arriving birds and those at higher latitudes (electronic supplementary material, table S1). Sex and the interaction between breeding latitude and breeding arrival date appeared in models with ΔAIC_c less than or equal to 4 but had weak support as their confidence intervals overlapped zero (electronic supplementary material, table S1). The effect of breeding arrival date on first egg date was the result of an among-breeding site effect (electronic supplementary material, table S4).

Fledge date in the year of deployment ranged from 13 June to 18 July (mean: July 1 ± 7 days; $n = 109$; figure 2; electronic supplementary material, figure S1). Birds with earlier first egg dates and those at lower breeding latitudes fledged young earlier than birds with later first egg dates and at higher breeding latitudes (electronic supplementary material, table S1). This relationship occurred both within- and among-breeding sites (electronic supplementary material, table S4). The differing slope between the within- and among-effects (estimate: 0.43 ± 0.14, CIs 0.14–0.73), imply there are two separate biological explanations. The among-breeding site effects probably resulted from latitudinal differences in the length of time between breeding initiation and fledge date that decreases as one goes farther north (electronic supplementary material, table S5), while the within-breeding site effect may reflect individual variation in the time between first egg dates and fledge dates.

(b) Breeding departure

Tree swallows departed the breeding grounds over a span of 37 days (range 21 June–29 July; mean: July 10 ± 6; $n = 100$; figures 1*b* and 2; electronic supplementary material, figure S1) and the top supported models included sex, breeding latitude, fledge date and the interaction between the latter two variables (electronic supplementary material, table S3). The interaction term (electronic supplementary material, table S1; figure 3*c*) suggested that when birds fledged young early in the season, there was little effect of breeding latitude, whereas late in the season, birds at high latitudes tended to depart quickly after fledging compared to southern breeding birds. For example, while all four of the birds at the most northern site in Alaska only spent approximately 2 days post-breeding before they departed for autumn migration, the mean number of days prior to departure for birds successfully breeding between 50 and 55°N was 8 ± 3 days (range: 5–17 days; $n = 45$), and 12 ± 3 days for birds breeding between 40 and 45°N (range: 3–20 days; $n = 25$). Birds that bred late (in the 75th percentile; >5 July) departed 7 ± 5 days (range: 2–16 days; $n = 25$) after fledging young, whereas those that bred early (25th percentile; <26 June) spent over twice as long at the breeding site after fledging young (18 ± 16 days post-breeding; range: 5–71 days; $n = 22$). The effects of the fledge date on breeding departure date were the result of within- and among-breeding site effects. These effects were similar and went in the same direction (electronic supplementary material, table S4). Females and males left within one day of each other (means: females: July 10 ± 8; males: July 11 ± 4).

(c) Timing of arrival and departure from the first stopover site

Similar to dates of departure from the breeding site, arrival dates at the first stopover site occurred over a span of 41 days (range: 21 June–30 July; mean: July 13 ± 7 days; $n = 102$; figures 1*b* and 2; electronic supplementary material, figure S1). Birds travelled a maximum of 3561 km (mean: 1055 ± 1010 km) between their breeding grounds and first stopover site. Individuals breeding west of the continental divide and in Alaska travelled the farthest distances (mean: 3011 ± 235 km; $n = 23$). On average, birds arrived at their first stopover site 3 ± 4 days (9 days when controlling for breeding latitude) after they departed the breeding site. The top supported models for predicting stopover arrival included sex, distance between breeding and stopover site, breeding latitude, departure date from the breeding site, the interaction between distance and departure date, and the interaction between breeding latitude and departure date (electronic supplementary material, tables S1 and S3). Swallows that travelled farther distances arrived at stopover sites later than those travelling short distances. The interaction between breeding latitude and breeding departure date suggested that swallows departing early from their breeding site arrived early at stopover sites, but the strength of this relationship declined with increasing breeding latitude (figure 3*d*). The relationship between stopover arrival and breeding departure was the result of within- and among-breeding site effects (electronic supplementary material, table S4). These effects were similar and went in the same direction. Females arrived at stopover sites on less than one day earlier than males when controlling for breeding latitude (means: female: July 12 ± 8 days; male: July 14 ± 6 days).

Unlike departure from breeding sites and arrival at stopover sites, there was considerably more variation in departure dates from first stopover sites. Departure dates occurred over a span of 119 days (range: 17 July–13 November; mean: September 25 ± 29 days; $n = 126$; figure 2; electronic supplementary material, figure S1) and the average length of stay at these sites was 75 days ± 28 days (range: 21–128 days, $n = 126$). The top supported models explaining departure date from stopover sites included sex, stopover latitude, arrival date at first stopover site, breeding latitude and the interaction between stopover latitude and arrival date (electronic supplementary material, tables S1 and S3). The interaction (electronic supplementary material, table S1; figure 3*e*) term suggested that the positive slope between arrival and departure weakened when swallows used more southerly stopover sites as their first stopover. Like stopover arrival date, the relationship between stopover departure and breeding arrival was the result of within-and among-breeding site effects (electronic supplementary material, table S4). Confidence intervals for breeding latitude and sex overlapped zero, suggesting they had little effect on stopover departure date (electronic supplementary material, table S1).

(d) Timing of arrival and departure from the non-breeding sites

Similar to departure dates from stopover sites, arrival dates at non-breeding sites were highly variable and occurred over 161 days (range: 19 July–27 December; mean: November 8 ± 20 days; $n = 115$; figure 2; electronic supplementary material, figure S1). Twenty-five per cent (29 out of 115) of birds flew from a stopover site to a non-breeding site in less than 15 days (25th percentile) at average speeds of 424 ± 262 km d^{-1} (range: 114–932 km d^{-1}). The other 75% (86 out of 114) travelled at much slower speeds (mean: 38 ± 23 km d^{-1}; range: 4–102 km d^{-1}) by either stopping at multiple sites for short periods of time or taking additional stopovers of 21 days or more. The top supported models predicting arrival at the non-breeding site included the distance between the stopover and non-breeding site, the stopover departure date, sex and the interaction between distance and stopover departure date (electronic supplementary material, table S1). Females arrived at non-breeding sites on average 10 ± 3.1 days earlier than males (mean female: November 4 ± 21; male: November 14 ± 17). The interaction between date of departure from the first stopover site and distance to non-breeding site (electronic supplementary material, table S1) suggested that when birds departed early from the stopover site, arrival at the non-breeding site was negatively influenced by migration distance (figure 3*f*). By contrast, when birds departed late from the stopover site, distance to the non-breeding site had little effect on arrival date, primarily because most late-departing birds appeared to reach non-breeding sites soon after their departure from stopover sites. Although breeding latitude appeared in models with ΔAIC_c less than or equal to 4, its confidence intervals overlapped zero, suggesting it had little effect on non-breeding arrival date (electronic supplementary material, table S1). Likewise, there were no within- and between-breeding site effects of stopover departure date on non-breeding arrival.

Departure date from the final non-breeding site was highly variable and occurred over a span of 107 days (10 January–27 April; mean: March 22 ± 22 days; $n = 122$; figure 3; electronic supplementary material, figure S1). Non-breeding latitude, sex, breeding latitude and non-breeding arrival date were in the top supported models predicting departure date from the final non-breeding site (electronic supplementary material, tables S1 and S3). Birds that spent the non-breeding season at southerly latitudes tended to depart earlier than those that spent the non-breeding season farther north. For instance, swallows departing from locations between 15 and 21°N departed, on average, 10 days earlier than birds departing from locations between 29 and 37°N. Males departed, 14 ± 3.5 days earlier than females (mean females: March 27 ± 21; males: March 16 ± 21). The predictor variables of breeding latitude and non-breeding arrival date had confidence intervals that overlapped zero, suggesting less certainty as predictors of non-breeding departure date (electronic supplementary material, table S1). There were no within- and among-breeding site effects of non-breeding arrival date on non-breeding departure date.

4. Discussion

Our results provide unique insights into how breeding latitude starts a cycle of cascading events first by regulating timing of breeding which then, in part, determines timing of arrival and departure at future stages in the annual cycle up until the end of the non-breeding period. Each of these timing relationships was mediated through interactions either with geographical location or distance travelled. For instance, the influence of breeding latitude on departure date from the breeding site depended on whether the young of adults fledged early or late in the year, and the influence of stopover arrival date on stopover departure date depended on stopover site latitude. Stopover departure date then affected arrival at non-breeding sites, but was mediated by how far an individual travelled between the first stopover and non-breeding site. Importantly, we provide evidence that this domino effect broke down during the non-breeding period where departure from the non-breeding sites was not based on prior timing events but was only influenced by the latitude of the non-breeding site and sex. We also show how these domino effects were a result of both within-and among-population variation. Overall, our study provides evidence of how pervasive domino effects can be, how breeding latitude drives such cascading effects and how they can eventually break down during the stationary non-breeding season.

In contrast to our work, evidence from other studies suggests that such a breakdown between timing events may be more common during migration in other species. For instance, while late-breeding wood thrush (*Hylocichla mustelina*) entered the tropics later than early breeders, the autumn migration period acted as a timing reset period because all individuals arrived at non-breeding sites at similar times [37]. Similarly, late breeding and departing Cory's shearwaters (*Calonectris diomedea*) arrived at their non-breeding grounds at the same time as early breeding individuals [30], and Hudsonian godwits (*Limosa haemastica*) that were 'late' during one period of the annual cycle were not necessarily late during other periods if individuals were able to 'catch-up' at stopover or non-breeding sites [38]. However, in a recent experimental brood enlargement study at two different latitudes, collared flycatchers with enlarged broods were able to mitigate the carry-over effects from the increased breeding demands during the non-breeding period [39]. Our results involving multiple populations at the continental level are consistent with what these other single or two-population studies have previously shown. There may be times within the annual cycle, such as during migration or non-breeding periods that act as 'catch-up periods', where any delays in the annual cycle are mitigated and late-breeding or otherwise delayed individuals may have opportunities to reset timing of future events in their annual cycle.

The breakdown of the domino effect during the non-breeding period suggests events or processes not measured during the non-breeding period may play an important role in determining the time of departure from the non-breeding grounds and subsequent arrival on the breeding grounds. Several studies have shown non-breeding habitat quality can influence spring migration timing and speed [40–42]. It is, thus, not surprising the non-breeding period was when timing relationships deteriorated because it was also the longest period of time when birds were 'stationary' and, therefore, had the longest interval between timing events. Our results also point to the possible importance of events, such as changes in resource abundance or degradation of habitat quality, within the non-breeding period driving subsequent timing of migration in this species.

We also show the timing of departure from the non-breeding grounds is primarily driven by non-breeding latitude, which may have important implications for understanding the effects of climate change on breeding phenology. Northern breeding populations of tree swallows may face strong timing trade-offs during the annual cycle because of the long migration distances and length of time they spend migrating compared to more southern populations. Vegetation phenology is advancing most rapidly in the north from rising global temperatures [43–45], and a timing mismatch may occur [8,46] if migratory animals have no cues at the non-breeding sites to gauge environmental conditions on the breeding grounds and time their breeding arrival accordingly. Therefore, populations that travel the farthest distances, such as northern populations, face the biggest risks of missing the short window of optimal breeding conditions. Swallows that return slowly to their breeding grounds (typically the individuals spending the non-breeding season at northern latitudes) may be better able to use non-breeding cues to time their arrival to the breeding site to match the timing of egg laying to food supply, which positively influences clutch size and fledging success in this species [7]. These findings suggest that northern breeding populations of tree swallows may be more prone to potential negative effects of phenological mismatches on reproduction, which, as we show may then carry over to affect the timing of other events throughout the annual cycle.

Timing of fledge dates, in our study, were largely owing to within-breeding site facultative adjustments in first egg dates. Regardless of when female tree swallows settle at breeding sites they time their first egg dates to gain benefits from the most favourable conditions and therefore end up breeding synchronously [47]. This optimal timing may differ based on local site-level conditions. However, the latitudinal phenological variation may drive the among-population effects. Thus, it is not the arrival date at the breeding site, *per se*, that influences the timing of future events (i.e. breeding departure, stopover arrival and stopover departure), but the within- and among-population effects of first egg date on fledge date, and breeding conditions or breeding latitude that probably begin the subsequent domino effects that carry over within- and among-populations.

In conclusion, we demonstrate how breeding latitude initiates timing events within the annual cycle (until the end of the non-breeding period) by influencing timing of breeding, which then carries over to influence timing of subsequent events in the annual cycle. However, timing of breeding departure, stopover departure and non-breeding arrival were also mediated by geographical location or migration distance. Such findings could not have been revealed without studying multiple populations spanning the breeding range of a species. This allowed us to examine variation in timing of events of the annual cycle, while controlling for intra-population variation, and identify differences and similarities in timing of events among breeding latitudes. We were able to identify which populations may face the greatest time constraints within the annual cycle and which may be more vulnerable to changing environmental conditions, particularly if individuals from those populations (i.e. at northern latitudes) are not able to adjust migration speed or distance travelled. We demonstrate that, while the latitude at which birds breed affects timing of subsequent events in the annual cycle, phenological relationships reset each year upon the initiation of spring migration back to the breeding grounds, emphasizing that high-quality stopover and non-breeding sites are probably critical for this migratory aerial insectivore and other migratory species.

Ethics. This research was approved by the University of Guelph's Animal Care Committee.

Data accessibility. Data are deposited in the Movebank Repository doi:10.5441/001/1.25551gr6 [48], and the Dryad Digital Repository at: http://dx.doi.org/10.5061/dryad.5v5b124 [49]. The R code supporting this article has been uploaded as part of the electronic supplementary material.

Authors' contributions. E.A.G. and D.R.N. designed the research and wrote the manuscript. E.A.G. analysed these data. S.M.K. processed the geolocator data and revised the manuscript. All other authors conducted fieldwork and helped with manuscript revisions.

Competing interests. We declare we have no competing interests.

Funding. Funding for the study was provided by Leaders Opportunity Fund Grants from the Canadian Foundation for Innovation (D.R.N., R.D.D.), Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants (D.R.N., R.G.C., R.D.D., M.B., D.G., F.P., M.L.L.), an NSERC Research Tools and Instruments Grant (D.R.N., M.B., R.D.D., D.G., M.L.L., F.P., D.S.), an NSERC Postdoctoral Research Fellowship (E.A.G.), an NSERC Industrial Research and Development Fellowship (D.W.B.), an NSERC Alexander Graham Bell Canada Graduate Scholarship (L.L.B.), the NSERC Canada Research Chairs Program (M.B., F.P.), the University of Guelph (D.R.N.), Environment and Climate Change Canada (R.G.C., O.L.), Bird Studies Canada (D.W.B., D.J.T.H.), the University of Northern British Columbia (R.D.D.), the British Columbia Knowledge Development Fund (R.D.D.), the Skaggs Foundation (T.B.), a National Science Foundation Grant DEB-0933602 (C.M.T.), a National Science Foundation Grant IOS-0745156 (C.M.V., D.V.), Fonds de Recherche du Québec—Nature et Technologies (M.B., D.G., F.P.), the James S. McDonnell Foundation (C.M.T.), the Alberta Conservation Association (G.L.H, H.E.T.), TD Friends of the Environment (G.L.H., H.E.T.), the Shell Environmental Fund (G.L.H., H.E.T.) and Nature Canada's Charles Labatiuk Nature Endowment Fund (G.L.H., H.E.T.). The development and analysis of some of the geolocators were supported by the National Science Foundation grant nos. IDBR 1152356 and DEB 0946685 (E.S.B.), and IDBR 1152131 (D.W.W.).

Acknowledgements. We thank the numerous field assistants, graduate students, undergraduate students and volunteers who assisted with fieldwork at all 12 breeding sites used in this study. We also thank C. Both and two anonymous reviewers for their comments on this manuscript.

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