TITLE: Non-breeding conditions induce carry-over effects on survival of migratory birds

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SUMMARY

Identifying the processes that limit populations is a foundational objective of ecology and an urgent need for conservation. For migratory animals, researchers must study individuals throughout their annual cycles to determine how environmental conditions limit demographic rates within each period of the annual cycle and also between periods through carry-over effects and seasonal interactions[1–6]. Our poor understanding of the rates and causes of avian migration mortality[7] hinders identification of limiting factors and reversal of widespread avian population declines[8,9]. Here, we implement new methods to estimate apparent survival (hereafter survival) during migration directly from automated telemetry data[10] in Kirtland's Warblers (*Setophaga*

kirtlandii) and indirectly from mark-recapture data in Black-throated Blue Warblers (*S. caerulescens*). Previous experimental and observational studies of our focal species and other migratory songbirds have shown strong effects of Caribbean precipitation and habitat quality on food availability[11–14], body condition[12–19], migration timing[11,12,15,16,20–23], natal dispersal[24,25], range dynamics[26], reproductive success[20,22,27], and annual survival[18–20,23,28–31]. Building on this research, we test the hypotheses that environmental conditions during the non-breeding period affect subsequent survival during spring migration and breeding. We found that reduced precipitation and environmental productivity in the non-breeding period strongly influenced survival in both species, primarily by reducing survival during spring migration. Our results indicate that climate-driven environmental conditions can carry over to affect survival in subsequent periods and thus likely play an important role in year-round population dynamics. These lethal carry-over effects may be widespread and are likely magnified by intensifying climate change.

RESULTS

Weekly survival was lower during migration than in stationary periods

We found that weekly survival probabilities for both species were lower during migration than in the stationary periods. In Kirtland's Warblers (*Setophaga kirtlandii*), we leveraged the species' restricted breeding range, small population size[32–34], and a continent-wide automated telemetry network (i.e., Motus Wildlife Tracking Network[10]) to directly estimate apparent survival (hereafter survival) during the stationary non-breeding (hereafter non-breeding), spring migration, and breeding periods using a novel extension of a multi-state robust-design Cormack-Jolly-Seber (CJS) model (Figure 1). In Black-throated Blue Warblers (*S. caerulescens*), we used

14 years of mark-recapture data from geographically- and demographically-linked populations[29–31,35,36] to estimate non-breeding, spring migration, breeding, and fall migration survival using a full-annual-cycle, integrated survival model[37]. Weekly survival probability for Kirtland's Warblers during spring migration was 0.899 (95% Credible Interval = 0.846-0.944), considerably lower than in the non-breeding or (0.968 [0.948-0.985]) or breeding (0.963 [0.944-0.979]) periods. Black-throated Blue Warblers also had lower weekly survival during spring (0.975 [0.942-0.996]) and fall migration (0.975 [0.940-0.997]), compared to the breeding (0.994 [0.985-0.999]) or non-breeding (0.997 [0.991-1.00]) periods.

Reduced environmental productivity and precipitation carry over to affect survival during migration and breeding

We found that environmental conditions in the Caribbean affected non-breeding survival of Kirtland's Warblers and carried over to influence survival during migration and breeding in both species (Figure 2, Figure S1). In Kirtland's Warblers, non-breeding home ranges with higher Enhanced Vegetation Index (EVI) values, a measure of environmental productivity[38], were associated with higher survival during the end of the non-breeding period (0.651 [0.370-0.855]; Bayesian probability of direction [hereafter Bayesian *pd*] ≥ 0.99), on spring migration (0.620 [0.335-0.835]; Bayesian $pd \geq 0.99$), and in the following breeding period (0.620 [0.341-0.832]; Bayesian $pd \geq 0.99$). In Black-throated Blue Warblers, precipitation during the non-breeding period, as indexed by the Southern Oscillation Index (SOI)[39–41], was not significantly associated with non-breeding survival for either sex (males: -0.68 [-2.88-1.24], Bayesian $pd = 0.76$; females: -0.34 [-2.03-1.19], Bayesian $pd = 0.67$). Survival probability on spring migration was positively associated with SOI in both sexes (males: 0.92 [0.02-2.04], Bayesian $p = 0.98$;

females: 0.72 [-0.27-1.96], Bayesian *pd* = 0.94). SOI was significantly and negatively associated with male survival in the subsequent breeding period (-1.47 [-3.34-0.34], Bayesian *pd* = 0.96), but only weakly associated with breeding survival of females (-0.88 [-3.17-1.10], Bayesian *pd* = 0.80). Thus, following dry, El Niño winters in the Caribbean, Black-throated Blue Warbler survival was lower during spring migration and at least for males, higher over the following breeding season.

DISCUSSION

Using new analytical approaches, we demonstrate that non-breeding period environmental conditions have lethal effects that carry over into migration and the subsequent breeding period in two species of migratory songbirds. These effects were evident at local and regional spatial scales and were confirmed in two species with different geographic ranges, using both direct and indirect methods for estimating seasonal survival. By extending a multi-state robust-design CJS model to incorporate the timing of one-way transitions during the annual cycle and account for the spatially heterogeneous layout of the automated-telemetry stations (see STAR Methods), we were able to directly estimate survival of Kirtland's Warblers during an entire migration, whereas previous studies of small birds have provided indirect estimates[25,28,29,42–44] or direct estimates from one leg of the migratory journey[45]. We found that poor environmental productivity within individual non-breeding home ranges in The Bahamas was associated with lower survival during the non-breeding, spring migration, and breeding periods. In Black-throated Blue Warblers, we extended previously-developed indirect estimation methods to assess the influence of environmental covariates on seasonal survival, the first such application of these methods in non-simulated data[37]. Spring migration survival of both sexes was lower following dry, El Niño winters in the Caribbean, and males showed higher breeding survival after dry winters. Collectively, these results support previous findings showing that non-breeding climate influences annual survival[28,30,46–49], and extend these findings by pinpointing where and when in the annual cycle the effects on mortality manifest. Our results have important implications for forecasting how climate change will influence the population dynamics of migratory birds. Moreover, we argue that they also highlight the need to estimate season-specific vital rates and to determine the factors that affect those vital rates in other imperiled taxa.

Seasonal survival on a rapidly changing planet

Our results suggest that the negative effects of non-breeding drought on survival during migration and the breeding period may be an important, but previously undocumented threat to the survival of birds during migration. The Caribbean has been drying since at least the 1950s[50] and climate change is predicted to increase both the frequency and severity of drought across this region[51–53]. A drying Caribbean has the potential to degrade non-breeding habitat quality and reduce food availability, thereby reducing the ability of individual birds to adequately prepare for migration and to survive through the breeding period.

Climate-induced impacts on population vital rates represent a looming and under-quantified threat for species' sustained existence[54] because the changes to seasonal survival that we documented have the potential to negatively affect population trajectories (Figure 3). Most migratory bird populations are already exhibiting precipitous declines, the drivers of which remain poorly understood[8]. Our findings that environmental conditions in the non-breeding period can lead to changes in vital rates across multiple seasons and that those vital rate changes could endanger population persistence (Figure 3) highlight the urgency for additional research focused on identifying the specific mechanisms that limit populations throughout the annual cycle.

What are the mechanisms of lethal carry-over effects?

Our results confirm predictions that environmental conditions during the non-breeding period can have a lethal carry-over effect during spring migration, but do not identify the precise mechanism(s) responsible. Previous work on songbirds has found that dry conditions and poor-quality habitat on the non-breeding grounds result in lower food availability[11–14] and reduced body condition prior to spring migration[12–19]. Limited food resources and poor body condition could increase non-breeding period mortality and are known to delay departure on spring migration[11,12,15,16,55]. Food and body condition in the non-breeding period also presumably limit the ability of birds to meet the physiological demands of spring migration and ultimately, to survive migration. Departing on migration late relative to conspecifics could further enhance risk of mortality if individuals attempt to compensate for late departure by increasing their migration rate[23]. Future research will be needed to confirm the precise mechanism(s), but our findings suggest that observed effects on survival during migration and breeding are the result of a chain of sublethal effects that begins on the non-breeding grounds.

The carry-over effects of non-breeding environmental conditions on spring migration survival continued to manifest during the breeding period in both species, but in opposite directions. Poor non-breeding conditions were associated with lower breeding survival in Kirtland’s Warblers but with higher breeding survival in male Black-throated Blue Warblers. We attribute this discrepancy to differences in the scale at which we estimated environmental conditions. At the individual level in Kirtland’s Warblers, high environmental productivity on individual non-breeding home ranges likely improved the chances of surviving spring migration (see above), and the following breeding period due to increased body condition, earlier arrival timing, and priority access to high-quality breeding territories[56,57]. At the population level in Black-throated Blue Warblers, reduced rainfall across the non-breeding range may result in fewer individuals reaching the breeding grounds (see above). This could lead to lower population density during the breeding period, which then increases survival during the breeding season. Previous investigations have not found evidence of density-dependent survival in Black-throated Blue Warblers at Hubbard Brook[31], but the demographic processes suggested by our integrated models may be operating at a spatial scale larger than the study site. Nevertheless, our results support the hypothesis that non-breeding environmental conditions can have important carry-over effects on survival during both migration and the subsequent breeding season.

A possible alternative explanation of our findings for Black-throated Blue Warblers is that reduced survival during migration is not a carry-over effect, but instead a direct effect of ENSO-driven weather during migration and breeding. Although the El Niño-Southern Oscillation (ENSO) has strong and predictable effects on dry and wet season precipitation in the Caribbean, including in Jamaica[39–41], it also has teleconnections across the hemisphere. Black-throated Blue Warblers migrate through the southeastern, eastern, and northeastern United States in April and May[58]. Along this migration route, effects of ENSO on temperature and precipitation are only apparent in the southeast between October and March, and are in the opposite direction from the effects observed in Jamaica (i.e., when conditions are dry in Jamaica, they are cool and wet in the southeast)[59,60]. This regionally variable effect, or lack thereof, of ENSO on weather along the migratory route suggests that a direct effect of ENSO during migration is unlikely. Nonetheless, we cannot entirely rule out that ENSO-related weather patterns along the migratory route, or other unmeasured factors, directly contribute or interact with non-breeding effects to influence survival during migration. However, our conclusion that ENSO-driven changes in Jamaican precipitation carries over to affect migration survival is also bolstered by multiple observational and experimental studies that have documented the effects of non-breeding precipitation and habitat quality on food availability, body condition, migration timing, natal dispersal, reproductive success, and range dynamics (see references above).

Implications

Estimating seasonal survival and documenting how climate-driven environmental conditions affect survival throughout the annual cycle are key to advancing our understanding of migratory bird population dynamics and the conservation of these imperiled species. As we demonstrate here, the Motus Wildlife Tracking System[10] provides new opportunities for directly estimating migration survival. However, continued expansion of the Motus network and analytical advances will be needed to realize this potential for the vast majority of other species, which have larger ranges and more complex migration patterns than Kirtland's Warblers[32,34]. In the meantime, the indirect approach we developed and implemented for estimating the effects of environmental conditions on seasonal survival in Black-throated Blue Warblers can be replicated for any species with the necessary data from demographically-linked populations. Regardless, more research and innovation in tracking technology will be needed to understand the immediate causes of mortality (e.g., starvation, collisions, predation).

Documenting survival throughout the annual cycle is a critical next step, but seasonal survival estimates must be combined with other demographic data (e.g., reproduction, dispersal, population size) to develop full-annual-cycle population models that can pinpoint where and when in the annual cycle populations are limited and/or regulated[25,43,61]. Such models will allow researchers to explore how processes throughout the annual cycle combine and interact in potentially nuanced ways to determine the population dynamics of migratory species. Only by further adoption of these approaches will we able to identify the multiple and likely interacting causes of widespread migratory species declines and begin to slow and reverse them through conservation and management. Similar efforts will be needed across migratory taxa, many of which are also experiencing alarming declines[5,62].

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AUTHOR CONTRIBUTIONS

All authors designed the study, NWC, PPM, and TSS performed the research, SWY and CSR provided new analytical methods and analyzed the data, NWC, SWY, and CSR wrote the manuscript, and all authors substantially edited the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Figure 1. Seasonal survival estimation and predicted effects of environmental conditions on spring migration survival

Conceptual figure illustrating: (A) non-breeding and breeding locations for the two species and differences in survival estimation methodology, (B) the periods where survival was either directly (solid) or indirectly (dashed) estimated throughout the annual cycle for each species, and (C) the predicted effects of non-breeding environmental conditions on spring migration survival. Artwork by Sally L. Bornbusch.

Figure 2. Reduced environmental productivity and precipitation carry over to affect survival during migration and breeding

Conditional effect (lines) and 95% credible intervals (shaded areas) of environmental conditions on apparent weekly survival. Conditional effect of March enhanced vegetation index (EVI) on weekly survival of Kirtland's Warblers (left) during late non-breeding (blue), migration (green), and breeding (red) periods. Tick marks along x-axis depict the distribution of observations across the domain of EVI. Conditional effects of non-breeding Southern Oscillation Index (SOI) on female (top right) and male (bottom right) Black-throated Blue Warblers during non-breeding (blue), spring migration (green), and breeding (red) periods. As with Kirtland's Warbler, tick marks along the x-axis depict the distribution of observations across the domain of SOI. See also Figure S1.

Figure 3. Potential effects of non-breeding grounds drying on population growth

Indicative population growth rate (i.e., lambda) as a function of non-breeding Enhanced Vegetation Index (EVI). To characterize the potential for variance in non-breeding environmental conditions to drive population growth trends via the survival dynamics described in this paper, we developed an ad hoc population projection model based on our conditional survival estimates and estimates from the literature. Briefly, this projection matrix estimates population growth as a single-age class, four-season "cyclic" model. We derived estimated per capita fecundity from Bocetti et al.[63] and a static estimate of fall migration survival from Rockwell et al.[28]. The conditional estimates for the other three seasons came from our fitted survival models and considered EVI conditions ranging from the 10-90% quantiles of EVI observed in our dataset. At or above median EVI, population growth is relatively stable and near 1 but drops quickly for below-normal EVI conditions. This suggests that drying conditions may impact population abundance via reduced survival. These findings should be treated as indicative of a possible effect and future work to develop a more complete population abundance model is underway.

STAR METHODS

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Nathan W. Cooper (coopern@si.edu).

Materials Availability

This study did not generate unique reagents.

Data and Code Availability

All data has been deposited at Figshare and is publicly available as of the date of publication. The DOI is listed in the key resources table. All original code has been deposited at GitHub and is publicly available as of the date of publication. The DOI is listed in the key resources table. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

We used mist nets and conspecific song playback to capture 136 adult male Kirtland's Warblers on their non-breeding grounds on Cat Island, The Bahamas (24.33º N, 75.45º W). We used mist nest to capture 314 (89 ♀, 205 ♂) adult Black-throated Blue Warblers at Hubbard Brook Experimental Forest in New Hampshire, USA (43.94°N, -71.70°W) and 116 (45 ♀, 71 ♂) adults at Copse Mountain, Jamaica, West Indies (18.29°N, -77.96°W). All handling of birds was approved by Animal Care and Use Committee Permits from the Smithsonian Institution and Dartmouth.

METHOD DETAILS

Field methods

From 2017-2019, we captured and color-banded male Kirtland's Warblers (2017 n = 58, 2018 n = 40, 2019 n = 38) across Cat Island, The Bahamas (24.67°N, -75.74°W). After capture, we attached a 0.35 g coded radio tag (NTQBW-2, Lotek Wireless) using a leg-loop harness[33]. In 2017, we used handheld telemetry to estimate departure date on spring migration by searching at least once every three days from April 1 through May 5[15]. In 2018 and 2019, we used an array of four automated-telemetry stations (hereafter stations) to determine departure date on spring migration[64,65]. We acquired detections during migration from the Motus Wildlife Tracking System[10], using the package *motus*[66] in Program R[67]. To resight individuals on the breeding grounds in the Lower Peninsula of Michigan (44.62°N, -84.27°W), where 95-97% of the Kirtland's Warbler population breeds[32], we used handheld telemetry and detections from 12 stations located in breeding habitat[33]. Once located, we attempted to re-sight each individual and determine their fate once per week through June.

Black-throated Blue Warblers were studied at Hubbard Brook Experimental Forest in New Hampshire, USA (43.94°N, -71.70°W) from 1986 – 2000 and at Copse Mountain, Jamaica, West Indies (18.29°N, -77.96°W) from 1986 –1998. Birds were captured in mist nets and color-banded. The Hubbard Brook study plot (64 ha) was searched for color-banded individuals every 1-7 days during breeding (mid-May to mid-August). Sampling on the Jamaica study plot (7 ha) occurred during 3–5-day periods in mid-October–early November, and during 2–5-day periods in mid-March. Following Sillett and Holmes[29], we built encounter histories from two periods per site: mid-May to early June and late July to mid-August at Hubbard Brook, and October and March in Jamaica. Although no banded individuals were encountered during both the breeding and non-breeding period, the Hubbard Brook and Jamaica populations have been shown to be geographically linked via stable isotopes[35] and light-level geolocators[36], and demographically linked via correlation of reproductive rates in Hubbard Brook and juvenile recruitment rates in Jamaica[29–31].

QUANTIFICATION AND STATISTICAL ANALYSIS

Kirtland's Warbler Seasonal Survival

To characterize non-breeding environmental conditions experienced by Kirtland's Warblers, we estimated an individual-specific Enhanced Vegetation Index (EVI) value as a proxy for relative environmental productivity[38]. We used EVI values measured during March because of previous research indicating the relevance of March rainfall for annual differences in arrival timing and reproductive success on the breeding grounds[20] and apparent annual survival[28]. We gathered EVI values from within a 250-meter radius of the centroid of individual non-breeding locations (calculated using the *sf* package[68]) in Program R[67] and took the mean of these values across both the spatial and temporal buffer to generate an individual-level covariate for survival modeling (see below). All environmental annotations were done using the *rstoat* package[69] in Program R[67], which draws from the NASA MODIS daily EVI dataset (https://modis.gsfc.nasa.gov/data/dataprod/mod09.php).

To estimate seasonal survival for Kirtland's Warblers, we constructed a variation of a three-state Cormack-Jolly-Seber (CJS) survival model[70–72]. We defined states based on individual migratory progression such that detections on Cat Island (known non-breeding grounds) were assigned to the non-breeding state, detections on the breeding grounds were assigned to the breeding state, and all other observations were considered migratory. Because our period of study extended from the end of the non-breeding period through breeding, we restricted transitions between states to be "one way" – individuals could only transition from non-breeding to migration and migration to breeding (and from any living state to the "dead" state). Kirtland's Warblers are obligate migrants; therefore, we modeled the transitions between states using the Weibull cumulative distribution function[73,74]. This function increases the probability of transition from one state to the next as time proceeds, asymptotically approaching one. Thus, individuals were not permitted to remain in a lower order state indefinitely but instead must eventually either proceed with migration or die. In this way, the model also estimated population-level migration phenology.

The clustered distribution of Motus stations resulted in detection patterns that superficially resembled "trap happy" and "trap shy" individuals; given that a bird was detected on one day, the probability of detection was substantially higher than for individuals that had not been detected on the previous day because detected birds were more likely to be in a high-density portion of the array (and vice versa). To account for this potential source of bias, we used the "robust design"[75], wherein primary occasions were defined as weeks and secondary occasions were defined as days.

We fit a model that estimated seasonal survival as a function of non-breeding EVI conditions for all three seasons. We also fit a null model that considered survival as constant within seasons. We used Deviance Information Criterion (DIC) to evaluate relative support between the fitted models[76]. We used uninformative priors for most parameters in the model, but parameters estimating constant seasonal survival probabilities were approximately based on Rockwell et al. [28] (note that exact moment-matching from those estimates resulted in impossible parameter combinations so we used more permissive prior distributions). We also constrained prior distributions associated with transition processes to exclude biologically implausible transitions (e.g., transitions from non-breeding to migration deep into the breeding season).

We fit models in a Bayesian frameworks using JAGS[77], which was called from within R using the *jagsUI* package[78].We drew four chains of 500,000 MCMC samples with a burn-in period of 50,000, thinned to every 250th sample to reduce serial autocorrelation within the chains. We considered models converged at R-hat <1.05.

Black-throated Blue Warbler Seasonal Survival

We used an integrated survival model[37] to estimate seasonal survival probabilities of male and female Black-throated Blue Warblers. For each data set (breeding and non-breeding), the integrated model fits a Cormack-Jolly-Seber (CJS) model to estimate apparent survival within and between stationary periods while accounting for imperfect detection[79]. In New Hampshire, the survival of individuals between re-sighting occasions was determined by either the 3-month breeding period survival probability (May – August; $\phi_{s,t}^{\mathrm{Sum}}$) or the 9-month between-breeding period survival (August – May; $\phi_{s,t}^{BB}$), where *s* denotes sex-specific survival probabilities in year *t*. In Jamaica, the survival of individuals between re-sighting occasions was determined by the 6-month non-breeding survival probability (October – April; $\phi_{s,t}^{\mathrm{Win}}$) or the 6-month between-non-breeding survival (April – Oct; $\phi_{s,t}^{BW}$). We accounted for imperfect detection by modeling the observed status of individuals as a function of the sex- and occasion-specific detection probabilities ($p_{s,t}^{j}$), where *j* denotes occasion (May, August, October, or March). In their original analysis of these data, Sillett and Holmes[29] found no support for sex-specific detection probabilities in October and March, so we did not model sex variation on that parameter. Furthermore, because observer effort was consistent during the May and October sampling periods, we followed Sillett and Holmes[29] and did not include annual variation in those detection probabilities.

The two survival models can be integrated by parameterizing the between-period survival probabilities in terms of the underlying seasonal survival rates:

$$\phi^{\mathrm{BW}}_{\mathrm{s,t}} = \phi^{\mathrm{Spr}}_{\mathrm{s,t}}\,\phi^{\mathrm{Sum}}_{\mathrm{t}}\,\phi^{\mathrm{Aut}}_{\mathrm{s,t}}$$

$$\phi^{\mathrm{BB}}_{\mathrm{s,t}} = \phi^{Aut}_{\mathrm{s,t}}\,\phi^{\mathrm{Win}}_{\mathrm{t+1}}\,\phi^{\mathrm{Spr}}_{\mathrm{s,t+1}}$$

which allows estimation of the latent 2-month spring and fall survival probabilities and the inclusion of covariates on seasonal survival probabilities[37]. We chose covariates based on previous research linking environmental conditions to annual survival in Black-throated Blue Warblers. In Jamaica, annual survival of Black-throated Blue Warblers from 1986-1999 was strongly associated with the phase of the El Niño Southern Oscillation (ENSO;[29,30]). During El Niño years in Jamaica, reduced rainfall[39,40] likely led to decreased availability of arthropod prey in the winter dry season and, hence, to lower survival. Wetter La Niña years likely resulted in increased food availability and higher survival. We hypothesized that ENSO mediates warbler survival via direct effects on non-breeding survival or by influencing body condition at departure, which should influence subsequent survival during spring migration or over the following breeding season. We included mean monthly values of the standardized Southern Oscillation Index (SOI) as a predictor of non-breeding, spring, and breeding survival probabilities for both sexes and predicted that survival would be positively associated with SOI (positive SOI values indicate La Niña conditions; negative values signify El Niño conditions).

Posterior distributions for parameters were estimated using Markov chain Monte Carlo implemented using the *nimble* package[80] in R[67]. Encounter histories were summarized using the multi-state array (m-array) format for computational efficiency. Model fitting revealed that the default random walk samplers used by nimble resulted in high correlation between the posterior samples for the latent fall and spring mean survival probabilities and thus poor mixing. Nimble's automated factor slice sampler resulted in lower correlation and improved mixing. We used the default samplers for all other parameters. We ran three chains for 75,000 iterations each after discarding the first 25,000 iterations as burn-in and saving every 5th sample to reduce autocorrelation in the posterior samples, resulting in 30,000 posterior samples of each parameter. Convergence was confirmed when R-hat was <1.05 and through visual inspections of trace plots.

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