

Seasonal survival estimation for a long-distance migratory bird and the influence of winter precipitation

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Received: 17 November 2015 / Accepted: 25 November 2016
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Abstract Conservation of migratory animals requires information about seasonal survival rates. Identifying factors that limit populations, and the portions of the annual cycle in which they occur, are critical for recognizing and reducing potential threats. However, such data are lacking for virtually all migratory taxa. We investigated patterns and environmental correlates of annual, oversummer, overwinter, and migratory survival for adult male Kirtland's warblers (*Setophaga kirtlandii*), an endangered, long-distance migratory songbird. We used Cormack–Jolly–Seber models to analyze two mark–recapture datasets: 2006–2011 on Michigan breeding grounds, and 2003–2010 on Bahamian wintering grounds. The mean annual survival probability was 0.58 ± 0.12 SE. Monthly survival probabilities during the summer and winter stationary periods were relatively high (0.963 ± 0.005 SE and 0.977 ± 0.002

SE, respectively). Monthly survival probability during migratory periods was substantially lower (0.879 ± 0.05 SE), accounting for ~44% of all annual mortality. March rainfall in the Bahamas was the best-supported predictor of annual survival probability and was positively correlated with apparent annual survival in the subsequent year, suggesting that the effects of winter precipitation carried over to influence survival probability of individuals in later seasons. Projection modeling revealed that a decrease in Bahamas March rainfall >12.4% from its current mean could result in negative population growth in this species. Collectively, our results suggest that increased drought during the non-breeding season, which is predicted to occur under multiple climate change scenarios, could have important consequences on the annual survival and population growth rate of Kirtland's warbler and other Neotropical–Nearctic migratory bird species.

Communicated by Markku Orell.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-016-3788-x) contains supplementary material, which is available to authorized users.

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Keywords Annual survival · Carryover effects · Kirtland's warbler · Non-breeding season · Population growth

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Introduction

Factors that limit populations of migratory animals remain poorly understood, largely due to the challenges of tracking individuals over long distances and across seasons, and to the difficulty of measuring vital rates of highly vagile organisms. Because changes in climate and/or habitats that migratory animals occupy in any portion of the annual cycle may affect their population dynamics (Sherry and Holmes 1995), identifying factors that limit their populations has proven to be challenging (Calvert et al. 2009; Robinson et al. 2010). This task is further complicated by the fact that events within one season may interact with events in subsequent, geographically disparate seasons to affect the ecology and demography of migratory animals (Fretwell 1972; Webster et al. 2002). Few reliable estimates of age- or season-specific survival exist for birds (Faaborg et al. 2010), or migratory species of many other taxa (Hedenström et al. 2011), especially for populations linked geographically throughout the year. Indeed, recent population declines observed in migratory animals ranging from salmonid fish to ungulates to birds (Sanderson et al. 2006; Bolger et al. 2008; Wilcove and Wikelski 2008; Sauer and Link 2011) emphasize the importance of quantifying seasonal demographic rates, identifying limiting factors, and reducing potential threats. Rigorous estimates of annual survival, and even oversummer and overwinter survival, of long-distance migratory birds have become more common in recent years (Faaborg et al. 2010), but few studies have been designed to estimate survival over the migratory periods (e.g., Klaassen et al. 2014; Casazza et al. 2015), and only one of a passerine (Sillert and Holmes 2002).

Climatic conditions experienced during each portion of the annual cycle—breeding, migration, and non-breeding—all have the potential to affect body condition and survival probabilities of individual migratory birds, and thus may have consequences for population dynamics. Previous research has linked variation in avian survival probabilities with fluctuations in breeding season temperatures and rainfall (Dugger et al. 2004; Robinson et al. 2007; Gullett et al. 2014), storms during migration that can cause direct mortality (Butler 2000; Newton 2007), and food limitation (Brown and Sherry 2006; Studds and Marra 2007, 2011). The survival rates of migratory birds are also influenced by large-scale climate phenomena (Sillert et al. 2000; Mazzerolle et al. 2005; Franke et al. 2011; LaManna et al. 2012) that affect global temperature and precipitation patterns. Understanding how these variables may impact demographic rates is especially important in the face of long-term climate change or increased climate variability, yet their effects on migratory animals remain poorly understood (Calvert et al. 2009).

The effects of climate in breeding, wintering, and en route areas cannot be considered in isolation, because events in one part of the year can carry over to affect migratory bird performance in later seasons (e.g., Baillie and Peach 1992; Marra et al. 1998; Gill et al. 2001; Bearhop et al. 2004; Norris et al. 2004; Rockwell et al. 2012). For example, dry season rainfall in the Neotropics can drive insect and fruit availability on wintering grounds, and thus individual body condition (Cooper et al. 2015). If birds are unable to build up the necessary reserves, the influence of winter climate on survival may be manifested as increased mortality during the subsequent spring migration (Sillert and Holmes 2002; Studds and Marra 2005) or breeding season. Annual survival rates of some Palearctic migrants are positively correlated to rainfall on their African wintering grounds, where food availability and thus birds' energetic reserves are likely to be limited (Peach et al. 1991, Baillie and Peach 1992; Szép 1995). Individual birds operating at an energy deficit after poor weather (Cowley and Siriwardena 2005) or delayed molt (Nilsson and Svensson 1996; Dawson et al. 2000) in temperate breeding areas may suffer increased mortality during the subsequent fall migration. Survival over the summer and winter stationary periods appears to be high in Neotropical–Nearctic migrants relative to the migratory periods (e.g., Sillert and Holmes 2002; Jones et al. 2004; Johnson et al. 2006), so carry-over effects of climate that influence survival during migration are likely to be ecologically important.

Migratory species with restricted ranges may be especially vulnerable to climate change that alters habitat or food availability if they lack alternative breeding and wintering sites. The Kirtland's warbler (*Setophaga kirtlandii*) is one such species, breeding primarily in a small region of northern Michigan and wintering in the Bahamas archipelago. Though still endangered, its status has improved dramatically, with the population size increasing by a factor of 10 since 1990 (USFWS 2016). However, we still lack substantial information about their basic ecology throughout the annual cycle. For example, earlier studies argued that the availability or quality of winter habitat is not limiting despite the absence of quantitative data (Mayfield 1992; Bocetti 1994; Sykes and Clench 1998). Summer limitation has been seemingly alleviated in this species through management efforts, improving both the quantity and quality of available breeding habitat via brown-headed cowbird (*Molothrus ater*; a brood parasite) removal (Kelly and DeCapita 1982; Walkinshaw 1983) and the creation of new jack pine (*Pinus banksiana*) stands (Probst and Weinrich 1993; Bocetti et al. 2002). Late winter rainfall in the Bahamas is important to Kirtland's warbler ecology, influencing both spring arrival dates and reproductive success (Rockwell et al. 2012), but we do not currently understand how

variation in temperature and rainfall on the species' limited breeding and wintering areas affects survival.

To understand how populations of migratory animals are limited, it is important to quantify season-specific survival rates and to examine how variation in factors throughout the annual cycle can affect those rates. Adult survival generally has a stronger influence on population growth than reproductive rates (Sæther and Bakke 2000), and thus represents a critical component of population dynamics. Here, we use two mark–recapture datasets (Michigan 2006–2011 and Bahamas 2003–2010) to: (1) quantify annual, over-summer, overwinter, and migratory period survival of the Kirtland's warbler, and (2) assess the influence of climate variables on annual survival rates. We predicted that survival probabilities would be lower during the migratory periods relative to the stationary periods (Sillert and Holmes 2002). We further combined our estimates of the influence of climate variables on survival rates with productivity data (Rockwell et al. 2012), to test the hypothesis that variation in climate can impact population growth.

Methods

Study species

Kirtland's warblers are small (13.7 ± 1.1 g) migratory songbirds and extreme habitat specialists. During the breeding season, they require large, dense, homogenous stands of young jack pine (Mayfield 1960; Probst et al. 2003). This historically fire-dependent species now requires intensive management and mechanical land clearing to maintain 5- to 23-year-old jack pine stands suitable for breeding habitat (Probst and Weinrich 1993; Probst et al. 2003). On the Caribbean wintering grounds, they also occupy disturbance-maintained, early successional habitats (Sykes and Clench 1998; Wunderle et al. 2010). The population size of Kirtland's warbler was very low throughout the 1970s and early 1980s (~200 singing males), partially due to their habitat specificity and a lack of wildfires. Management efforts on the breeding grounds have enabled the population to increase at a rate of about 8.5% per year since 1990. In June 2015, the population was estimated at approximately 2365 singing males (USFWS 2016).

Study sites

We worked on a series of study sites in Michigan and in the Bahamas. During the breeding season, we used ten 30-ha study plots located in Alcona, Iosco, Oscoda, and Ogemaw counties in northern Lower Michigan. Field sites were characterized by fairly homogenous stands of young jack pine, interspersed with a few deciduous trees (see Rockwell

et al. 2012 for details and map). The non-breeding season portion of this study was conducted in southern Eleuthera Island in the central Bahamian archipelago. Vegetation was characterized by evergreen and semi-deciduous broad-leaf trees and shrubs, which formed a thick brush known as coppice (Correll 1979). Research was conducted on six study sites located at established overwintering areas where at least four individuals were found within 200 m of each other. We also found and captured birds at nearby locations and revisited other sites where Kirtland's warblers had previously been found (see Wunderle et al. 2010 for details). We conducted intensive marking and resighting of color-banded warblers in both breeding and wintering locations.

Marking and resighting efforts

In Michigan, we used resighting of 331 marked individuals to estimate the annual and over-summer survival from 2006 to 2011. Male Kirtland's warblers were target netted and captured upon spring arrival to breeding territories, given a numbered aluminum band and a unique combination of UV-resistant Darvic color bands, and aged as either first-time breeders (second year; SY) or returning adults (after second year; ASY) (Rockwell et al. 2012). We were unable to reliably capture females. We visited plots every three days from 1 May to 7 June to band new males (2006–2010), and searched for previously banded males every three days until 31 July (2007–2009). In 2006 and 2010–2011, we resighted banded males in the month of May only. Thus, in some years we measured 2 months of over-summer survival (1 May–1 July) and 10 months of overwinter + migration survival (Table 1) and exponentiated the monthly summer estimate over the 4 months that actually comprise the summer stationary period for this species. In other years we measured the annual survival only (1 May–1 May; 12 months). In addition, we systematically searched, using playback, areas within 400 m of the plot edges once a month. Band retention was very high and most bands were resighted at very short distances with binoculars; thus, the error rates of band reads were minimal or non-existent. Efforts were made to eliminate floaters from our dataset by only including capture histories of males that established territories on our study plots (i.e., sang in one area for at least two weeks). Thus, transient males that disappeared immediately following banding were not included in the analysis.

In the Bahamas, we used capture and resighting of 215 Kirtland's warblers to estimate overwinter survival from 2003 to 2010. Warblers were captured from 1 October 2003 through 30 April 2009, with additional captures in February to April 2010 (Table 1). Both passive and target nettings were used to capture birds (details in Wunderle et al. 2014). Netting was completed from sunrise to 0930–1000 EST for at least two mornings and an afternoon (1600 to

Table 1 Summary information regarding the structure of the Michigan and Bahamas mark–recapture datasets for Kirtland’s warblers (n = sample size)

Dataset	Years	n	Demographic parameters	Encounter occasions	Survival period(s) estimated
Michigan	2006–2011	331	Age	12	Annual, oversummer
Bahamas	2003–2010	215	Age, sex	45	Overwinter

In Michigan, encounter occasions occurred once in early May (2006, 2010, 2011), or three times per year in early May, June, and July (2007–2009)

In the Bahamas, encounter occasions occurred monthly from October 2003 to April 2009 (seven times per year). The final winter of 2010 had only three encounter occasions; these occurred in February, March, and April only

sunset) at each site every month. All individuals were given a unique band combination and released. We classified age at capture as either a first-winter juvenile (hatch year; HY) or a returning adult (after hatch year; AHY). To resight marked birds, intensive searches of the study sites were conducted following each netting session. Searches were conducted primarily from sunrise to 0930–1000 EST, during which time observers traversed access trails and roads to locate banded birds. Generally, five to nine mornings were spent searching a study site by two to five independent observers during each netting session, with effort allocated according to the site’s size and number of warblers. In the Bahamas, we estimated survival over two seasons: a 6-month winter period (1 October–1 April), and a 6-month oversummer + migration period.

Observations of marked individuals from both datasets were recorded monthly, to facilitate comparisons between survival intervals of different lengths. While nearly 50 individual birds were resighted in both Michigan and the Bahamas during this study, only 12 of these were included in both mark–recapture datasets. This sample size was insufficient for combining all observations into a single analysis.

Survival analyses

We modeled survival (ϕ) and detection (p) probabilities for both datasets using Cormack–Jolly–Seber (CJS) models in Program MARK (White and Burnham 1999). We used an information theoretic approach, choosing Akaike’s information criterion for small datasets (AIC_c) as the model-selection criterion (Burnham and Anderson 2002). The goodness of fit of the global models for the Bahamas and Michigan datasets were tested using Program RELEASE within MARK. The variance inflation factor (\hat{c}) was calculated via the median c -hat procedure in MARK, and then used to adjust AIC_c values through quasi-likelihood ($QAIC_c$) when necessary due to minor departures from goodness of fit (Burnham and Anderson 2002). For the 2006–2011 Michigan dataset, we also used Program MARK to assess the relationship between annual survival rates and our set of hypothesized climate variables.

We analyzed the Michigan dataset using a hierarchical modeling procedure: we started with two model subsets, kept the best models from those subsets, and combined them in a final model set (see Bulluck and Buehler 2008; Smith and Wilson 2010). The first model subset examined the influence of all possible combinations of age (SY vs. ASY), season (oversummer vs. overwinter + migration), and time (year or month) on survivorship, compared to a constant survival model. We allowed detection probability to vary by season and time (month or year). We did not model p as a function of age, because behaviors that affect conspicuousness of individuals did not vary by age (Rockwell, pers. obs.), and any SYs that were never detected again after initial banding were eliminated from the dataset. The Michigan dataset did not include effects of sex because only males were studied. The second model subset examined potential sources of variation in annual survival probability. This subset included summer and winter temperature and precipitation variables, as well as large-scale climate indices based on a priori ideas of what climate variables may affect survival (e.g., Silllett et al. 2000; Dugger et al. 2004; Newton 2007; Franke et al. 2011; Rockwell et al. 2012). All climate data were obtained from the National Climatic Data Center (Nassau Airport and Mio WWTP MI stations). Exact wintering locations for all Kirtland’s warblers are unknown, but the vast majority are thought to winter in the Bahamas. Climate throughout the archipelago is correlated to that in Nassau (Sealey 2006), including precipitation measured in some years at our Eleuthera field site (White and Wunderle, unpublished data). We considered two other sources of annual variation in survival: population size in June, obtained from the annual survey of singing males (USFWS 2016), and a simple linear trend over time. These were compared to a constant survival model, a model of survival allowed to vary randomly by year, and a set of climate models, for a total of 18 a priori candidate models (Table 2; Online Resource 2).

For the 2006–2011 Michigan dataset, we carried over models from either subset that had a $\Delta QAIC_c < 2$ (Burnham and Anderson 2002) into the final model set. We also added new models containing different combinations of

Table 2 Definition of each explanatory variable used to predict survival and/or recapture probabilities of Kirtland's warblers

Variable	Definition
Subset 1: demographic and time parameters	
Age	Michigan: second-year (first-time breeder; SY) vs. after second year (returning adult; ASY). Bahamas: hatch year (bird in its first winter; HY) vs. after hatch year (returning adult; AHY)
Sex	Male vs. female (available for Bahamas dataset only)
Season	Michigan: summer vs. overwinter + migration. Bahamas: winter vs. oversummer + migration
Year	Annual variation in survival
t	Monthly variation in survival, i.e., fully time-dependent
Subset 2: weather and annual parameters	
March rain	Total precipitation (cm) in the Bahamas in March
Late winter rain	Total precipitation (cm) in the Bahamas in late winter (1 Feb–31 Mar)
SOI	Mean monthly value of the Southern Oscillation Index in the current year
SOI $n - 1$	Mean monthly value of the Southern Oscillation Index in year $n - 1$
Winter rain	Total winter precipitation (cm) in the Bahamas (1 Oct–1 Apr)
Hurricane	Binary variable representing whether there was a hurricane that year in the Bahamas
Wintermaxtemp	Mean winter high temperature in the Bahamas (1 Oct–1 Apr)
Winter 90°F	Number of winter days in the Bahamas exceeding 90°F (1 Oct–1 Apr)
Winter NAO	Mean value of the North Atlantic Oscillation (NAO) during the winter months
Summer rain	Total precipitation (cm) in Mio, MI in summer (1 May–31 July)
May rain	Total precipitation (cm) in Mio, MI in May
Maymintemp	Mean May minimum temperature in Mio, MI
May freeze	Number of May days in Mio, MI that fell below freezing
Linear	Annual linear trend over time
Year	Annual differences in survival
Popsiz	Population size in June, obtained from the annual survey of singing males

variables found in highly ranked models from either subset. We calculated model-averaged estimates of monthly survival from the Michigan and Bahamas final model sets, and then exponentiated monthly survival by the number of months in each period of interest (e.g., oversummer period = 4 months, overwinter period = 6 months) to determine the cumulative survival rate for each period. Annual survival is the product of survival probabilities during each phase of the annual cycle: $\phi_{\text{annual}} = \phi_{\text{overwinter}} \times \phi_{\text{oversummer}} \times \phi_{\text{migration}}$. To estimate survival over the 2-month migratory period, we used the equation above and solved for $\phi_{\text{migration}}$. Direct observation of five color-banded Kirtland's warbler males revealed a mean maximum spring migration period of 15.8 days (Ewert et al. 2012). Duration of fall migration is often longer (e.g., Stutchbury et al. 2009; Hecksher et al. 2011). Therefore, we considered fall and spring migration to have a combined length of 2 months, although these two periods were not separately estimable with our analytical approach. All survival estimates are given as: estimate \pm standard error (SE). Standard errors of monthly survival probabilities were calculated by Program MARK, while standard errors of survival parameters that are functions of other parameters were calculated using the Delta method (Seber 1982; Powell 2007).

To explore how climate could affect population growth rate (λ), we focused on March rainfall in the Bahamas, as this was the best-supported survival model (see "Results"). We determined the effect of March rainfall on survival probability by using its model-averaged slope estimate and the logit link function. We then combined this with reproductive data from Rockwell et al. (2012) to model the effects of different levels of rainfall declines on lambda (λ), using the equation $\lambda = \phi_{\text{adult}} + \text{fecundity} \times \phi_{\text{juvenile}}$ (Pulliam 1988). We used 0.35 as the baseline estimate of ϕ_{juvenile} for these calculations (Bocetti and Rockwell, unpublished data) and assumed that it covaried with ϕ_{adult} . We then modeled the effects of 5, 10, 25, and 50% decreases in March rainfall on population growth rate (λ). Because we do not have data from banded females, our model uses the mean number of male offspring per male from Rockwell et al. (2012) as our measure of fecundity.

Results

We used capture histories for 534 color-banded Kirtland's warbler males, including 331 individuals captured in Michigan from May to July (2006–2011), to model

Table 3 AIC results of subset 1, subset 2, and final model sets of monthly survival (ϕ) and recapture probabilities (p) for male Kirtland’s warblers in Michigan from 2006 to 2011

Model	QAICc	Delta QAICc	w_i	K
Subset 1: demographic and time parameters				
$\phi(\text{season}) p(t)$	1377.4	0	0.203	13
$\phi(\text{age}) p(t)$	1378.1	0.67	0.145	13
$\phi(\text{year}) p(t)$	1378.3	0.93	0.127	15
$\phi(\text{age} + \text{season}) p(t)$	1378.6	1.18	0.112	14
$\phi(\text{age} + \text{year}) p(t)$	1378.7	1.29	0.106	16
$\phi(\text{season} + \text{year}) p(t)$	1378.8	1.36	0.103	16
$\phi(\text{season} + \text{age} + \text{year}) p(t)$	1379.0	1.61	0.090	17
Subset 2: weather and annual parameters				
$\phi(\text{Marchrain}) p(t)$	1374.7	0	0.236	13
$\phi(\text{latewinterrain}) p(t)$	1376.2	1.51	0.111	13
$\phi(\text{SOI } n - 1) p(t)$	1376.2	1.56	0.108	13
Final set				
$\phi(\text{Marchrain}) p(t)$	1374.67	0.00	0.129	13
$\phi(\text{Marchrain} + \text{season}) p(t)$	1375.36	0.69	0.091	14
$\phi(\text{Marchrain} + \text{age}) p(t)$	1375.91	1.23	0.069	14
$\phi(\text{latewinterrain}) p(t)$	1376.19	1.51	0.060	13
$\phi(\text{SOI } n - 1) p(t)$	1376.23	1.56	0.059	13
$\phi(\text{latewinterrain} + \text{season}) p(t)$	1376.54	1.87	0.051	14
$\phi(\text{SOI } n - 1 + \text{season}) p(t)$	1376.55	1.88	0.050	14

Includes the number of estimable parameters (K), QAICc values, differences between current QAICc and QAICc value for the best model (ΔQAICc), and QAICc weights (w_i). Variables in parentheses give parameterization for ϕ and p (see Table 1 for variable definitions). Variables from models in subsets 1 and 2 that were $<2 \Delta\text{QAICc}$ from the top model were carried over into the final model set. Goodness-of-fit test for the global, full group \times time model ($\phi_{\text{age} \times t}, p_{\text{age} \times t}$) indicated a minor lack of fit to the data ($\chi^2_{df=1} = 31.4, p = 0.07$), so a \hat{c} adjustment was used ($\hat{c} = 1.40$). Models with ΔQAICc values >2 are not shown; see Electronic Supplemental Material for full AIC table (Online Resources 1–3)

survival probabilities. In the first model subset assessing demographic and time effects on Michigan birds, the seasonal survival model received the most support (QAICc weight = 0.20). However, models with effects of age and year had nearly equivalent support in the data

($\Delta\text{QAICc} < 1$), suggesting that these variables may also be important. All models with $\Delta\text{QAICc} < 10$ included detection probabilities that varied by month (t) (Online Resource 1). In the second model set examining the effects of climate and other annual variables on survival, the March rain model received the strongest support, having twice the QAICc weight (0.24) as the second-ranked model (0.11) (Table 3). Late winter rainfall and mean monthly values of the Southern Oscillation Index (SOI; a measure of the strength of El Niño conditions) also received statistical support as predictors of survival.

The final Michigan model set, using combinations of variables found in the top-ranked models from the first two subsets, contained 30 candidate models. The top three best-supported models all included apparent annual survival as a function of March rainfall (Table 3), and March rainfall had the highest relative variable importance (Table 4). Effects of season and age in the second- and third-ranked models are likely to be uninformative parameters (Arnold 2010). Models including effects of late winter rain and mean monthly SOI of the previous year also had values of $\Delta\text{QAICc} < 2$ (Table 3). Because several models were well supported by the data, we used model averaging to obtain survival and slope parameter estimates. March rain ($\beta = 0.13 \pm 0.06$ SE) was positively related to annual survival in the subsequent year. Thus, annual survival probability decreases when March rainfall in the Bahamas is reduced (Fig. 1). Late winter rain ($\beta = 0.05 \pm 0.03$ SE) was positively related, and SOI ($\beta = -0.22 \pm 0.14$ SE) of the preceding year was negatively related to annual survival probabilities, but their 95% confidence intervals overlapped zero. The mean annual survival for ASY males (0.580 ± 0.12) was somewhat higher than for SY males (0.553 ± 0.13), while survival over the 4-month summer period was similar across age classes (0.862 ± 0.06 and 0.851 ± 0.07 ; Table 5).

In the second dataset, we used capture histories of 215 Kirtland’s warblers to estimate overwinter survival in the Bahamas during the October–April stationary period (2003–2010). The top three models both included additive or interactive effects of age and season on survival probabilities (cumulative QAICc weight = 0.77)

Table 4 Model-averaged parameter estimates and unconditional standard errors (SE) for each climate variable carried over into the final model set, estimating survival probability for Kirtland’s warblers captured in Michigan, 2006–2011

Variable	Estimate	SE	Lower 95% CI	Upper 95% CI	Relative variable importance
March rain	0.126	0.063	0.001	0.254	0.417
Late winter rain	0.050	0.031	−0.012	0.112	0.234
SOI $n - 1$	−0.221	0.141	−0.499	0.058	0.242

Relative variable importances are the summed Akaike weights of each model containing that variable (each variable is represented in an equal number of models in the final model set)

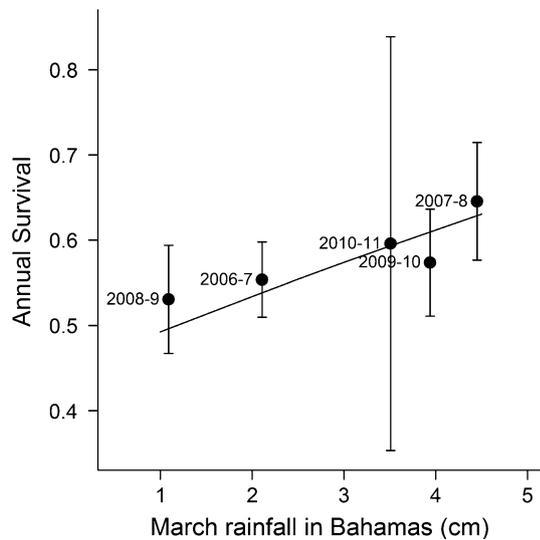


Fig. 1 Total March precipitation in the Bahamas predicts apparent annual survival probability of adult male Kirtland’s warblers in the subsequent year. *Data points* are model-averaged annual survival estimates from the final model set for mark–recapture data collected in Michigan, 2006–2011. *Data labels* show the annual intervals over which apparent survival was estimated. *Error bars* represent ± 1 SE, calculated using the Delta method. SE of year 2010–2011 is larger because survival and detection probabilities during this last time interval were not separately estimable for all models. *Trend line* is derived from the model-averaged effect of March rain from the final Michigan model set

(Table 6). The fourth-ranked model also included an effect of sex, but as an uninformative parameter (Arnold 2010). Annual differences in winter survival were not well supported. Sex and season were the best-supported factors affecting detection probabilities (Table 6). Because multiple models received substantial support in the data, we again used model averaging to obtain survival estimates. AHY males appeared to survive the 6-month winter period at much higher rates than HY

males (0.871 ± 0.06 and 0.687 ± 0.07 , respectively; Table 5). We did not find evidence for sex-specific overwinter survival differences (AHY males: 0.871 ± 0.06 , AHY females: 0.856 ± 0.07 ; Table 5).

We used mean annual (2006–2011) and oversummer (2007–2009) survival estimates for ASY males, and the mean overwinter (2003–2010) survival estimate of AHY males, to calculate survival over the migratory periods ($\phi_{\text{annual}} = \phi_{\text{summer}} \times \phi_{\text{winter}} \times \phi_{\text{migration}}$). The estimated survival probability of adult male Kirtland’s warblers during the migratory phase, considered here to be the two months of fall and spring migration combined, was 0.773 ± 0.12 . The monthly survival probabilities for adult males in each season were: oversummer, 0.963 ± 0.005 ; overwinter, 0.977 ± 0.002 ; and migration, 0.879 ± 0.05 (Fig. 2). Monthly survival and seasonal survival are both lower during the migratory period relative to the stationary periods, with approximately 44% of mortalities occurring during this portion of the annual cycle.

To explore the effect of late winter rainfall on population dynamics, we projected the effect of different levels of March rainfall on population growth rate (λ). For every 1-cm reduction in March rain, the logit of apparent annual survival is predicted to decrease by 0.126 (see “Results”), and reproductive success is predicted to decrease by 0.23 fledglings per male per year (Rockwell et al. 2012). For example, at the mean level of March rainfall during the study period (3.04 cm), we would predict adult survival to be 0.58, juvenile survival to be 0.35 (Bocetti and Rockwell, unpublished data), and the number of male fledglings per male to be 1.42 (half the number of total fledglings; Rockwell et al. 2012). Using Pulliam’s (1988) formula, the population growth rate at the current mean of March rain would be 1.08 ($\lambda = 0.58 + 1.42 \times 0.35$). With 5, 10, 25, and 50% reductions in March rainfall, population growth rates (λ) are predicted to be 1.05, 1.02, 0.94, and 0.82, respectively.

Table 5 Model-averaged estimates of annual, oversummer, and overwinter survival for Kirtland’s warblers in Michigan from 2006 to 2011 or the Bahamas from 2003 to 2010

Age	Annual	Oversummer	Overwinter	Overwinter (female)
Adult (ASY or AHY)	0.580 ± 0.12	0.862 ± 0.06	0.871 ± 0.06	0.856 ± 0.07
Yearling or hatch year (SY or HY)	0.553 ± 0.13	0.851 ± 0.07	0.687 ± 0.07	0.624 ± 0.05

Michigan data (annual and oversummer) use ASY vs. SY age classes, while Bahamas data (overwinter) use AHY vs. HY age classes (see Table 2). Data from females were only available from the Bahamas (overwinter). Annual survival probabilities (1 May–1 May) were calculated as the product of all monthly survival estimates in a given year (summer monthly estimate² \times [overwinter+migration monthly estimate]¹⁰, or monthly estimate¹², depending on the year). The oversummer period is considered to be 1 May–31 August; we raised the measured summer monthly estimate from two months to the fourth power to better reflect the actual length of the summer stationary period. Overwinter survival probabilities (1 October–1 April) were calculated by raising the monthly estimate for a given winter to the sixth power. Data are presented as mean $\phi \pm$ SE; standard errors of annual and seasonal survival probabilities were calculated using the Delta method

Table 6 Models of monthly survival (ϕ) and recapture probabilities (p) for Kirtland's warblers in the Bahamas from 2003 to 2010

Model	AICc	Delta AICc	w_i	Model Likelihood	K
$\phi(\text{age} \times \text{season}) p(\text{sex} + \text{season})$	1859.39	0.00	0.38	1.00	7
$\phi(\text{age} \times \text{season}) p(\text{sex} \times \text{season})$	1860.43	1.03	0.23	0.60	8
$\phi(\text{age} + \text{season}) p(\text{sex} + \text{season})$	1861.12	1.73	0.16	0.42	6
$\phi(\text{sex} + \text{age} + \text{season}) p(\text{sex} + \text{season})$	1861.15	1.75	0.16	0.42	7
$\phi(\text{sex} \times \text{age} \times \text{season}) p(\text{sex} \times \text{season})$	1864.49	5.09	0.03	0.08	12
$\phi(\text{age} \times \text{season}) p(\text{season} \times \text{year})$	1867.66	8.27	0.01	0.02	21
$\phi(\text{sex} \times \text{age} \times \text{season}) p(\text{season} \times \text{year})$	1867.68	8.29	0.01	0.02	25
$\phi(\text{age} + \text{season} + \text{year}) p(\text{sex} + \text{season})$	1868.30	8.91	0.00	0.01	13

Includes the number of estimable parameters (K), AIC_c values, differences between current AIC_c and AIC_c value for the best model (ΔAIC_c), and AIC_c weights (w_i). Subscripts give parameterization for ϕ and p ; age = two age classes (AHY or HY), sex = male or female, year = annual variation, t = monthly variation, and season = overwinter (1 Oct–1 Apr) or summer + migration (1 Apr–1 Oct). The global, full group \times time model ($\phi_{\text{sex*age*t}}, p_{\text{sex*age*t}}$) fit the data well ($\chi^2_{167} = 137.6$, $p = 0.92$). Models with AIC_c values >10 are not shown; see Electronic Supplemental Material for full AIC table (Online Resource 4)

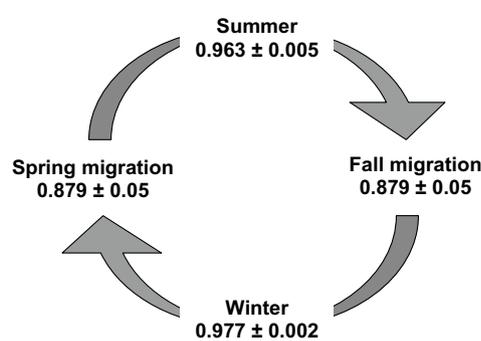


Fig. 2 Monthly survival probabilities during four seasonal intervals in the annual cycle of adult male Kirtland's warblers. Summer is the 4-month period from 1 May to 31 August, winter is the 6-month period from 1 October to 31 March, spring migration is considered to take place during the month of April, and fall migration during the month of September. Monthly summer survival estimate is the mean \pm SE of years 2007–2009 measured in Michigan; monthly winter survival estimate is the mean \pm SE of years 2003–2010 measured in the Bahamas. Survival estimates during spring and fall migratory periods are not separately estimable and are calculated as the square root of the overall 2-month migration period estimate (0.773 ± 0.12 SE). Standard errors were calculated using the Delta method

Discussion

We estimated season-specific survival of a highly range-restricted migratory songbird using data from both breeding and non-breeding sites. Our study presents the first published estimates of survivorship of the endangered Kirtland's warbler based on modern CJS models. This is also one of the few studies to estimate seasonal survival throughout the annual cycle for a long-distance migratory bird. The apparent annual survival probability for adult male Kirtland's warblers was 0.58 ± 0.12 SE, similar to published CJS estimates for other, non-endangered warbler species (reviewed in Faaborg et al. 2010). We found that

late winter rainfall in the Bahamas, particularly in March (the month prior to spring migration), was an important predictor of annual survival. We found survival during the migratory period to be the lowest out of any phase of the annual cycle, accounting for 44% of annual mortality.

Our finding that rainfall during the non-breeding season predicts annual survival of Kirtland's warblers corroborates theoretical (Sherry and Holmes 1995) and empirical evidence (Baillie and Peach 1992; Sillett et al. 2000; Saino et al. 2004; Studds and Marra 2007, 2011; Wilson et al. 2011; Rockwell et al. 2012) that migratory bird populations can be limited by winter weather. The link between winter rainfall, food supply, and overwinter performance of migratory birds is well supported (e.g., Strong and Sherry 2000; Marra and Holmes 2001; Latta and Faaborg 2002; Brown and Sherry 2006; Smith et al. 2010; Studds and Marra 2007, 2011; Wunderle et al. 2014). Rainfall levels can drive variation in winter food resources, such as the abundance of fruit or phytophagous insects (Janzen 1973; Wolda 1978; Studds and Marra 2007, 2011; Wunderle et al. 2014). Reduced rainfall can then lead to reduced body condition (Brown and Sherry 2006; Studds and Marra 2007, 2011; Wunderle et al. 2014; Cooper et al. 2015) and slower rates of fat deposition (Smith et al. 2010) in overwintering migratory birds. March may represent a critical time period for overwintering migrants; it is when birds must physically prepare for spring migration, and yet also face declines in insect abundance coinciding with the peak of the winter dry season experienced by many tropical regions. Birds in poorer condition at the end of the late winter dry season may then be less likely to survive the subsequent spring migration (Sillett et al. 2000; Sillett and Holmes 2002; Studds and Marra 2005). Kirtland's warblers may be especially vulnerable to this effect because they occupy seasonally dry winter habitats within a limited geographic region.

Such carryover effects may also explain the lower survival probability of male Kirtland's warblers during the migratory periods (0.773 ± 0.12) relative to the summer (0.862 ± 0.06) and winter (0.871 ± 0.06) stationary periods. Though individuals of this species only spend an estimated two months on migration, this phase accounts for the greatest proportion of total annual mortality (Fig. 2). Of 100 adult male warblers observed on the breeding grounds on 1 May, 42 of them are expected to perish by the following May. Of these, about 18.5 would die during spring or fall migration. We suggest that this is not solely due to the energetic demands and dangers of migration itself, but may be influenced by winter climate in the Bahamas, particularly rainfall. Occupation of drier winter habitats leads to limited food resources and reduced physical preparedness for migration (Brown and Sherry 2006; Studts and Marra 2005, 2007, 2011; Smith et al. 2010). Recent field studies have shown that the body condition of overwintering Kirtland's warblers is positively correlated with rainfall in the previous month (Wunderle et al. 2014). During dry winters, fewer individuals may be able to gain sufficient body mass to survive the subsequent spring migration, which would have important consequences for population dynamics (Peach et al. 1991; Szép 1995; Sillett et al. 2000; Sillett and Holmes 2002; Mazerolle et al. 2005). If our hypothesis regarding the carryover effect of winter rainfall is correct, we would expect to see higher mortality during spring migration than fall. However, we did not observe a sufficient number of non-transient, marked individuals at both the summer and winter field sites to allow us to parse apparent survival into spring vs. fall migration.

Our estimate of monthly survival probability during the migratory periods (0.879 ± 0.05) is greater than that of a congener, the black-throated blue warbler (*Setophaga caerulescens*) that overwinters in the Greater Antilles. More than 85% of apparent annual mortality in *S. caerulescens* occurred during migration (Sillett and Holmes 2002), compared to 44% in our study. Kirtland's warblers are large compared to other Parulids (mean body mass of 13.7 g for *S. kirtlandii*, Mayfield 1992; 9.8 g for *S. caerulescens*, Holmes et al. 2005). Their greater body reserves and a migratory route with relatively short overwater segments (Petrucha et al. 2013) may make them better able to accommodate periods of adverse weather or uncertain food supply during migration.

Kirtland's warblers had high apparent survival rates during the winter and summer stationary periods, similar to previous studies of marked Parulids (Sillett and Holmes 2002; Jones et al. 2004; Johnson et al. 2006). However, our estimates were lower than those for species with fixed winter and summer home ranges, like black-throated blue warbler. In contrast, Kirtland's warbler depends on ephemeral habitats on its breeding and wintering grounds,

suggesting that CJS estimates of stationary survival probabilities may be biased as low by permanent emigration (Lebreton et al. 1992, Sandercock and Jaramillo 2002). Non-breeding home ranges of Kirtland's warblers are flexible and can change throughout the winter in response to variation in fruit resources (Wunderle et al. 2010, 2014), which may result in more permanent emigrations during the non-breeding season. They also exhibit less site fidelity during the breeding season, returning to the same territories until the jack pine is greater than ~15 years old, and then dispersing to younger habitat patches (Donner et al. 2010). Our estimates of ϕ_{summer} and ϕ_{winter} are lower than those for black-throated blue warblers (Sillett and Holmes 2002), but our estimates of ϕ_{annual} and $\phi_{\text{migration}}$ are higher. These differences are probably due to a combination of real effects (e.g., relatively large body size of *S. kirtlandii*) and reduced philopatry resulting in underestimation of survival probability. Thus, our estimates for annual, oversummer, and overwinter survival should be considered minimum estimates, and that for migration a maximum. A complete understanding of season survival patterns for Kirtland's warbler awaits technological advances, such as satellite transmitters light enough to be placed on small songbirds year round.

Sex- and age-specific overwinter survival probabilities were generally consistent with patterns of social dominance by older males and sexual habitat segregation on wintering grounds observed in other species (Wunderle 1995; Marra 2000; Marra and Holmes 2001; Latta and Faaborg 2001, 2002). Empirical evidence exists for these patterns in Kirtland's warblers as well. Adult males increase pre-migration body condition significantly faster than females and exhibit stronger site fidelity in the Bahamas (Wunderle et al. 2014), suggesting that females may be relegated to poorer winter habitats where survival is lower. Age was better supported than sex as a factor affecting overwinter survival, but our estimates of overwinter survival of yearling (HY) birds were based on small sample sizes.

We have demonstrated that March rainfall on tropical wintering grounds is an important factor associated with annual survival of a long-distance migratory species. Our results corroborate other studies demonstrating that migratory bird populations can be limited by events during the non-breeding season. The Caribbean experiences a late winter dry season linked to decreased insect availability for Neotropical–Nearctic migratory birds (Lefebvre et al. 1994; Parrish and Sherry 1994; Brown and Sherry 2006; Smith et al. 2010). Furthermore, the Bahamas have experienced a decline in rainfall from 1959 to 1990 (Martin and Weech 2001), and climate change models predict significant future drying trends throughout the Caribbean region (Neelin et al. 2006). Long-term drought, or an increase in the severity or length of the dry season in the Bahamas,

has the potential to reduce both survival (this study) and productivity (Rockwell et al. 2012) of Kirtland's warblers, negatively affecting population size via two pathways. Our projection model revealed that if March rainfall falls by more than 12.4% from the current mean levels, the population of Kirtland's warblers may decline due to winter drought alone. While the status of this endangered bird has improved greatly in recent years, emerging threats such as climate change must be taken into consideration in conservation plans for this species and others. Many Neotropical–Nearctic migrants winter in the Caribbean, and increased drought during the non-breeding season could have important consequences on the annual survival and population growth rate of many Neotropical–Nearctic migratory bird species.

Our study adds to the growing body of evidence that events outside of breeding have persistent demographic effects implicated in population declines in multiple migratory taxa, including birds (Szép 1995; Wilson et al. 2011), reptiles (Crowder et al. 1994), fish (Wilson 2003), ungulates (Bolger et al. 2008), and marine mammals (Kraus et al. 2005). Information on season-specific mortality and its causes is thus of vital conservation importance for migratory animals, yet these data are unavailable for most species (Calvert et al. 2009; Hedenström et al. 2011). Such knowledge is critical for recognizing and mitigating threats that occur throughout the annual cycle, and for identifying conservation priorities. Climate change, for example, affects migratory animals in different ways during the breeding, non-breeding, and migratory periods, depending on the ecology of the organism in question (e.g., Walther et al. 2002; Butler 2003; Visser and Both 2005; Seebacher and Post 2015). Full annual cycle biology therefore provides a powerful framework for understanding how populations of migratory animals are limited throughout the year, and should continue to be a research priority.

Acknowledgements We thank the two anonymous reviewers whose comments substantially improved this manuscript. This research was completed with approval from the Kirtland's Warbler Recovery Team and the IACUCs of the University of Maryland and Smithsonian National Zoological Park. All applicable institutional and/or national guidelines for the care and use of animals were followed. The Michigan portion of this research was supported by the American Ornithologists' Union, Cooper Ornithological Society, Manomet Center for Conservation Science, Smithsonian Institution, University of Maryland, U.S. Fish and Wildlife Service, and USDA Forest Service. We thank 15 enthusiastic field assistants for their hard work at Michigan study sites. We are grateful to C. Studds and J. Hostetler for assistance with fieldwork and statistics, respectively. We additionally thank the dedicated team of eight Bahamian student interns and ten field assistants who carried out field work on Eleuthera, as well as E. Carey of the Bahamas National Trust. We greatly appreciate the local support provided by Bahamian landowners and commonage committees for permitting access to their lands. Funding for Eleuthera work was provided by International Programs of the USDA Forest Service, The Nature Conservancy, and the Puerto Rican Conservation

Foundation, working in cooperation with the Bahamas National Trust, the College of the Bahamas, and the University of Puerto Rico. The National Climatic Data Center of the National Oceanic and Atmospheric Association is available online at <http://www.ncdc.noaa.gov/IPS/mcdw/mcdw.html>.

Author contribution statement SMR, PPM, TSS formulated the idea. SMR, PPM, JMW, CIB developed the methodology. SMR, JMW, DC, JDW, DNE performed the field work. SMR and TSS analyzed the data. SMR and all other authors prepared the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest other than the funding sources listed in "Acknowledgments".

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