

ABSTRACT

Title of Document: CARRY-OVER EFFECTS FROM THE NON-BREEDING SEASON INFLUENCE SPRING ARRIVAL DATES, REPRODUCTIVE SUCCESS, AND SURVIVAL IN AN ENDANGERED MIGRATORY BIRD, THE KIRTLAND'S WARBLER (*SETOPHAGA KIRTLANDII*)

Sarah Mary Rockwell, Doctor of Philosophy,
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Directed By: Dr. David Inouye, Department of Biology

I used a unique model system to evaluate potential sources of population limitation in migratory birds that travel seasonally between temperate breeding grounds and tropical non-breeding grounds. The Kirtland's warbler (*Setophaga kirtlandii*) is an endangered species that is well-studied during its breeding season in northern Michigan, but how winter events may carry over to affect demographic processes remains unknown. Stable-isotope analyses of birds' tissues collected upon spring arrival revealed inconsistent yearly effects of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and δD signatures on arrival schedules. Males departing from more mesic winter habitats (depleted $\delta^{13}\text{C}$), consuming more insects (enriched $\delta^{15}\text{N}$), and wintering further south (enriched δD) arrived earlier to temperate breeding grounds. However, these patterns were not significant across all years. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures between age

classes were suggestive of age-related dominance relationships in winter. Winter habitat and diet differences among males within years did not seem to have strong carry-over effects, but mean spring arrival dates were delayed following drier winters, suggesting that carry-over effects in this species may be driven more by interannual variation in rainfall. There was a strong male age by rainfall interaction, with first-time breeders responding more strongly to changes in rainfall than experienced adults. Regardless of age, drier winters and delayed arrival and nest initiation were significantly associated with fewer offspring fledged in the subsequent breeding season. Analysis of our 5-year mark-recapture dataset showed that apparent survival is also positively associated with winter rainfall in the Bahamas. Kirtland's warbler survival probabilities are relatively high within the summer and winter stationary periods, but are lower during migration. Combining my survival and productivity data into a simple projection model revealed that the population growth rate of this species may become negative if Bahamas March rainfall drops more than 18% from its current mean. Climate change models predict continued drying trends in the Caribbean, which could have negative consequences on the population dynamics of the Kirtland's warbler. These results emphasize the importance of understanding the effects of climatic variation on demographic rates, and underscore the need for continued research on the ecology of migratory animals throughout the annual cycle.

CARRY-OVER EFFECTS FROM THE NON-BREEDING SEASON INFLUENCE
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AN ENDANGERED MIGRATORY BIRD, THE KIRTLAND'S WARBLER
(*SETOPHAGA KIRTLANDII*)

By

Sarah Mary Rockwell

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Advisory Committee:
Dr. David Inouye, co-chair
Dr. Peter Marra, co-chair
Dr. Michelle Dudash
Dr. Karen Lips
Dr. Mary Ann Ottinger
Dr. Scott Sillett

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Preface

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All research was conducted in accordance with permits issued by the U.S. Fish and Wildlife Service, the USDA Forest Service, Michigan Department of Natural Resources, and the USGS Bird Banding Laboratory, with the support of the Kirtland's Warbler Recovery Team. Protocols were approved by the Institutional Animal Care and Use Committees of the Smithsonian National Zoological Park and the University of Maryland.

Dedication

This dissertation is dedicated to my parents, David and Susan Rockwell, who never told me to go to medical school... and to my brothers, Brian and Charlie Rockwell, who have been my best friends from the beginning. This work would not have been possible without their love and support.

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Overview

Migratory behavior is exhibited by the majority of birds breeding at temperate latitudes. It is an evolutionary adaptation allowing migratory birds to exploit abundant but transitory resources at northern latitudes, yet also requiring them to move, forage and avoid predators in multiple habitat types across temperate and tropical regions. Identifying the factors that limit population sizes of migratory animals is important for creating effective management plans, yet these factors are rarely well-understood, due in part to the logistical challenges inherent in studying small organisms that move across large spatial scales. Migratory birds can be affected by alteration of habitat or climate in areas occupied during any part of the annual cycle – breeding grounds, overwintering areas, and stopover sites used during migration. This makes them especially vulnerable to global climate change, simply because of the wide range of geographic areas and habitats that they depend on throughout the year. Understanding the effects of variation in climate and habitat quality on demographic processes is the first step towards predicting how species may respond and adapt to persistent climate change, yet the complexity of the annual cycle combined with logistical constraints has made this task challenging.

Historically, research on the factors limiting populations of migratory birds has been biased towards breeding ground studies. There is evidence that summer food availability, habitat fragmentation, and nest predation may all limit reproductive success and consequently population size. Other work has suggested that migrants are limited by declines in habitat availability on tropical wintering grounds, weather conditions (particularly rainfall) in winter, or through the effects of winter food

supply on body condition. The emerging consensus is that studying regulatory mechanisms in each season independently may be misleadingly simple, as these periods of the annual cycle are also inextricably linked. Events within one season may also carry over to influence aspects of fitness in subsequent seasons, a phenomenon referred to as a seasonal interaction.

The overall goal of this research was to assess potential carry-over effects originating from winter conditions (such as habitat occupation, diet, and climate) on demographic processes of a migratory songbird. The Kirtland's warbler (*Setophaga kirtlandii*; formerly *Dendroica kirtlandii*) is a federally endangered species that occupies restricted ranges in both the breeding and non-breeding seasons. It is locally common on its summer grounds in northern Michigan, but highly habitat-specific, exclusively using stands of young Jack pine (*Pinus banksiana*) for nesting. However, it has been notoriously difficult to find on its winter range in the Bahamas archipelago, where it was only known from scattered single sightings until a substantial population was discovered for the first time in 2002. Kirtland's warblers are quite large for a parulid species, and are omnivorous in both summer and winter, making them somewhat unique. They exhibit a high rate of breeding site fidelity until their Jack pine stand ages past the point of suitability, then they readily disperse to younger stands. They exhibit some territorial behavior in winter, but their home ranges remain flexible in response to changes in ephemeral food resources.

The limited breeding and non-breeding ranges of the Kirtland's warbler make it an excellent study species. At a broad scale, the species exhibits very high migratory connectivity, meaning that nearly the entire population spends the winter in

a relatively small area, then all migrate to an equally restricted summer region. In other words, my study population on the breeding grounds is known to occupy a fairly small geographic area in winter, making it easier to estimate winter conditions affecting the population without having to generalize across a large winter range. In addition, their site fidelity made it possible to collect data on the same individuals across multiple years. The longitudinal nature of this study gave me the important advantage of being able to parse out effects of individual quality, and measure an individual male's response to changing winter conditions across different years. The ecological research conducted in the Bahamas since 2002 afforded me a unique opportunity to combine information on oversummer, overwinter, and annual survival to estimate survival over the migratory periods, which has only been done for one other species of migratory songbird. Such estimates of season-specific vital rates are particularly needed for threatened and endangered species if conservation goals include identifying limiting factors and reducing potential threats.

In chapter 1, I tested the use of stable isotopes to remotely infer information about previous seasons, by taking advantage of the fact that animals assimilate habitat- ($\delta^{13}\text{C}$), diet- ($\delta^{15}\text{N}$), and latitude-specific (δD) isotope ratios into their tissues through the resources they consume. I assessed the carry-over effects of within-year differences in winter habitat use and diet among individuals by collecting tissues grown in winter from incoming males in spring, and analyzing their stable-isotope ratios. When all years were pooled, males with more depleted $\delta^{13}\text{C}$ signatures arrived earlier to spring breeding grounds. Because habitat moisture is strongly linked to the abundance of fruit and insects in the tropics, this means that males wintering in more

mesic sites were likely able to maintain a level of body condition that allowed them to depart earlier from wintering grounds. However, this pattern was only significant in two out of five years, suggesting that $\delta^{13}\text{C}$ may only be a weak indicator of habitat quality in species adapted to dry habitats, like the Kirtland's warbler. Males with more enriched $\delta^{15}\text{N}$, indicating a diet with a greater proportion of arthropods, also tended to arrive earlier, but the pattern was not significant in any individual year, implying that the importance of insect vs. fruit resources during pre-migratory fattening is more complicated in this species than previously thought. Results from δD were suggestive of a leapfrog migration pattern, with individuals wintering further south passing over and preceding those that wintered further north to temperate breeding grounds, but this pattern was also inconsistent across years. However, adult males did tend to have more depleted $\delta^{13}\text{C}$ (indicating occupation of higher-quality, more mesic habitats), and more enriched $\delta^{15}\text{N}$ (indicating a greater proportion of insects in the diet), suggesting that they may exclude first-winter males from the best territories and/or food resources.

In chapter 2, I evaluated carry-over effects driven by interannual variation in rainfall that may affect winter habitat quality and food availability among years for the entire population of Kirtland's warblers. I found that second-year males (first-time breeders) were highly sensitive to changes in rainfall, significantly advancing arrival after wetter winters, probably due to the well-established link between winter rainfall, food availability and pre-migratory body condition. Older males, on the other hand, maintained arrival schedules regardless of the level of winter rainfall. This is further evidence for age-related dominance effects, where older males may exclude younger

males from high-quality habitats that resist seasonal desiccation and maintain levels of food abundance, though it is possible that older males simply have more experience in habitat selection and greater foraging efficiency. Drier Bahamian winters were associated with fewer offspring fledged in the subsequent breeding season across all age classes. If female arrival dates are similarly limited by winter rainfall, then adult males may suffer reduced reproductive success following drier winters despite their ability to maintain arrival schedules. In contrast, I found no relationship between winter rainfall and body condition upon spring arrival, suggesting that differences in body condition among males that are present at the end of the winter period are made up for later, perhaps by lengthening spring migration. To our knowledge, this is the first longitudinal study to examine the effects of winter rainfall on spring arrival dates, body condition, and reproductive success in a Neotropical migratory bird, and we found evidence for important carry-over effects driven by winter rainfall.

In chapter 3, I estimate apparent survival, parse survival probabilities into each phase of the annual cycle, and assess the influence of summer and winter climate on annual survival. Rigorous estimates of annual survival of migratory songbirds require long-term study of marked populations, and are therefore rare, while season-specific survival rates have only been estimated by one other study to date. I provide a minimum estimate of annual survival of adult male Kirtland's warblers of 0.58 ± 0.12 , which is similar to other non-endangered warbler species. I also found that survival rates outside of the summer and winter stationary periods are the lowest of any part of the annual cycle. The two months spent on migration

account for half of all annual mortalities. Importantly, in a model selection framework, March rainfall in the Bahamas explained variation in survivorship better than any other winter or summer climate variable that I included in my model sets. March rainfall was positively correlated with apparent annual survival in the subsequent year. In fact, I suggest that the high mortality rate I found during the migratory periods is not solely due to the challenges of migration alone, but may in fact be a carry-over effect that is tightly linked to winter rainfall in the Bahamas. During dry late winter periods, fewer individuals may be able to gain sufficient body mass to survive the subsequent spring migration. In the previous chapter, I found that drier winters are also associated with reduced reproductive success, so if drying trends in the Bahamas continue as predicted, it could have multiple negative impacts on the population dynamics of the Kirtland's warbler.

The research outlined here, and reported in detail in the following three chapters, emphasizes the importance of understanding seasonal interactions and factors affecting migratory bird ecology throughout the annual cycle. Carry-over effects of wintering conditions can drive ecologically relevant variation in demographic processes. In the light of recent population declines observed in many taxa of migratory species, including songbirds, improving our understanding of the full life cycle biology of migratory animals should continue to be a conservation and research priority.

Chapter 1: The use of stable isotopes in predicting winter diet, winter origin, and spring arrival timing at northern breeding grounds for an endangered migratory songbird

Abstract.

Identifying the factors that limit or regulate populations of small migratory animals has proven to be challenging, requiring information on each portion of the annual cycle, as well as how events within one season carry over to affect individuals and populations in subsequent seasons. We tested the use of stable isotopes to remotely infer information about previous seasons, by taking advantage of the fact that animals assimilate habitat- ($\delta^{13}\text{C}$), diet- ($\delta^{15}\text{N}$), and latitude-specific (δD) isotope ratios into their tissues through the resources they consume. The Kirtland's warbler is an omnivorous migratory songbird that overwinters in xeric, second-growth scrub habitats in the Bahamas archipelago. We captured 257 male Kirtland's warblers during 321 arrival events on Michigan breeding grounds from 2006-2010 to determine the influence of winter habitat type, diet, and latitude on the timing of spring arrival. $\delta^{13}\text{C}$ in red blood cells was positively associated, and $\delta^{15}\text{N}$ was negatively associated, with arrival dates when all years were pooled, indicating that males departing from wetter winter habitats, and those that consumed a greater proportion of insects, arrived earlier to temperate breeding areas. However, the relationship between $\delta^{13}\text{C}$ and arrival dates was only significant in 2 out of 5 years, suggesting that $\delta^{13}\text{C}$ may only be a weak indicator of habitat quality for this species. Similarly, the relationship between $\delta^{15}\text{N}$ and arrival date was not significant in any

individual year. δD was significantly negatively correlated with spring arrival dates in 2006 and when both years were combined, but not significant in 2007, suggesting a possible leap-frog migration pattern. Overall, we found some (albeit weak) evidence for the ability of $\delta^{15}C$, $\delta^{15}N$, and δD to infer information about conditions during the prior non-breeding season in this species. Stable isotope analysis has proven to be a powerful tool for elucidating seasonal interactions. However, this technique may not be appropriate for all species, and its usefulness may vary depending upon the non-breeding season conditions to which birds are subject. Improving our understanding of the full life cycle biology of migratory birds should continue to be a conservation and research priority, so exploring both direct and indirect methods for doing so remains essential.

Introduction

Factors that limit and regulate animal populations remain poorly understood for most animal species (Faaborg et al. 2010, Hedenström et al. 2011). For migratory organisms that travel hundreds or thousands of kilometers between seasons, identifying limiting factors is especially problematic, requiring information on events occurring in multiple locations as well as their carry-over effects to subsequent seasons (Sherry and Holmes 1995, Newton 2004). One contributing problem is our inability to track small organisms, such as individual migratory birds, over large spatial scales, impeding our capacity to quantify migratory connectivity and examine critical seasonal interactions that underlie population regulation (Webster and Marra 2005). Conventional mark-recapture techniques using color bands have not been

widely successful; despite large banding efforts, recovery rates between seasons remain extremely low for most non-game bird species (Webster et al. 2002), although comprehensive analyses have yet to be done. Other extrinsic markers, such as satellite tags and radio transmitters, have been useful in the study of raptors, shorebirds, and waterfowl. New light-level geolocators are light enough to track small passerines over long distances (e.g., Stutchbury et al. 2009a, Heckscher et al. 2011, Ryder et al. 2011, Stanley et al. 2012), but they require recapturing individuals in the following year, leading to low sample sizes. Additionally, this technology can only provide data on geographic location, not ecological factors like habitat or diet. The complexity of the annual cycle combined with these logistical constraints has contributed to the exceptional difficulty of identifying limiting factors for migratory bird populations.

Recently, the application of stable isotopes has revolutionized our ability to link events in winter and summer by taking advantage of the fact that animal tissues reflect the unique isotopic composition of the supporting food web occupied during tissue synthesis (Rubenstein and Hobson 2004). The stable isotope ratios of several light elements vary systematically across habitats, diets, and geographic locales. For example, the ratio of ^{13}C to ^{12}C (known as $\delta^{13}\text{C}$) is higher in C_4 and CAM plants than in C_3 plants due to the different metabolic enzymes used (Marshall et al. 1994). C_3 plants experiencing drought stress also preferentially uptake ^{13}C and discriminate against ^{12}C (Lajtha and Marshall 1994). Thus, $\delta^{13}\text{C}$ enrichment occurs in xeric environments where these types of plants dominate (Marra et al. 1998). Habitat-specific carbon signatures are then passed up the food chain through fruits or phytophagous insects to primary and secondary consumers. As a result, organisms

assimilate a habitat-specific stable-carbon isotope ratio ($\delta^{13}\text{C}$) into their tissues (Hobson 1999), which reflects the moisture regime of the plant community in the habitat occupied while tissues were grown. Habitat suitability for several migratory bird species during the breeding season varies along this same wet-to-dry moisture gradient that can be measured by $\delta^{13}\text{C}$ (Marra et al. 1998).

Stable-nitrogen isotope ratios (ratio of ^{15}N to ^{14}N , written as $\delta^{15}\text{N}$) vary predictably among different trophic levels, and thus can provide a signal of diet (Minagawa and Wada 1984, Hobson 1999). The heavier nitrogen isotope becomes more concentrated at higher trophic levels, so birds feeding primarily on insects will have tissues with more enriched $\delta^{15}\text{N}$ signatures than birds consuming proportionally more fruit. The ratio of deuterium to light hydrogen isotopes (^2H to ^1H , written as δD) in precipitation varies systematically on a north-south gradient in eastern North America. Rain water becomes progressively more depleted in deuterium as you move further north, so the latitude where birds' tissues were synthesized can be inferred by their δD signatures (Chamberlain et al. 1997, Hobson and Wassenaar 1997). These isotopic "fingerprints" can persist indefinitely in metabolically inert tissues like feathers, or for 6-8 weeks in slow-growing tissues such as claws. Stable isotopes in red blood cells (separated from plasma, which turns over more quickly) have a half-life of 30 days (Hobson and Clark 1993). Direct observation of winter departure and breeding ground arrival of five color-banded Kirtland's warbler males revealed a mean maximum spring migration period of 15.8 days (Ewert et al. 2012). Thus, birds arriving at breeding areas in spring are expected to have tissues that still reflect the

isotopic composition of their overwintering habitats and diets (Hobson and Clark 1992, Hobson and Wassenaar 1997, Norris et al. 2005).

Stable-isotope techniques have permitted major advances in studying migratory connectivity and the role of carry-over effects between seasons in migratory animals. For instance, Marra et al. (1998) found that American redstarts (*Setophaga ruticilla*) wintering in wet, forested habitats had depleted $\delta^{13}\text{C}$ values relative to individuals in drier scrub habitats. Enriched $\delta^{13}\text{C}$ values were associated with an inability to maintain body mass over the winter period and delayed winter departure (Marra et al. 1998, Studds and Marra 2005, Smith et al. 2010). Occupation of high-quality, mesic habitats in winter, as indicated by depleted $\delta^{13}\text{C}$, carries over to result in: improved energetic condition during spring migration (Bearhop et al. 2004), advanced spring arrival on temperate breeding grounds and improved condition upon arrival (Marra et al. 1998), advanced breeding condition (Tonra et al. 2011), earlier breeding dates (Norris et al. 2004), greater reproductive success (Norris et al. 2004, Reudink et al. 2009), and higher return rates (Studds and Marra 2005) in two species of migratory birds.

Conditions during the non-breeding season can also vary between years, and additional studies have used measures of conditions experienced in winter other than isotopes. Winter precipitation, the Southern Oscillation Index (SOI), and Normalized Differential Vegetation Index (NDVI) also drive seasonal interactions influencing reproduction, survival, and population size (Ryel 1981; Peach et al. 1991; Baille and Peach 1992; Szép 1995; Sillett et al. 2000; Nott et al. 2002; Saino et al. 2004; Mazerolle et al. 2005; Studds and Marra 2007, 2011; Wilson et al. 2011; LaManna et

al. 2012; Rockwell et al. 2012). Taken together, these studies of the effect of spatial and temporal variation in winter habitat conditions (particularly moisture) provide compelling evidence that events during the non-breeding period can result in ecologically relevant seasonal interactions - carry-over effects between winter, spring migration, and the subsequent breeding season.

The use of stable-isotopes to infer prior habitat use has primarily been developed with common species, but has yet to be tested with threatened or endangered species, such as the Kirtland's warbler (*Setophaga kirtlandii*). This species is well-studied and intensively managed on its breeding grounds (Bocetti et al. 2002), but its non-breeding season ecology is relatively poorly known, in part because wintering individuals have been difficult to locate. Only ~200 individuals were recorded on their non-breeding grounds from 1851-2002 (Currie et al. 2003). Recently, a substantial winter population was discovered for the first time, on the southern portion of the island of Eleuthera, Bahamas (Currie et al. 2003). Kirtland's warblers use primarily dry, second-growth habitats such as broadleaf scrub and low coppice in the winter (Sykes and Clench 1998; Haney et al. 1998; Wunderle et al. 2007, 2010), though a few individuals have been observed occupying Caribbean pine (*Pinus caribaea*) habitats with short understories (Lee et al. 1997). At the Eleuthera field site, Kirtland's warblers consume a substantial portion of fruit (69% of 499 foraging observations) as well as arthropods (Wunderle et al. 2010), but the importance of fruit vs. insects in their winter diet is unknown. Different study sites vary substantially in the degree to which they retain moisture, and thus food

abundance, throughout the late winter dry season, and individual warblers will shift home ranges to track these resources (Wunderle et al. unpub. data).

A greater understanding of how the non-breeding season limits and regulates the population size of the Kirtland's warbler, and how limiting factors originating in winter produce biologically important carry-over effects, is essential to creating effective, long-term management strategies. Furthermore, no previous studies have examined the carry-over effects of winter diet or winter latitude on breeding ground processes in a migratory songbird, though several have used measures of habitat quality that are likely correlated to food abundance (e.g., Marra et al. 1998, Norris et al. 2004). We sampled male Kirtland's warblers upon arrival to Michigan breeding areas to examine the effects of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and δD on patterns of spring arrival to breeding grounds. On Eleuthera, Kirtland's warblers occupy sites that differ in their ability to retain moisture (J. M. Wunderle, pers. comm.). We predicted that incoming males in Michigan would have $\delta^{13}\text{C}$ signatures positively correlated with spring arrival dates, such that those departing from wetter, higher-quality winter habitats are able to arrive earlier. Kirtland's warblers are omnivorous in winter (Wunderle et al. 2010), and we also hypothesized that consumption of a greater proportion of insects would constitute a higher-quality diet, enabling a bird to depart earlier on spring migration. Thus, we predicted a negative relationship between $\delta^{15}\text{N}$ signatures and spring arrival dates because individuals consuming more insects in late winter would arrive earlier to temperate breeding grounds than those that consumed more fruit. Many migratory bird species exhibit a leapfrog migration pattern (e.g., Bell 1996, Kelly et al. 2002, Kelly 2006, Reichlin et al. 2010), where birds departing on

migration from more extreme ends of the species' range bypass in time and/or space those that bred or wintered towards the middle of the range. We predicted that this might be true for Kirtland's warblers as well, resulting in a negative correlation between δD signatures and spring arrival dates, as individuals wintering further south in the Bahamas island chain pass over those wintering further north, and precede them on temperate breeding grounds.

Methods

Study Species and Sites. The Kirtland's warbler is a ground-nesting passerine that was federally listed as an endangered species in 1973 (Byelich et al. 1976). It is one of the largest species of parulids, weighing about 13.8g (Mayfield 1992). This species occupies a narrow range of breeding habitat, nesting almost solely in the pine barrens of about 16 counties in the northern lower peninsula of Michigan (Mayfield 1992). Kirtland's warblers prefer to use large (> 32 ha), fairly dense, homogenous stands of Jack pine (*Pinus banksiana*) interspersed with regular small clearings for nesting habitat. Stands must be relatively young (between 5-20 years old) to attract breeding adults (Byelich et al. 1976), so this species depends on natural wildfires or human management to clear areas for the regeneration of young Jack pine. The strength of their breeding habitat specialization has likely contributed to their limited breeding range and endangered status (Mayfield 1983). Habitat loss and heavy nest parasitism by the Brown-headed cowbird (*Molothrus ater*) reduced the population of Kirtland's warblers to ~200 singing males in 1971, but intensive management on the breeding grounds allowed the population to rebound to ~1800 singing males in 2012

(USFWS 2012). Virtually nothing was known about the winter ecology of this species until 2002, when a substantial overwintering population was discovered for the first time, on the island of Eleuthera in the Bahamas (Currie et al. 2003). Kirtland's warblers live in early successional habitats in winter as well as summer, occupying second-growth, broadleaf scrub or low coppice that is maintained by fire, hurricanes, and human disturbance (Haney et al. 1998; Sykes and Clench 1998; Wunderle et al. 2007, 2010). Kirtland's warblers readily shift locations over the course of the winter as they track ephemeral and diminishing food resources. They are more omnivorous in winter than other warblers, consuming a substantial amount of wild sage (*Lantana involucrata*), snowberry (*Chiococca alba*), and black torch (*Erithalis fruticosa*) fruit in addition to arthropods (Wunderle et al. 2010). Home ranges may overlap considerably, especially in late winter when food is at its most patchy and scarce (Wunderle et al. unpub. data). However, their restricted wintering range means that large-scale spatial variation in stable-carbon and -nitrogen isotopes is unlikely to confound local habitat or diet signatures (Still et al. 2003, Bearhop et al. 2004).

Our study was carried out on ten 30-ha plots located in the northern lower peninsula of Michigan (Alcona, Crawford, Iosco, Ogemaw, and Oscoda counties). Plots were dominated by young Jack pines that were nearly all planted as 2-year old trees after whole-tree harvesting of the stand. Deciduous tree species such as pin oak (*Quercus ellipsoidalis*) and sand cherry (*Prunus pumila*) also occur. Ground cover such as blueberry (*Vaccinium angustifolium*), bearberry (*Arctostaphylus uva-ursi*), sweet fern (*Comptonia peregrina*), and sedge (*Carex pensylvanica*) may provide

important forage and nesting cover for Kirtland's warblers (Bocetti 1994; see Rockwell et al. 2012 for full details).

Plot surveys and arrival dates. We conducted aural surveys of our study plots every three days to detect the arrival of new males from 2006 – 2010, starting on May 1 of each year. During each plot survey, multiple observers simultaneously walked along transects placed 200-300m apart, moving across the study area and listening for singing males. Male Kirtland's warbler song is loud, and can easily be heard across these distances in habitats with a short canopy (Probst et al. 2005). Each singing male was then located and observed with binoculars to determine whether it was banded. We recorded arrival dates as the first day in the 3-day survey interval in which an individual was first seen (e.g., males first observed on May 1, 2, or 3 were recorded as arrival date 1). Days numbered starting with May 1 are used throughout (1 = May 1).

Capture and tissue collection. Male Kirtland's warblers were captured using mist-nets and conspecific song playback, and marked with a unique combination of three color bands and one numbered aluminum band. Males were captured soon after arrival (always < 8 days, though 74% were captured on the first day they were observed, and 92% were captured by the second site visit after arrival). Males were aged as either first-time breeders (second-years; SY) or adults returning to breed (after second-years; ASY) using plumage characteristics (Probst et al. 2007). We were unable to capture females reliably or determine their arrival dates, as they are much less conspicuous in the field and do not respond consistently to playback. Morphometric measurements were taken at the time of capture. Body condition upon

arrival was calculated by taking the first principal component (PC1) of tarsus, wing, tail and culmen length, regressing it over mass, and recording the linear residual. Approximately 100 μ l of blood was taken from each individual via brachial venipuncture and collected in heparinized 75 μ l glass capillary tubes. Blood samples were placed on ice while in the field, then centrifuged to separate plasma and hematocrit, and stored at -4°C before preparation for isotope analyses. Because forecrown feathers of many migratory birds, including Kirtland's warblers, are molted on the wintering grounds (Mayfield 1992, J. M. Wunderle pers. comm.), we collected three of the foremost crown feathers by plucking them with tweezers. Isotopic signatures in red blood cells of birds have turnover times of nearly 8 weeks (half-life of 29.8 days; Hobson and Clark 1993), and feathers are metabolically inert after growth (Hobson and Wassenaar 1997). Spring migration is fairly rapid in Kirtland's warblers (Ewert et al. 2012), so birds captured within a week of arrival were assumed to have tissues retaining the isotopic composition of their wintering grounds (Norris et al. 2005).

Stable isotope analysis. Stable isotope analysis was completed at the Facility for Stable Isotope Research in Queen's University, Kingston, Ontario (2006-2007), and at the Stable Isotope Mass Spectrometry Facility at the Smithsonian Institution, Suitland, MD (2008-2010). Measurements of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and δD were performed using continuous flow isotope ratio mass spectrometers. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analyzed in all 5 years, and δD was analyzed in 2006 and 2007 only. Feather samples were prepared by washing them with a 2:1 chloroform:methanol solution to remove surface oils and left to dry under a lab hood for 24 hours. Red blood cell samples, separated

from plasma via centrifugation, were freeze-dried and crushed. All tissue samples were weighed and loaded into tin capsules (carbon and nitrogen) or silver capsules (hydrogen). Hydrogen samples were then allowed to equilibrate with the local atmosphere for 48 hours, and then baked in an oven at 100°C for 24 hours to remove any surface moisture. Samples were combusted in an NCS 2500 Elemental Analyzer (Finnegan TC/EA) and introduced online into a Finnegan MAT 252 Mass Spectrometer (Queen's University), or by using a Thermo Scientific Delta V Advantage mass spectrometer coupled with a Costech ECS 4010 elemental analyzer via a ConFlo IV gas interface (Smithsonian Institution). One in-house standard was run for every four unknowns. Isotope ratios are reported relative to international standards (Pee Dee belemnite for carbon, atmospheric N₂ gas for nitrogen, and Vienna Standard Mean Ocean Water for hydrogen). Isotope ratios (R) are expressed in parts per mil, using standard delta (δ) notation, where $\delta = (R_{\text{sample}} / R_{\text{standard}}) - 1$ x 1000.

Statistical methods. The effects of various blood isotope values on spring arrival dates were analyzed using general linear mixed models with random intercepts fit for each bird. Because we sampled many individual birds across multiple years, this repeated measures approach was necessary to account for the lack of independence among some observations. The longitudinal nature of this study also helped control for any effects of individual quality. The full models for arrival dates also included fixed effects of age, blood isotope ratio ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or δD), and their two-way interaction, as well as random effects of year and study site. We determined the significance of explanatory variables by iteratively removing them from the full

model, and then comparing the reduced to the full model via chi-squared likelihood ratio tests with one degree of freedom. Non-significant random variables and interactions were not included in final models. All statistical analyses were performed with R Version 2.12.1 (R Foundation for Statistical Computing, Vienna, Austria).

Results

From 2006 to 2010, we recorded spring arrival dates and collected tissue samples 321 times for 257 individual Kirtland's warbler males (2006, $n = 51$; 2007, $n = 73$; 2008, $n = 88$; 2009, $n = 64$; 2010, $n = 45$). These 321 sampling events included 220 observations of ASY males, 96 of SY males, and 5 of individuals of unknown age. Males returning to northern breeding areas had arrival dates ranging from May 2 to June 5, with a global mean of day 14.6 ± 0.36 SE after May 1. ASY males preceded SY males at Michigan breeding grounds ($t_{167} = 8.78$, $P < 0.001$), with median arrival dates of May 13 and May 19, respectively. Stable-carbon isotope ratios ($\delta^{13}\text{C}$) in red blood cells ranged from -27.3‰ to -22.6‰ , with the exception of one potential outlier at -20.8‰ . Values of $\delta^{15}\text{N}$ ranged from 1.5‰ to 7.5‰ , and values of δD ranged from -61‰ to -17‰ with a possible outlier at -77‰ . Adult males tended to have blood more depleted in $\delta^{13}\text{C}$ (wetter winter habitats; $t_{181} = 1.70$, $P = 0.09$), and more enriched in $\delta^{15}\text{N}$ (more arthropods in diet; $t_{203} = 1.77$, $P = 0.08$) than SY males, though these differences were only marginally significant (Figure 1). ASY and SY males did not differ in their δD signatures ($t_{147} = 0.29$, $P = 0.77$; Figure 1).

When pooled across all years, male Kirtland's warblers with more depleted $\delta^{13}\text{C}$ isotope values, indicating an origin in wetter winter habitats, arrived earlier in

the spring than those with more enriched values (blood $\delta^{13}\text{C}$: $\chi^2 = 1006.9$, $\text{df} = 1$, $P < 0.001$; Figure 2). The slope of this relationship was positive as predicted ($\beta = 0.58 \pm 0.37$ SE), and did not vary by age (age \times blood $\delta^{13}\text{C}$: $\chi^2 = 1.3$, $\text{df} = 1$, $P = 0.25$). The random variables bird ID, study site, and year also contributed a significant amount of explanatory power to the model. When all years were pooled, males with more enriched $\delta^{15}\text{N}$ isotope values, indicating a greater proportion of insects in their late winter diets, arrived in advance of those with more depleted $\delta^{15}\text{N}$ signatures (blood $\delta^{15}\text{N}$: $\chi^2 = 1022.1$, $\text{df} = 1$, $P < 0.001$; Figure 3). The relationship between these variables was in the predicted negative direction ($\beta = -0.66 \pm 0.36$), and the slope did not differ across age classes (age \times blood $\delta^{15}\text{N}$: $\chi^2 = 0.93$, $\text{df} = 1$, $P = 0.33$). The random effects of bird ID, study site, and year influenced arrival dates in this model as well. Combining 2006 and 2007, male Kirtland's warblers with more enriched δD signatures, or those originating from islands further south, tended to arrive earlier (crown δD : $\chi^2 = 2340.8$, $\text{df} = 1$, $P < 0.001$; Figure 4). However, one potential outlier at -77‰ had a high degree of influence on this relationship (Figure 4). When this point was removed, the pattern was no longer significant (crown δD : $\chi^2 = 0.83$, $\text{df} = 1$, $P = 0.36$). There was no interaction between age and δD in crown feathers (age \times crown δD : $\chi^2 = 1.12$, $\text{df} = 1$, $P = 0.29$), but breeding site and year both added significant explanatory power to the model.

Because arrival dates varied significantly by year in each isotope model, we next examined the relationship between isotope ratios and arrival dates in each year separately. We again used linear mixed models, but this time without the random effects of bird ID and year, because we only sampled each individual once in any

given year. $\delta^{13}\text{C}$ values in red blood cells did not consistently predict spring arrival timing. The relationship was significant in 2006 ($t_{41} = 2.17$, $P = 0.036$) and 2010 ($t_{35} = 2.19$, $P = 0.035$), but not in 2007 ($t_{58} = 0.68$, $P = 0.50$), 2008 ($t_{75} = 0.26$, $P = 0.79$), or 2009 ($t_{55} = 0.68$, $P = 0.50$; Figure 2). Stable nitrogen isotope ratios were not significantly associated with arrival dates in any individual year (2006: $t_{41} = 0.74$, $P = 0.46$; 2007: $t_{58} = 1.36$, $P = 0.18$; 2008: $t_{73} = 0.96$, $P = 0.33$; 2009: $t_{55} = 0.30$, $P = 0.77$; 2010: $t_{35} = 0.65$, $P = 0.52$; Figure 3). The negative relationship between stable-hydrogen isotope ratios and arrival dates was significant in 2006 ($t_{41} = 2.52$, $P = 0.02$), but not in 2007 ($t_{48} = 1.31$, $P = 0.20$; Figure 4). The strength of the relationship in 2006 dropped to near-significant when the high-leverage point at -77‰ was removed ($t_{41} = 1.85$, $P = 0.07$).

Discussion

Overall, we found inconsistent yearly effects of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and δD signatures on arrival schedules of migratory Kirtland's warblers arriving to Michigan breeding grounds in spring. When all years were pooled, relationships between isotopes and arrival dates fit our predictions, with males foraging in more mesic winter habitats, consuming more insects, and wintering further south arriving earlier to temperate breeding grounds, but these patterns were not significant across all years. We also found that older males tended to have more depleted $\delta^{13}\text{C}$ (indicating occupation of wetter habitat), and more enriched $\delta^{15}\text{N}$ (indicating more arthropods in the late winter diet) in their tissues than SY birds returning from their first winter. This pattern is consistent with age-related dominance relationships (Marra 2000, Marra and Holmes

2001), and habitat segregation (Latta and Faaborg 2002, Townsend et al. 2011) found in other species of wintering migrants, where younger birds are excluded from the highest-quality winter habitats, possibly contributing to the later arrival dates of younger males (Rockwell et al. 2012). ASY birds and birds in their first winter season did not segregate on a broad latitudinal scale, but rather on a finer habitat scale, with adults occupying wetter habitats and eating more insects. This pattern could occur either through behavioral dominance (Marra 2000, Marra and Holmes 2001), or greater habitat selection experience and/or foraging efficiency of adults.

Carry-over effects driven by variation in winter rainfall among years are known to influence spring arrival timing in Kirtland's warblers, with males advancing arrival following wetter winters (Rockwell et al. 2012). Our data provide some evidence that within-year differences in winter habitat quality among males may also influence spring arrival dates, at least in some years. Winter rainfall predicts fruit abundance and body condition of Kirtland's warblers at various wintering sites on the island of Eleuthera, Bahamas (J. White and J. Wunderle, unpub. data). Habitat quality for many species of overwintering migratory birds is affected by moisture and its strong relationship with the abundance of food resources (Janzen 1973, Wolda 1978, Brown and Sherry 2006, Studds and Marra 2007, 2011). In turn, food availability is known to influence multiple measures of migratory bird performance, including winter site persistence (Strong and Sherry 2000, Latta and Faaborg 2002), body condition (Strong and Sherry 2000, Marra and Holmes 2001, Latta and Faaborg 2002, Studds and Marra 2005, Brown and Sherry 2006, Smith et al. 2010), and departure dates from wintering areas (Studds and Marra 2005, 2007, 2011). Thus, blood $\delta^{13}\text{C}$

values sometimes predict arrival schedules of Kirtland's warblers because males with depleted $\delta^{13}\text{C}$ may have overwintered in wetter habitats, where they likely experienced greater food availability, and were able to maintain levels of winter body condition that allowed them to depart earlier on spring migration.

However, our results are somewhat in contrast to other recent studies that have linked isotopic measures of winter habitat quality to body condition, timing of spring arrival, and reproductive success in multiple species of Neotropical migratory birds (Marra et al. 1998, Norris et al. 2004, Bearhop et al. 2004, Reudink et al. 2009, Smith et al. 2010). While male Kirtland's warblers exhibited a substantial range of blood $\delta^{13}\text{C}$ values (-27.3‰ to -22.6‰) upon spring arrival, suggesting that birds overwintered in Neotropical habitats with varying moisture levels, the relationship between winter habitat moisture and arrival dates was not consistent across all years. Instead, blood $\delta^{13}\text{C}$ values significantly predicted spring arrival dates in only two out of the five years of this study. It is unclear why these relationships were only significant in 2006 and 2010, which were neither particularly dry nor particularly wet years. The aforementioned studies had the important advantage of using study species that have been the focus of long-term research on their wintering ecology, so potential sources of isotopic variation were better understood. In contrast, the full winter range and variety of habitat types occupied by Kirtland's warblers in winter, including the geographic origins of most of the individuals in the present study, are unknown. While detailed ecological research has been conducted on Kirtland's warblers overwintering in southern Eleuthera since 2002, the study population of <50 birds may only represent 1-3% of the total population. A few Kirtland's warblers have been

observed wintering in Caribbean pine habitats with low, open understories (Lee et al. 1997), and it is possible that other individuals may overwinter in different habitat types with unknown isotopic profiles. Ground-truthing of expected isotope values in precipitation and birds' tissues across multiple islands and habitats in the Bahamas would aid the interpretation of isotope data in future research efforts.

Additional reasons may explain why stable-carbon isotopes do not reliably explain carry-over effects of winter habitat in Kirtland's warblers. For example, Kirtland's warblers appear to be less strictly territorial in winter than previously studied model species, and instead will readily shift home ranges in response to spatial and temporal variation in resource abundance (Wunderle et al. 2010). Stable isotopes in red blood cells should reflect habitats occupied and resources consumed in the week or two immediately prior to spring departure, but this may not be the same home range where the bird spent critical portions of the winter period. Other tissues, such as claw material, integrate stable-isotope ratios over a longer time frame, but the relationship between $\delta^{13}\text{C}$ in claws and arrival dates was not consistent either (significant in 2010, and when all years were pooled; S. M. Rockwell, unpub. data). The omnivorous winter diet of Kirtland's warblers may further complicate the interpretation of carbon. $\delta^{13}\text{C}$ in tissues can become more enriched when individuals feed on prey items at higher trophic levels (Haramis et al. 2001, Podlesak et al. 2005). If this is true for Kirtland's warblers, then the $\delta^{13}\text{C}$ enrichment caused by consuming more insects may confound the $\delta^{13}\text{C}$ depletion due to occupation of more mesic habitats. This would reduce the facility of $\delta^{13}\text{C}$ to reflect habitat moisture alone, and

make it more difficult to detect the negative trend we expected between $\delta^{13}\text{C}$ and spring arrival schedules.

It may be that stable-carbon isotopes are simply less indicative of habitat quality in species that regularly use xeric habitats in winter (Boone et al. 2012). Kirtland's warblers are known to overwinter in xeric secondary growth and low coppice in the Bahamas (Sykes and Clench 1998, Wunderle et al. 2010). Perhaps the variation in moisture across winter sites in the Bahamas is not enough to strongly affect $\delta^{13}\text{C}$, and the variation we observed in $\delta^{13}\text{C}$ was due to an unknown and unmeasured source. If most Kirtland's warbler individuals occupy fairly uniform xeric habitats, then carry-over effects influencing spring arrival, reproduction, and survival may be driven more by interannual variation in rainfall that affects the entire population (Rockwell et al. 2012, see also Chapters 2 and 3), rather than by within-year differences in habitat quality among individuals. Boone et al. (2012) found no relationship between $\delta^{13}\text{C}$ and energetic condition or arrival timing of Magnolia warblers at a spring stopover site in Ohio, though they collected data in only one year. They concluded that stable-carbon isotopes may only be a weak indicator of winter habitat quality in migratory bird species adapted to dry habitat types, and our results are consistent with this finding. Either $\delta^{13}\text{C}$ is only associated with Kirtland's warbler arrival schedules in some years, or perhaps multiple years of data are needed to obtain the power necessary to detect a weak effect.

We similarly found an inconsistent pattern between spring arrival dates and stable-nitrogen isotopes in birds' tissues. Kirtland's warblers are unusual among parulids in that they eat substantial amounts of fruit and insects in both the breeding

and non-breeding seasons (Donner et al. 2009, Wunderle et al. 2010). The range of nitrogen isotopes that we found in Kirtland's warbler red blood cells indicates that different individuals consumed varying proportions of fruit vs. insect resources. When all years were pooled, the relationship between $\delta^{15}\text{N}$ and spring arrival dates was significantly negative, indicating that birds with a greater proportion of insects in their late winter diets were able to arrive earlier at spring breeding grounds. However, this relationship was not significant in any individual year. All five years of data were needed to detect the effect of $\delta^{15}\text{N}$, suggesting a weaker influence than we expected. We initially hypothesized that the higher fat and protein content of insects would make them a preferred food source when preparing for migration by increasing muscle mass and body fat. Behaviorally dominant wintering Hermit Thrush (*Catharus guttatus*) are able to maintain a more insectivorous diet from early to late winter, and consume fruit only when insects are less available (Diggs et al. 2011). In fact, fruit alone has been considered insufficient for maintaining body mass in other species of omnivorous songbirds (Levey and Karasov 1989, Blem 1990, Long and Stouffer 2003, Pearson et al. 2003).

However, there is some empirical evidence that both fruit and insects are important in Kirtland's warblers' winter diets, so the fact that we found an inconsistent or weak effect of $\delta^{15}\text{N}$ may be expected. Kirtland's warblers are found in early successional habitats in the Bahamas that have a greater abundance of key fruiting plants (particularly wild sage), and they have been observed to consume fruit frequently (69% of 499 foraging observations; Wunderle et al. 2010). The warblers also tend to track fruit abundance, with their numbers declining on sites where fruit

declines, and increasing on sites where fruit persists or increases over the winter (Wunderle et al. unpub. data). Thus, what constitutes a high-quality diet for wintering Kirtland's warblers may be more complicated than we previously thought. If insects are not clearly a higher quality food source during pre-migratory fattening, but rather a combination of fruit and insects is required, then perhaps we would expect to see a relatively weak effect of $\delta^{15}\text{N}$ on spring arrival timing. Additionally, severe nutritional stress can elevate $\delta^{15}\text{N}$ ratios because of increased protein catabolism (Hobson et al. 1993). If this was a factor, stressed birds consuming greater proportions of fruit could have higher $\delta^{15}\text{N}$ signatures than expected.

We found a negative relationship between δD and spring arrival timing overall and in 2006 alone, suggesting that males occupying more southerly islands in the Bahamas tended to arrive earlier to spring breeding areas, consistent with our predictions. This result corroborates other studies finding evidence for leapfrog migration patterns in other bird species, both in the New and Old Worlds (e.g., Bell 1996, Kelly et al. 2002, Kelly 2006, Reichlin et al. 2010; but see Mazerolle and Hobson 2007, Wilson et al. 2008, Langin et al. 2009). Leapfrog migration has both spatial and temporal aspects; a subpopulation of migrants wintering further south may bypass other subpopulations wintering further north by either migrating earlier, settling further north to breed, or both. In this case, birds departing from southern islands in the Bahamas may have passed over and preceded those wintering on northern islands in spring arrival (the breeding range of Kirtland's warblers is so narrow that all individuals breed at essentially the same latitude). However, there was no such relationship in 2007, nor when a potential outlier with a strong influence on

the overall pattern was removed, so our results are equivocal. The resolution of δD in precipitation within the relatively narrow latitudinal range of the Bahamas may not be high enough to differentiate between island regions. Based on the weak nature of the relationships we found between $\delta^{13}C$ and $\delta^{15}N$ and arrival dates, it may simply require more than two years of data to fully resolve δD patterns. Additional research on the carry-over effects of winter δD signatures could help determine the islands that better support overwintering Kirtland's warblers, and thus the islands on which to focus conservation efforts.

We found that $\delta^{13}C$, $\delta^{15}N$, and δD significantly predicted spring arrival timing of incoming Kirtland's warbler males in some years. Additionally, $\delta^{13}C$ was positively associated, and $\delta^{15}N$ was negatively associated, with arrival dates when all years were pooled. Other studies have found clearer significant relationships between winter habitat quality, as measured by $\delta^{13}C$, and body condition, spring arrival dates, return rates, and reproductive success of migratory birds (Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004, Studds and Marra 2005, Reudink et al. 2009, Smith et al. 2010). American redstarts (*Setophaga ruticilla*) and Northern waterthrush (*Parkesia noveboracensis*), in particular, are well-known to occupy a diversity of winter habitat types, ranging from wet mangrove forests to dry scrub (Marra et al. 1998, Studds and Marra 2005, Smith et al. 2010). For Kirtland's warblers that primarily winter in dry scrub habitats, interannual variation in rainfall drives arrival timing, reproduction, and survival (Rockwell et al. 2012, Rockwell et al. *in prep*), but the influence of $\delta^{13}C$ is less pronounced, suggesting it may be a weak indicator of habitat quality for this species. No previous studies have examined the carry-over

effects of winter $\delta^{15}\text{N}$ or δD , but these isotopes have the potential to further our knowledge of the integrated, year-round ecology of migratory birds that are omnivorous in winter, or that occupy a winter range with predictable patterns in precipitation δD .

Stable isotope analyses that remotely infer information about winter events have proven to be a powerful tool for elucidating the far-reaching effects of seasonal interactions, and have immensely improved our understanding of the full life cycle biology of migratory birds, yet they may not be appropriate for all species, under all wintering conditions. We emphasize the importance of understanding the natural history of the study species in the period of the annual cycle about which you infer information. Efforts to create isotopic maps for additional areas of the Caribbean and Central America will also aid in interpreting isotopic data. Continued research on the carry-over effects of winter events on spring arrival timing, survival, reproduction, and other aspects of migratory bird performance will help determine for how many species isotopic measurements of winter conditions are useful. Such information on seasonal interactions and the factors affecting migratory bird ecology throughout the annual cycle is critical for understanding population dynamics and creating effective conservation plans.

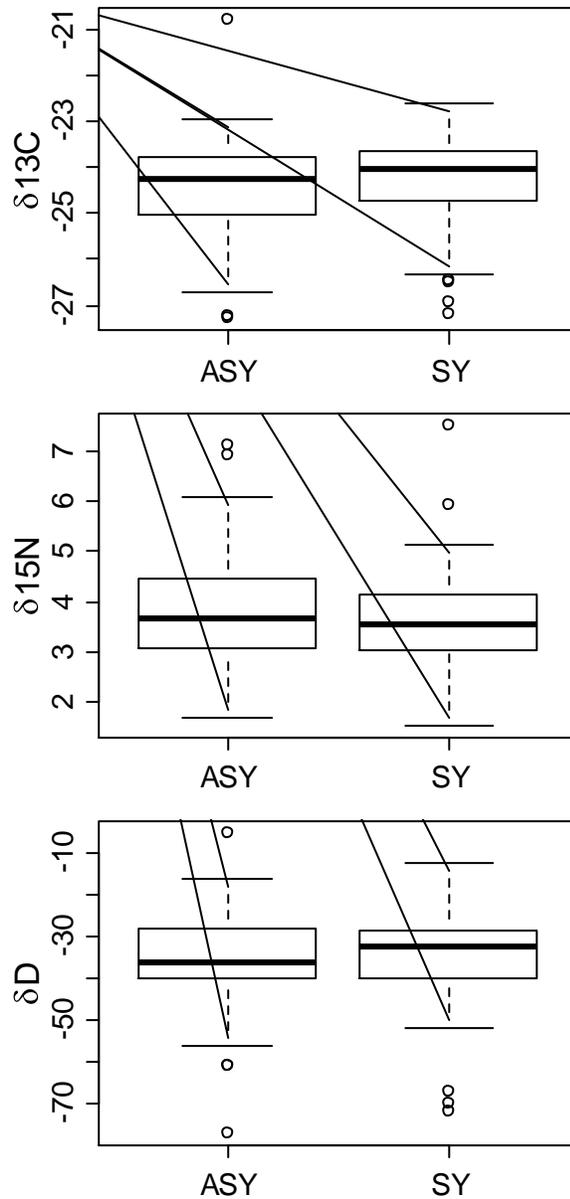


Figure 1. Variation in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and δD isotope ratios of Kirtland's warbler males captured upon arrival to Michigan breeding grounds from 2006 – 2010. Measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are from red blood cell samples, while δD values are from crown feathers molted in winter. Boxplots show the median and interquartile range, whiskers represent the interquartile range $\times 1.5$, and dots show datapoints outside of that range. Differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between age groups are marginally significant ($0.05 < P < 0.1$).

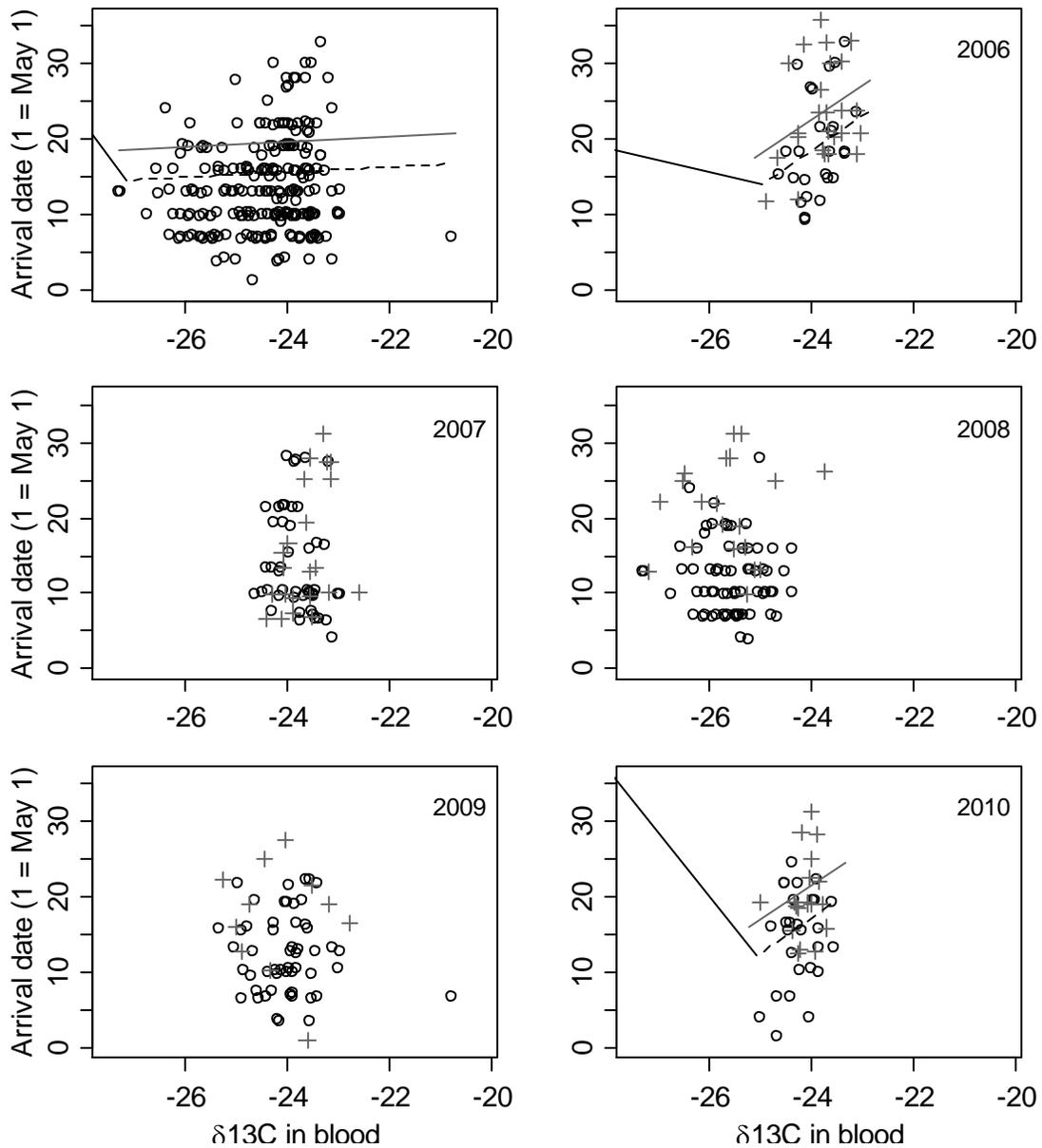


Figure 2. Relationships between $\delta^{13}\text{C}$ in red blood cells and spring arrival timing for male Kirtland's warblers sampled upon arrival to Michigan breeding grounds from 2006 – 2010. Each data point represents an individual bird, with ASY males as open circles and SY males as gray crosshatches. Top left panel shows data from all years combined; other panels show data from individual years. Fitted lines are from general linear mixed models including $\delta^{13}\text{C}$ and age as fixed effects, and breeding site (all panels) and individual bird ID and year (top left panel only) as random effects. Fitted lines are only shown where relationships are significant. ASY males are fitted with dashed black lines and SY males are fitted with solid gray lines.

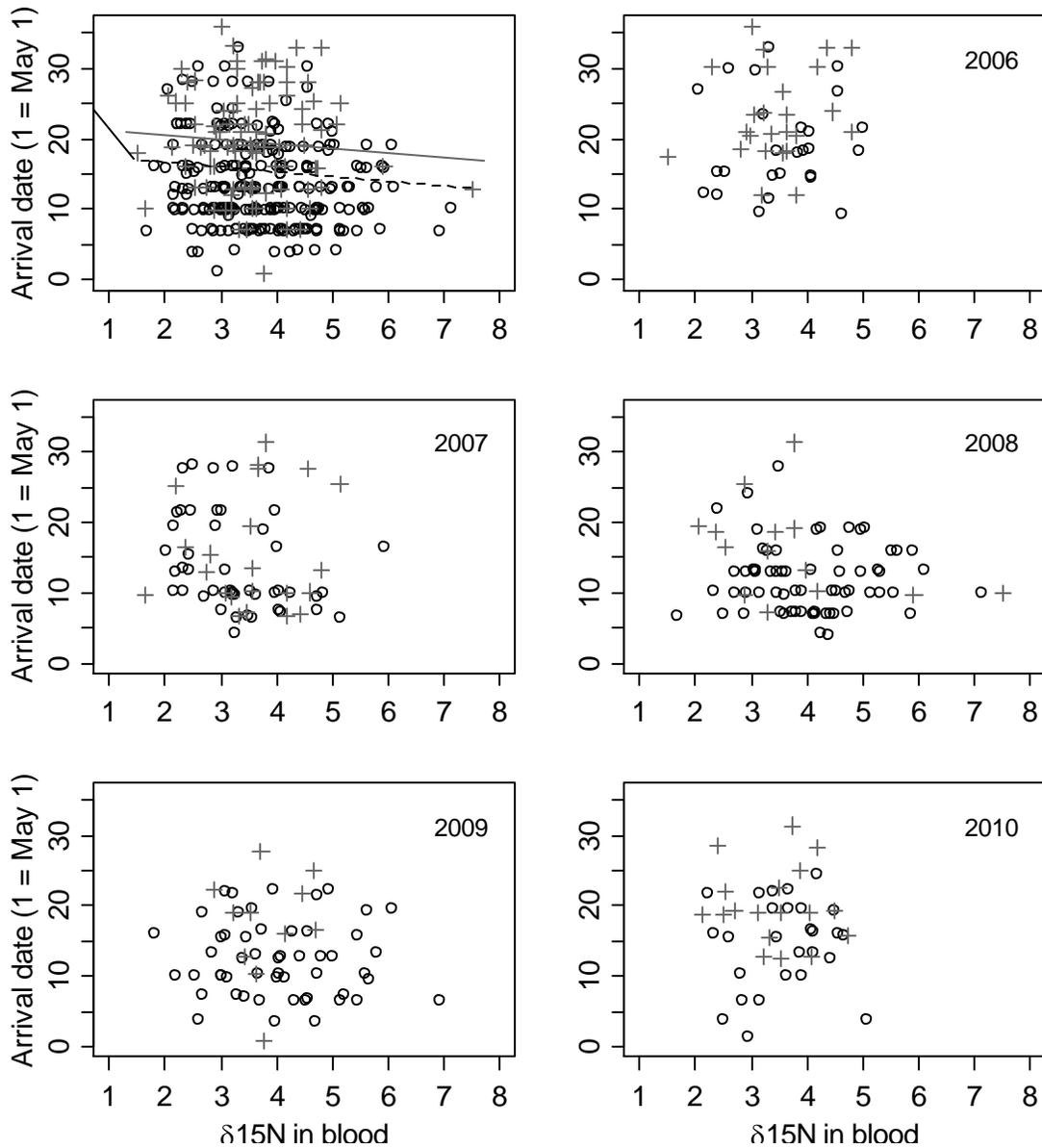


Figure 3. Relationships between $\delta^{15}\text{N}$ in red blood cells and spring arrival timing for male Kirtland's warblers sampled upon arrival to Michigan breeding grounds from 2006 – 2010. Each data point represents an individual bird, with ASY males as open circles and SY males as gray crosshatches. Top left panel shows data from all years combined; other panels show data from individual years. Fitted lines are from general linear mixed models including $\delta^{15}\text{N}$ and age as fixed effects, and breeding site (all panels) and individual bird ID and year (top left panel only) as random effects. Fitted lines are only shown where relationships are significant. ASY males are fitted with black dashed lines and SY males are fitted with gray solid lines.

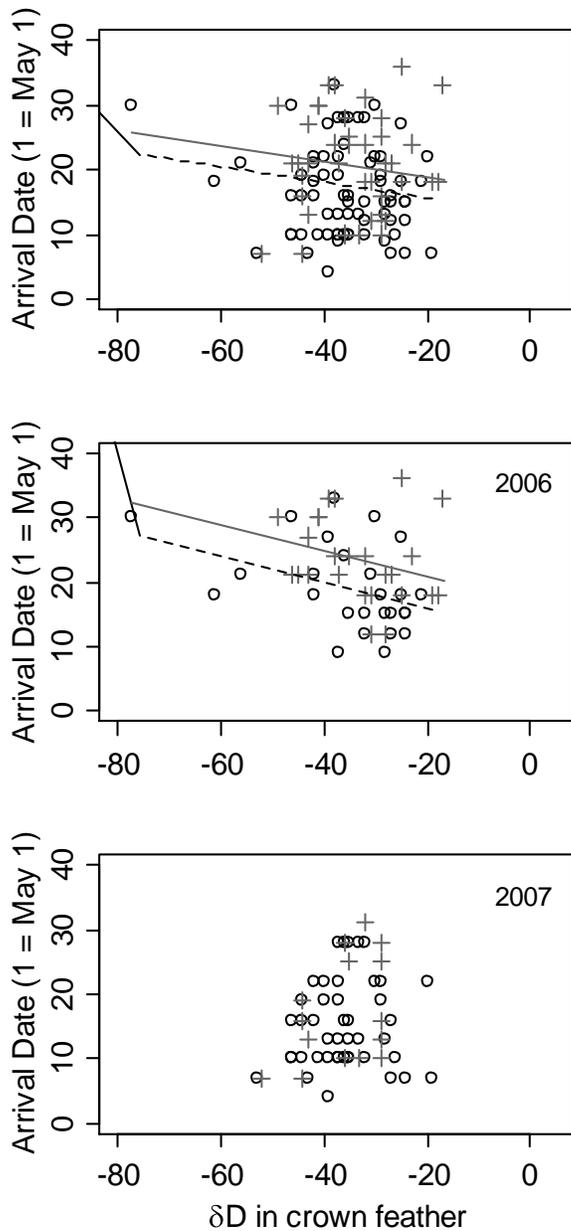


Figure 4. Relationships between δD in crown feathers and spring arrival timing for male Kirtland's warblers sampled upon arrival to Michigan breeding grounds from 2006 – 2007. Each data point represents an individual bird, with ASY males as open circles and SY males as gray crosshatches. Top panel shows data from all years combined; other panels show data from individual years. Fitted lines are from general linear mixed models including δD and age as fixed effects, and breeding site (all panels) and individual bird ID and year (top panel only) as random effects. Fitted lines are only shown where relationships are significant. ASY males are fitted with black dashed lines and SY males are fitted with gray solid lines.

Chapter 2: Carry-over effects of winter climate on spring arrival date and reproductive success of an endangered migratory bird, the Kirtland's warbler

Abstract.

Understanding how animals will adapt to climate change requires understanding how climate variables influence their biology year-round, and how events in different seasons interact. Migratory birds may be especially vulnerable due to the wide range of geographic areas that they depend on throughout the annual cycle. This study examines the potential effects of non-breeding season climate change on the breeding biology of the Kirtland's warbler (*Setophaga kirtlandii*), an endangered songbird that breeds in northern lower Michigan and winters in the Bahamas. Our objectives were to determine whether spring arrival dates on the breeding grounds are correlated with late winter rainfall in non-breeding areas and whether this has consequences for reproductive success. We used data on spring arrival dates and number of fledglings per year, sampling many individuals across multiple years, to show that males arrive on breeding grounds later following drier winters. There was a strong male age by rainfall interaction, indicating that first-time breeders were much more sensitive to changes in rainfall than experienced adults. Regardless of age, however, drier winters and delayed arrival and nest initiation were significantly associated with fewer offspring fledged. These results are important because the Caribbean region is currently experiencing a significant drying trend, and climate change models predict that the severity of this drought will continue to increase. Any resulting adjustments to the timing of migration could constrain spring

arrival dates and limit reproductive success for the endangered Kirtland's warbler, as well as other Neotropical migrants wintering in the Caribbean.

Introduction

Global climate change has clear and ecologically relevant effects on a diverse range of taxa (Walther et al. 2002, Parmesan 2006, Geyer et al. 2011). Understanding how species change, adapt and perhaps persist in the face of climate change first requires understanding how climate variables themselves influence an organism's biology during each phase of its life history. Neotropical-Nearctic migratory birds spend about 3-4 months on breeding areas, 6-7 months on wintering grounds, and 1-2 months on spring and fall migration each year. The wide range of geographic areas and habitats that they depend on throughout the annual cycle may make migratory birds especially vulnerable to the effects of climate change. Understanding how climate and climate change might influence the population dynamics of birds that travel between temperate breeding grounds and tropical wintering grounds has proven to be difficult, yet this information is critical for developing adaptive management plans. While many studies have highlighted the effects of warming in northern areas on the timing of arrival and breeding (Crick et al. 1997, Dunn and Winkler 1999, Butler 2003, Cotton 2003, Hüppop and Hüppop 2003, Ahola et al. 2004, Sparks et al. 2005), and the potential negative consequences for productivity (Visser et al. 1998, Both and Visser 2001, Both et al. 2010), researchers have only recently begun to recognize the importance of winter climate on migratory bird ecology (Sillett et al.

2000; Saino et al. 2004, 2007; Both et al. 2006; Studds and Marra 2007, 2011; Wilson et al. 2011).

A growing body of evidence suggests that ecological factors during the non-breeding season, including climate, can carry over to affect individuals and population processes in subsequent seasons (Runge and Marra, 2005), potentially limiting population sizes of migratory birds (Ryel 1981, Peach et al. 1991, Baillie and Peach 1992, Szép 1995). Measures of winter precipitation and primary productivity in Africa have been correlated with spring arrival and nest initiation dates of European migrants, suggesting that variation in overwintering precipitation among years can drive the timing of migration and breeding (Møller 2004, Saino et al. 2004, Gordo et al. 2005). Poor winter habitat quality is associated with poorer body condition during migration (Bearhop et al. 2004), delayed spring arrival on temperate breeding grounds and poorer condition upon arrival (Marra et al. 1998, Gill et al. 2001), later breeding dates (Norris et al. 2004, Saino et al. 2004), reduced reproductive success (Norris et al. 2004, Reudink et al. 2009), and lower return rates of migratory birds (Studds and Marra 2005). These carry-over effects likely originate from variation in resource abundance on the wintering grounds. Differences in food availability across non-breeding season habitats affect multiple measures of overwintering migratory bird performance, including site persistence (Strong and Sherry 2000, Latta and Faaborg 2002), body condition (Strong and Sherry 2000, Marra and Holmes 2001, Latta and Faaborg 2002, Studds and Marra 2005, Brown and Sherry 2006, Smith et al. 2010), and corticosterone levels (Marra and Holberton 1998). The ability to maintain body condition throughout the non-breeding season in particular appears to

constrain an individual birds' ability to depart on spring migration (Marra et al. 1998; Studds and Marra 2005, 2007, 2011).

Rainfall is a major factor driving this variation in winter food abundance, particularly the availability of phytophagous insects (Janzen 1973; Wolda 1978; Studds and Marra 2007, 2011). Many areas of the Neotropics experience a period of late winter drought that is linked to seasonal declines in insect availability (Lefebvre et al. 1994, Parrish and Sherry 1994, Brown and Sherry 2006, Smith et al. 2010). Reduced rainfall at the end of the winter dry season limits food resources at the same time that birds must build muscle and fat reserves in preparation for an energetically demanding migration. Measures of rainfall have been directly linked to body condition (Studds and Marra 2007) and rates of fat deposition (Smith et al. 2010) in overwintering migratory birds, across both habitats and years. In a longitudinal study of individual American redstarts (*Setophaga ruticilla*), differences in winter rainfall among years influenced both insect biomass on territories and spring departure dates (Studds and Marra 2011). Additional evidence from redstarts shows that spatial variation in rainfall across their winter range explains spring arrival dates in different breeding populations (McKellar et al. *in review*).

Overwinter rainfall is also positively correlated with annual survival (Peach et al. 1991, Szép 1995) and population size on the breeding grounds (Peach et al. 1991, Baillie and Peach 1992), in Palearctic migratory species. Similarly, the focal species of this study, the Kirtland's warbler, showed a positive relationship between winter rainfall and the number of singing males observed on the breeding grounds in the subsequent spring, from 1971-1980 (Ryel 1981). Additionally, the population

abundance of American redstarts in eastern North America increased after years of higher rainfall and primary productivity in the Caribbean where they overwinter (Wilson et al. 2011). The El Niño Southern Oscillation Index (SOI), a large-scale climate index related to winter rainfall in the Neotropics (Rogers 1988), is correlated with adult survival, fecundity, and recruitment of young in several Neotropical migratory bird species, with the direction of the relationship dependent on how the wintering grounds are affected by SOI (Sillett et al. 2000, Nott et al. 2002, Mazerolle et al. 2005). Taken together, these studies demonstrate the critical importance of the winter period. Weather conditions at this time, regardless if measured by rainfall or indirectly by SOI, have important consequences for populations of migratory birds. Winter rainfall has biologically relevant effects on individuals, likely through its effects on food abundance, which can carry over to affect multiple aspects of individual condition and demographic processes in subsequent seasons.

This study examines the effects of winter climate on spring arrival dates, body condition, and reproductive success in the Kirtland's warbler, an endangered songbird that breeds in northern lower Michigan and winters primarily in the Bahamas. Management of breeding habitat has led to a substantial increase in the warbler population. However, limiting factors on the Bahamian wintering grounds and how they carry over to influence breeding ground events remain poorly studied in this species, which could undermine current conservation efforts. To provide information for threat analyses and improve management plans, it is essential to explore how events in winter may affect Kirtland's warblers in subsequent seasons. Here, using a longitudinal analysis (i.e., the same color-banded birds across years), we test the

hypothesis that spring arrival dates, condition upon arrival, and reproductive success are correlated with late winter rainfall in the Bahamas. The Kirtland's warbler is an excellent study species for these questions. Its limited winter range allows us to use rainfall measures from a specific geographic area that our study population on the breeding grounds is known to occupy in winter, unlike other studies that must estimate weather conditions generalized across a large winter range. We predicted that individual males would arrive later on northern breeding grounds and in poorer condition following winters with less rainfall, and that this would have negative consequences for within-year reproduction. To our knowledge, this is the first longitudinal study to examine the effects of winter rainfall on spring arrival dates, body condition, and reproductive success in a Neotropical migratory bird.

Methods

Study species. The Kirtland's warbler is a large parulid that breeds almost exclusively in northern Michigan (Mayfield 1992), with a few small satellite populations in Wisconsin (Trick et al. 2008) and Ontario (Richard 2008). This warbler is a disturbance-adapted species, specializing in Jack pine (*Pinus banksiana*) barrens that were historically maintained by wildfires. They prefer large (> 32 ha), fairly homogenous stands of Jack pine that grow on well-drained, sandy soils. Stands must be relatively young (between 5-15 years old) to attract Kirtland's warblers, and the canopy in these areas is fairly short (1.4 – 5.0 m) (Mayfield 1960, Walkinshaw 1983). Kirtland's warblers spend the non-breeding season throughout the Bahamian archipelago, including the Turks and Caicos (Sykes and Clench 1998). They occupy

early successional habitats in winter as well, such as second-growth, broadleaf scrub or low coppice, which are maintained by anthropogenic disturbance, fire, and hurricanes (Sykes and Clench 1998, Wunderle et al. 2007). Unlike most other warblers, Kirtland's consume both fruit and arthropods in the breeding and non-breeding periods (Deloria-Sheffield et al. 2001, Wunderle et al. 2010).

Heavy brood parasitism by the Brown-headed cowbird (*Molothrus ater*), and limited availability of young Jack pine habitat due to modern fire suppression practices led to a precipitous decline in Kirtland's warbler numbers. They were listed as a federally endangered species in 1973 (Byelich et al. 1976). Currently, 190,000 acres are designated Kirtland's Warbler Management Areas, and these are managed on a 50-year rotation so that 38,000 acres of pine barrens are of an appropriate age for nesting at all times (Bocetti et al. 2002). Nearly all stands are whole-tree harvested and then replanted with 2-year old Jack pines. These management efforts, plus several natural wildfires, greatly increased the amount of suitable habitat available to Kirtland's warblers in recent decades. In addition, an extensive cowbird control program has significantly improved nesting success (Kelly and DeCapita 1982, Walkinshaw 1983, Kepler et al. 1996). In response, the population has since increased steadily from an estimated 200 singing males in the 1970s and 1980s to approximately 1800 in 2011 (USFWS 2011).

Field sites. Our study sites included ten 30-ha plots located in Alcona, Crawford, Iosco, Ogemaw, and Oscoda counties in northern Lower Michigan (Figure 5). Each plot was established using GPS, and the borders were marked with forest flagging. Study plots were characterized by young Jack pine stands (6-15 years old)

interspersed with deciduous trees, particularly northern pin oak (*Quercus ellipsoidalis*) and sand cherry (*Prunus pumila*). Ground cover species found in the understory of this habitat, such as lowbush blueberry (*Vaccinium angustifolium*), bearberry (*Arctostaphylos uva-ursi*), sweet fern (*Comptonia peregrina*), and Pennsylvania sedge (*Carex pensylvanica*) provide important forage and nesting cover (Walkinshaw 1983, Bocetti 1994, Probst and Donnerwright 2003).

Capturing birds and determining arrival dates. Study plots were monitored every three days beginning May 1 for the arrival of new males from 2006 - 2010. Plots were surveyed by multiple observers walking along transects 200-300m apart across the study area and listening for singing males. Male Kirtland's warbler song is loud and can easily be heard across these distances (Probst et al. 2005). Each singing male was located and observed to determine whether it was banded. Arrival dates were recorded as the first day in the 3-day survey interval in which the bird was first seen (e.g., males first observed on May 1, 2, or 3 were recorded as arrival date 1). Days numbered starting with May 1 are used throughout (1 = May 1). We recorded a total of 483 arrival dates for 306 individual males (2006, $n = 51$; 2007, $n = 99$; 2008, $n = 118$; 2009, $n = 113$; 2010, $n = 102$). Males were captured soon after arrival (always < 7 days, though 74% were captured on the day of first observation, and 92% were captured by the second site visit after arrival). We used mist nets and song playback to target-net males, and then marked them with a unique combination of three color bands and one numbered USGS aluminum band. Males were aged as either first-time breeders (second-years; SY) or adults returning to breed (after second-years; ASY) using plumage characteristics (Probst et al. 2007). Morphometric

measurements (mass, tarsus, wing, tail, and culmen length) were taken at the time of capture. Body condition upon arrival was measured by taking the linear residual of the first principal component (PC1) of tarsus, wing, tail and culmen length regressed over mass. We were unable to reliably capture or determine arrival dates for females, which are much less conspicuous in the field and do not respond consistently to playback.

Reproductive success. From 2007 – 2009, we located nests of banded males and monitored them to record reproductive success. Nests were checked approximately every 3 days to determine critical events such as clutch initiation, hatching, and fledging dates. Nest initiation, or first-egg date, was defined as the day the first egg was laid in the first nest attempt of the year for an individual male. Nests initiated after the third week of June could not be positively determined to be first nest attempts, and were excluded from analyses using first-egg date. In cases where the nest was found with eggs or nestlings, first-egg date was estimated by subtracting the mean length of the nestling and/or incubation periods from the fledging or hatching date (Mayfield 1992). Reproductive success per nest was measured by the number of potential fledglings present on day 6 of the 9-day nestling period. Because depredation typically means the loss of the entire nest, the number of nestlings present on day 6 can be used as the best estimate of the number of successful fledglings (Bocetti 1994). Fledging of young was confirmed by returning to the parental territory after 1-3 days and looking for fledglings or indicative parental behaviors (food-carrying, alarm calls, etc.). If we were unable to confirm the fledging of any young after four additional visits, we recorded the nest fate as depredated.

Second nest attempts and re-nests after depredation were also located, and annual reproductive success for each male was recorded as the total number of fledglings for the breeding season. We determined yearly reproductive success 232 times for 169 individual males (2007, $n = 53$; 2008, $n = 96$; 2009, $n = 83$).

Climate Data. Monthly precipitation data for the Bahamas (Nassau Airport station) were retrieved from the National Climatic Data Center of the National Oceanic and Atmospheric Association (<http://www7.ncdc.noaa.gov/IPS/mcdw/mcdw.html>). To evaluate which metric to use in our final models, we initially tested several measures of winter rain in the Bahamas, including total winter rainfall (October-April), late winter rainfall (February-April), and March rainfall. Models including March rainfall had the best fit given the data for explaining both arrival dates and reproductive success, as determined by Akaike's Information Criterion (AIC). March (the month immediately prior to spring departure) may reflect the peak of the critical winter drought period, and March rainfall has been shown to be the best predictor of departure dates from nonbreeding areas in other migratory species (Studds and Marra 2011). March rainfall in the Bahamas ranged from 1.09 to 5.41 cm over the course of the study.

Statistical analyses. The effects of March rainfall on spring arrival date and reproductive success of Kirtland's warblers were analyzed using general linear mixed models with random intercepts fit for each bird. This repeated measures approach accounted for the lack of independence among birds that were sampled in multiple years, and controlled for individual effects. The full models also contained fixed effects for age, March rainfall, and their two-way interaction, and a random effect of

study site. We determined the significance of each variable by iteratively removing it from the full model and comparing the reduced to the full model using a chi-squared likelihood ratio test with one degree of freedom. Non-significant interactions were not included in final models. We tested the effect of March rainfall on body condition during spring arrival in the same way, except that time of capture was added as a covariate.

We used the same approach to analyze the relationship between arrival dates and first-egg dates or reproductive success. The full general linear mixed model included random effects of individual bird ID and breeding site, and fixed effects for age, arrival date, and their two-way interaction. Variable significance was assessed as described above, and non-significant interactions were removed from final models. All analyses were performed with program R (R Core Development Team 1999). All error estimates are given as standard errors (SE).

Results

Arrival dates and reproductive success. Male Kirtland's warblers returning to northern breeding areas had arrival dates ranging from May 2 to June 5, with a global mean of day 14.6 (± 0.36 days SE). We observed a total of 483 spring arrival events for 306 individual males, recording 120 arrival dates of second-year males and 363 of older males. One male was recorded in all 5 years, 11 were recorded in 4 years, 37 in three years, 66 in two years, and the remaining 191 individuals were observed in only one year. Males that arrived earlier on spring breeding grounds had mates that initiated clutches earlier (arrival date: $\chi^2 = 89.8$, $df = 1$, $P < 0.001$; Figure 6a). Early

arriving males also fledged more offspring (arrival date: $\chi^2 = 89.5$, $df = 1$, $P < 0.001$; Figure 6b), and the slope of this relationship did not vary with age (arrival date \times age: $\chi^2 = 0.15$, $df = 1$, $P = 0.70$). A 10-day delay in arrival was on average associated with 0.74 fewer fledglings raised, equivalent to a difference in reproductive success of more than 2.5 fledglings/year across the range of spring arrival dates in this study ($\beta = -0.074 \pm 0.03$ SE; Figure 6b). Additionally, clutch size of the first nest attempt of the year decreased significantly with first-egg date (first-egg date: $\chi^2 = 18.83$, $df = 1$, $P < 0.001$).

Winter rainfall, spring arrival, and body condition. Adult male Kirtland's warblers arrived at spring breeding grounds in advance of second-year males (age: $\chi^2 = 41.18$, $df = 1$, $P < 0.001$) within the range of March rainfall observed in our study, but there was a strong rainfall \times age interaction (rainfall \times age: $\chi^2 = 10.48$, $df = 1$, $P = 0.001$). Second-year males delayed arrival by 1.4 days for every 1 cm reduction in March rainfall (SY males: $\beta = -1.42 \pm 0.40$ SE; Figure 7a), while arrival dates of adult males remained relatively constant (ASY males: $\beta = -0.12 \pm 0.19$ SE; Figure 7a). The random variable, breeding site, also added a significant amount of explanatory power to the model (site: $\chi^2 = 11.04$, $df = 1$, $P < 0.001$).

The body condition of males arriving in Michigan was positively related to Bahamian March rainfall ($\beta = 0.02 \pm 0.02$ SE), but the effect size was small and not significant (rainfall: $\chi^2 = 1.09$, $df = 1$, $P = 0.30$). Adult males arrived in significantly better body condition than second-year males (age: $\chi^2 = 5.15$, $df = 1$, $P = 0.023$), and males arriving at different breeding sites did not differ in condition (site: $\chi^2 = 0$, $df = 1$, $P = 1$).

Winter rainfall and reproductive success. To determine the effect of winter rainfall on the number of young fledged, we recorded annual reproductive success 232 times for 169 individual males, including 50 SYs, and 182 ASYs. The reproductive success of five males was recorded in all three years, 53 were recorded in two years, and the remaining 111 individuals were recorded in one year. Male annual reproductive success ranged from 0 to 10 offspring, with a global mean of 3.3 (± 0.16 SE). No males had more than two successful nests, and only one male attempted three nests within a single breeding season. Adult males raised significantly more fledglings than second-year males (age: $\chi^2 = 28.39$, $df = 1$, $P < 0.001$), and all males fledged more offspring following Marches with more rainfall (rainfall: $\chi^2 = 7.1$, $df = 1$, $P = 0.007$). On average, Kirtland's warbler males raised 0.23 additional fledglings for every 1 cm increase in March rainfall ($\beta = 0.23 \pm 0.09$ SE; Figure 7b), and this pattern did not vary between age classes (rainfall \times age: $\chi^2 = 0.11$, $df = 1$, $P = 0.74$). The random effect of breeding site also influenced reproductive success (site: $\chi^2 = 16.42$, $df = 1$, $P < 0.001$).

Discussion

We found strong evidence for carry-over effects originating from winter rainfall that influenced arrival dates and the number of young fledged in the endangered Kirtland's warbler. This is the first longitudinal study to document a relationship between winter rainfall, spring arrival dates, and reproductive success of individual migratory birds. Young males arrived in northern breeding areas later following winters with less March rainfall in the Bahamas, and both young and older

males had reduced reproductive success following drier winters. Our ability to test the response of the same individual males to variation in winter rainfall across multiple years allowed us to account for variation due to individual quality. We also incorporated full reproductive histories of banded individuals, including second nests and nests with second females (polygyny), providing the most accurate measure of reproductive success per male possible in the absence of information on extrapair paternity. In addition, the small and highly connected wintering and breeding areas of this species allowed us to use late winter rainfall estimates from a more geographically accurate wintering area. We were able to better isolate the winter conditions that our study population experienced, unlike other studies that must estimate winter locality and associated weather conditions across a large winter range.

The relationship between March rainfall and arrival time was much stronger for SY than ASY males (Figure 7a), with younger males delaying arrival by 1.4 days for every one centimeter reduction in precipitation. Two non-mutually exclusive explanations for this pattern are possible. First, ASYs may be socially dominant, and claim winter territories that are more likely to retain moisture, even through the late winter drought season. Young males that occupy poorer quality habitats in winter would then be disproportionately affected by the decrease in rainfall and food availability in drier winters. In support of this, ASY males do exhibit higher overwinter site persistence and increase pre-migration body condition faster than SY males and females, suggesting that such dominance relationships exist (J. M. Wunderle, unpubl. data). However, Kirtland's warblers appear to have flexible home ranges in winter rather than strict territories like other well-studied migratory species,

such as the American redstart (Marra and Holmes 2001). Instead, some individuals will readily shift locations over the course of the winter as they track diminishing food resources (Wunderle et al. 2010). Home ranges can overlap considerably, especially in late winter when fruit and insects become scarce because of seasonal drought (Wunderle et al. 2010). A second hypothesis is that SY males may simply have less experience in tracking these patchy resources, and are therefore unable to maintain body condition and advance migratory fattening as well as ASY males in dry conditions (Smith et al. 2010). Adult Kirtland's warbler males increase pre-migration body condition significantly faster than young males (J. M. Wunderle, unpubl. data), which is consistent with both hypotheses. In either case, young males in poorer condition prior to spring migration are likely to arrive later on breeding grounds following drier winters, while the arrival schedules of older males are less affected by winter drought conditions.

We found that males of all age classes were able to increase productivity by an average of 0.23 fledglings per year for every one centimeter increase in March rainfall (Figure 7b). Within the observed range of precipitation during our study (1.09 to 5.41 cm), this could account for a difference of one fledgling per male per year. This pattern cannot be explained exclusively through earlier male arrival following wet winters, because only younger males advanced arrival in response to increased winter rain. Older males that were able to maintain arrival schedules regardless of winter rainfall levels still experienced reduced reproductive success following drier winters. This is likely because females arrived later or in poorer condition after winters with less rainfall. Arrival date and body condition of females may have more

influence on reproductive success because of their need to acquire the resources necessary to produce a clutch. Kirtland's warbler females may occupy poorer quality habitats that are less buffered against seasonal desiccation, making them more vulnerable to winter drought, similar to SY males. Social dominance of adult males over younger males and females (Marra and Holmes 2001) and sexual habitat segregation in winter (Wunderle 1995, Latta and Faaborg 2002) has been documented in other migratory bird species. The fact that adult males increase pre-migration body condition faster than females (J. M. Wunderle, unpubl. data), suggests that older males may exclude females from the best winter habitats in Kirtland's warblers as well. Unfortunately, we were unable to reliably capture females or record their arrival dates, so the prediction that female arrival dates would also be sensitive to winter rainfall remains untested.

We found no relationship between March rainfall and the body condition of males upon spring arrival, even though preliminary evidence from the Bahamas indicates that winter drought in February-March is significantly associated with reduced body condition of Kirtland's warblers in March-April, prior to departure (J. M. Wunderle, unpubl. data). It is possible that individuals in poor condition prior to spring departure may be forced to stay longer on the wintering grounds or migrate slower to compensate for a body condition deficit after dry winters. This would result in later arrival for some males, but relatively equal post-migration body condition. Without departure dates from the Bahamas, we could not determine whether the later spring arrival dates we documented were the result of delayed spring departure or an extended migratory period. If either strategy allows males the time they need to

forage and sufficiently regain muscle tissue and improve body condition, then we would expect to see the differences we observed in spring arrival dates without corresponding variation in body condition upon arrival.

Kirtland's warbler males had mates that delayed clutch initiation by 0.39 days for each day the male arrived later at spring breeding grounds (Figure 6a).

Reproductive success also decreased significantly with later spring arrival, at a rate of 0.74 fewer fledglings per year for each 10-day delay in arrival (Figure 6b). This difference is likely to be biologically important, because the range of arrival dates of males in our study was over 30 days, leading to a difference in male annual reproduction of more than 2 whole fledglings (Figure 6b). We were unable to evaluate the number of offspring sired via extrapair paternity; thus, there were unmeasured components of reproductive success. However, early-arriving males of other migratory species tend to sire more extrapair offspring than late-arriving males (Reudink et al. 2009), which would exacerbate differences due to arrival dates. This likely only made our test more conservative, rather than changed the overall patterns we found. The timing of breeding is a major determinant of fitness in migratory birds, and our results corroborate many other studies reporting a negative correlation between spring arrival or clutch initiation dates and reproductive success (Perrins 1970, Lozano et al. 1996, Potti 1998, Poirier et al. 2004, Smith and Moore 2005, Reudink et al. 2009). The penalties of later arrival can occur through several mechanisms. Late-arriving males may have reduced access to the best territories and/or mates (Møller 1994, Lozano et al. 1996, Smith and Moore 2005). Delayed arrival may decrease the length of the breeding season, reducing the frequency of re-

nests and second clutches (Marra et al. 1998, Visser et al. 2003, Norris et al. 2004). A delay in the timing of breeding may shift the period of peak nestling demand past the time of peak food availability, disrupting an important synchrony between these events (Visser et al. 1998, Both and Visser 2001). Finally, clutch sizes tend to be smaller later in the season, and hatching failure of some species may be greater (Perrins 1970, Martin 1987, Rowe et al. 1994). The clutch size of the first nest attempt of the year of Kirtland's warblers decreases significantly with first-egg date, even among the same individual males (see Results). In fact, there appears to be a threshold where males that arrive after a certain date are unable to complete more than one successful nest per season. No males arriving after May 19 were able to raise more than 5 fledglings in a year, the clutch size of a typical nest (Figure 6b), or to complete two successful nesting cycles (S. M. Rockwell, unpubl. data).

Our findings support other studies suggesting that migratory bird populations are limited by winter climate. Winter rainfall and food availability are tightly linked in the tropics (Janzen 1973; Wolda 1978; Studds and Marra 2007, 2011), and this relationship can affect overwinter performance of migratory birds (Strong and Sherry 2000; Marra and Holmes 2001; Latta and Faaborg 2002; Studds and Marra 2005, 2007, 2011; Brown and Sherry 2006; Smith et al. 2010). In turn, poor overwinter condition and delayed departure dates from wintering grounds can lead to later spring arrival and poorer condition upon arrival (Marra et al. 1998). Wetter conditions in migratory birds' wintering grounds, measured by the El Niño Southern Oscillation Index (SOI), are associated with increased number of young in the subsequent breeding season (Mazerolle et al. 2005, Nott et al. 2002). Winters with more rainfall

are also correlated with greater population sizes of migratory birds in the following year (Ryel 1981, Baille and Peach 1992, Peach et al. 1991, Wilson et al. 2011). Our finding that winter rainfall is correlated with arrival dates on breeding areas and reproductive success augments existing evidence that winter weather can carry over to affect population processes during the subsequent breeding season (Peach et al. 1991, Baille and Peach 1992, Szép 1995, Saino et al. 2004, Reudink et al. 2009, Wilson et al. 2011, McKellar et al. *in review*). Previous research has demonstrated that winter rain could regulate the population size of Kirtland's warblers even when they numbered far fewer than they do today (Ryel 1981). Combined with our results and evidence from current field studies in the Bahamas showing that winter home ranges overlap as the drought season progresses (Wunderle et al. 2010), and that adult males may competitively exclude others from accessing resources (J. M. Wunderle, unpubl. data), this means that the Kirtland's warbler population is likely to be at least partially limited by events on the wintering grounds.

We have demonstrated that variation in rainfall in subtropical wintering areas among years influences reproductive success of Kirtland's warblers thousands of kilometers away on temperate breeding grounds. While the duration of this study (five years) was not sufficient to detect long-term trends in either winter climate or reproductive success, the dependence of this species on such a restricted winter range increases the population's vulnerability to future climate change in that region. Significant drying trends in the Caribbean are predicted by several climate models (Neelin et al. 2006). The Bahamas have already experienced a decline in precipitation from 1959-1990, with rainfall decreasing by 10% on Inagua Island and by 14% on

Long Island (Martin and Weech 2001), likely causing a corresponding reduction in food resources in the pre-migratory period. Any resulting constraints on the timing of migration and spring arrival are likely to further limit productivity, with negative effects on the population dynamics of the endangered Kirtland's warbler. Many other Neotropical migrants also winter in the Caribbean, and all of these species have the potential to be negatively affected by prolonged drying trends as well. Our study highlights the importance of creating conservation partnerships to protect quality habitats for migratory birds on wintering areas as well as breeding areas. To better understand how migratory animals are affected by a changing climate, it is essential to study factors throughout the annual cycle. Only through such a comprehensive and integrated approach will be able to make accurate predictions regarding how populations will respond to and possibly adapt to a changing climate.

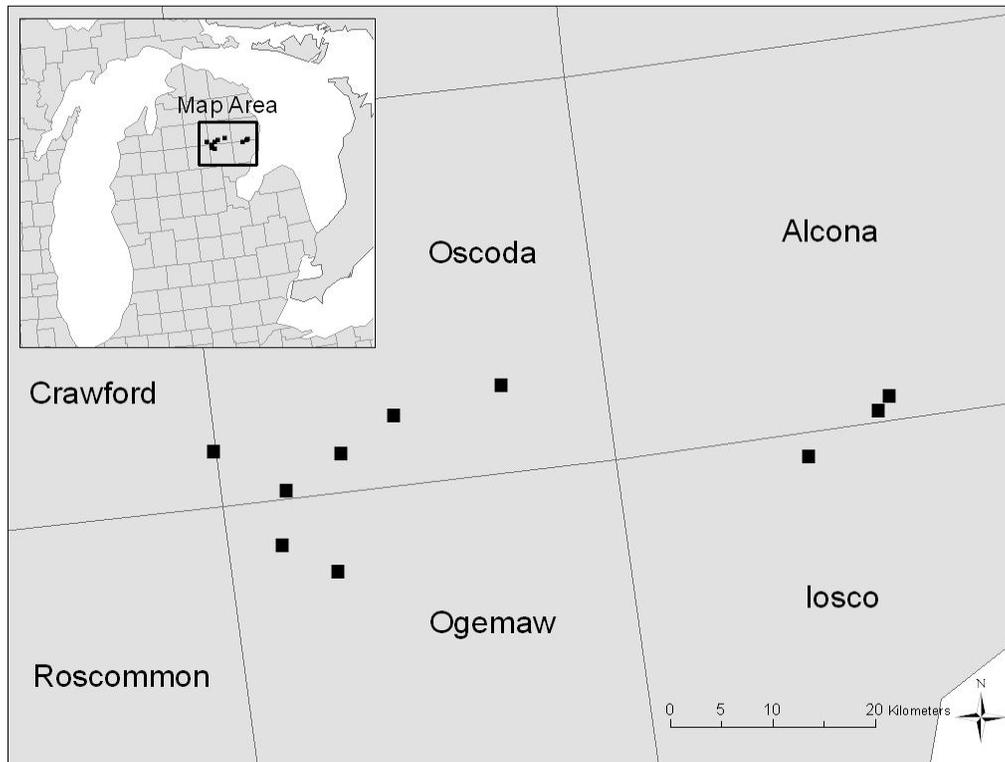


Figure 5. Distribution of ten 30-hectare study sites, located within Kirtland's Warbler Management Areas in the northern lower peninsula of Michigan, and used from 2006-2010.

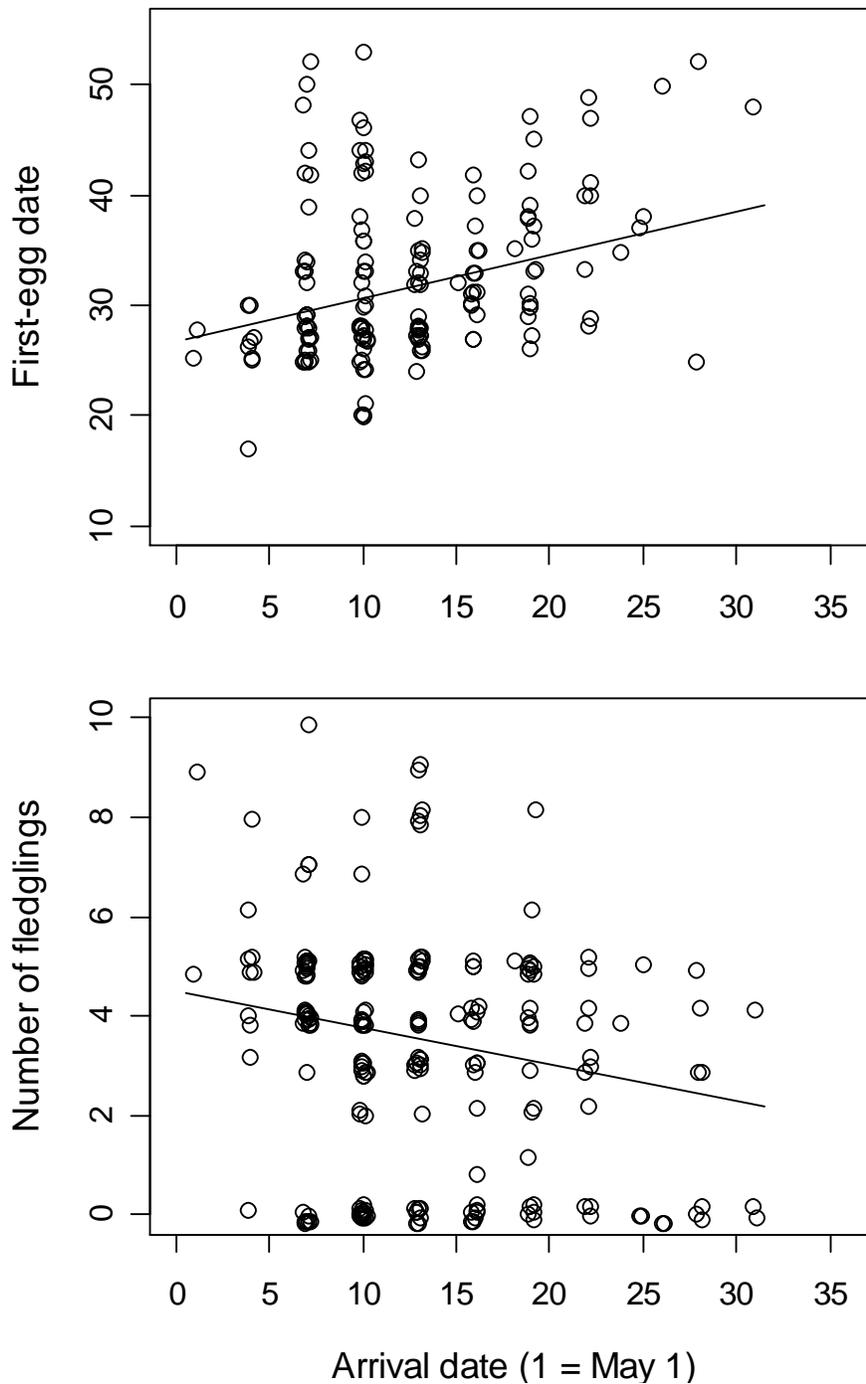


Figure 6. Spring arrival dates at breeding grounds explain (a) first-egg dates and (b) yearly reproductive success (number of fledglings per male per season) of male Kirtland's warblers of all age classes combined. Data were collected in northern Lower Michigan from 2007-2009. Each data point represents an individual bird. Fitted lines are from repeated measures general linear mixed models with age and arrival date as fixed effects, and breeding site and individual bird ID as random effects.

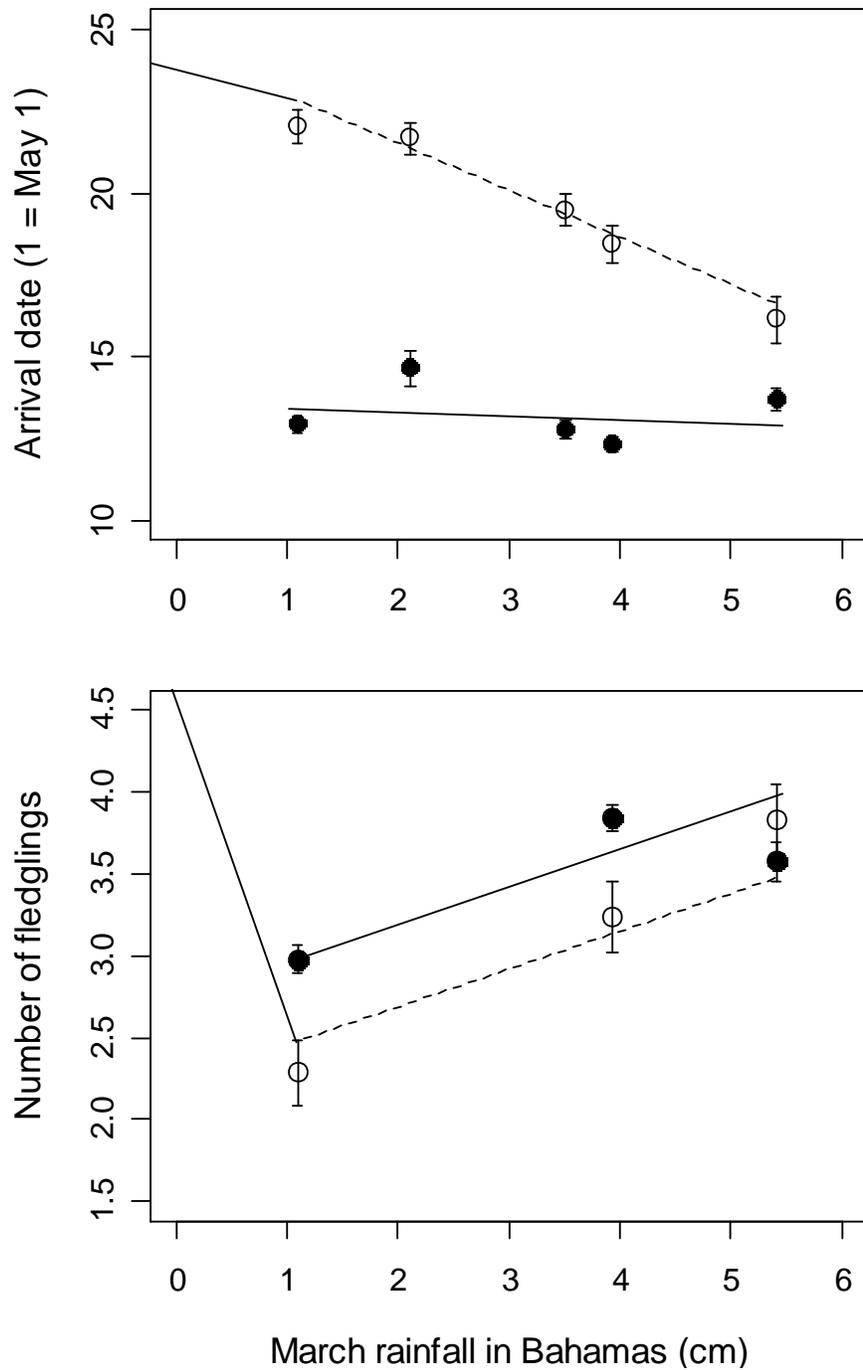


Figure 7. Total March rainfall in the Bahamas predicts (a) spring arrival dates from 2006-2010 and (b) yearly reproductive success (number of fledglings per male per season) from 2007-2009 of male Kirtland's warblers in northern Lower Michigan. Data points are predicted values (mean \pm SE) from a repeated measures general linear mixed model with age and March rainfall as fixed effects, and breeding site and individual bird ID as random effects. ASY males are represented by filled circles with a solid fitted line, while SY males are represented by open circles with a dashed fitted line.

Chapter 3: Carry-over effects of winter precipitation drive annual survival of a migratory songbird, with estimation of seasonal survival rates

Abstract.

Conserving and managing populations of migratory animals requires information about seasonal survival rates, data that are lacking for virtually all avian species. Here we estimate annual, oversummer, overwinter, and migratory period survival for the Kirtland's warbler (*Setophaga kirtlandii*), an endangered songbird that breeds in northern lower Michigan and winters in the Bahamas archipelago. We also assess the influence of multiple summer and winter climate variables on annual survival. We used Cormack-Jolly-Seber models to analyze two mark-recapture datasets (Michigan 2006-2011 and Bahamas 2003-2010), encompassing a total of 554 individuals over 8 years. Mean annual survival probability of adult male Kirtland's warblers was 0.58 ± 0.11 SE from 2006 to 2011. Survival rates during the summer and winter stationary periods were relatively high (0.862 ± 0.06 SE and 0.902 ± 0.06 SE, respectively). Survival during the migratory periods was lower (0.745 ± 0.18 SE), accounting for ~50% of all annual mortality. We modeled the effects of multiple winter, summer, and large-scale climate variables on annual Kirtland's warbler survival, in relation to a constant-survival model. In a model selection framework, March rainfall in the Bahamas was the best-supported model of survival, and was positively correlated with apparent annual survival in the subsequent year, suggesting that winter precipitation carried over to influence survival probability in later seasons. Projection modeling revealed that a >18% decrease in March rainfall from its current

mean may cause population growth rates of this species to become negative. Our results suggest that increased drought during the non-breeding season, which is predicted to occur under several climate change scenarios, could have important ecological consequences on annual survival and population growth rate of the endangered Kirtland's warbler.

Introduction

Factors that limit populations of migratory animals remain poorly understood, largely due to the difficulty of tracking individuals over long distances and across seasons, and measuring their vital rates. Migratory behavior is exhibited by the majority of birds breeding at temperate latitudes, allowing them to exploit abundant but transitory resources in the north, yet also requiring them to move, forage and avoid predators in multiple habitat types across temperate and tropical regions. Changes in climate and/or habitats that migratory birds occupy in any portion of the annual cycle may affect their population dynamics (Sherry and Holmes 1995, Newton 2007), so identifying the 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 of migratory animals (Fretwell 1972, Webster et al. 2002).

Few reliable estimates of age- or season-specific survival exist for migratory bird species (Faaborg et al. 2010), especially for populations linked geographically throughout the year. Such estimates are particularly needed for threatened and

endangered species if conservation goals include identifying limiting factors and reducing potential threats. Our lack of knowledge regarding how migration shapes variation in survival rates, and when during the annual cycle that mortalities occur, extends to other migratory taxa (Hedenström et al. 2011). Indeed, recent population declines observed in species of migratory animals ranging from salmonid fish to ungulates to migratory birds (Sanderson et al. 2006, Bolger et al. 2008, Saracco et al. 2008, Wilcove and Wikelski 2008, Sauer and Link 2011) emphasize the importance of quantifying seasonal demographic rates and identifying when during the annual cycle populations of these species are most limited. While rigorous estimates of annual survival have become more common in recent years (e.g. Bayne and Hobson 2002, Cilimburg et al. 2002, Dugger et al. 2004, Jones et al. 2004, Mazerolle et al. 2005, Stutchbury et al. 2009b), few reliable estimates of oversummer or overwinter survival exist for Neotropical migratory birds (but see Conway et al. 1995, Marra and Holmes 2001, Sillett and Holmes 2002, Latta 2003, Jones et al. 2004, Johnson et al. 2006, and Calvert et al. 2010), and only one study to date has estimated survival over the migratory periods (Sillett 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 migratory birds, and thus may have consequences for population dynamics. Previous research has linked avian survival probabilities to local weather variables, such as cold temperatures in early spring (Newton 2007, Robinson et al. 2007), summer rainfall (Dugger et al. 2004, Cowley and Siriwardena 2005), and storms or heavy rains during migration (e.g., Perrins et al.

1985, Wiedenfield and Wiedenfield 1995, Butler 2000, Newton 2007). Heavy rain or prolonged hot, dry weather during either stationary period can cause direct mortality (Newton 2007), or reduce foraging efficiency (Cowley and Siriwardena 2005) and food availability (Janzen 1973; Wolda 1978; Brown and Sherry 2006; Studds and Marra 2007, 2011). Survival rates of migratory birds are also influenced by global climate phenomena, represented by indices such as the El Niño Southern Oscillation (ENSO; Sillett et al. 2000, Mazerolle et al. 2005, LaManna et al. 2012) and North Atlantic Oscillation (NAO; Franke et al. 2011) that integrate temperature and precipitation information across a broader scale. Understanding how these variables may impact demographic rates is especially important as global climatic conditions are expected to undergo long-term directional change and/or increased variability, yet their effects remain poorly understood (Calvert et al. 2009).

However, 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., Peach et al. 1991, Baillie and Peach 1992, Marra et al 1998, Gill et al. 2001, Bearhop et al. 2004, Norris et al. 2004, Harrison et al. 2011, Rockwell et al. 2012). For example, dry season rainfall in the Neotropics can drive insect availability on wintering grounds, and thus individual body condition. 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 (Sillett et al. 2000, Sillett and Holmes 2002, Studds and Marra 2005) or breeding season. Annual survival rates of some Palearctic migrants are also 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). Carry-over effects originating from breeding season climate may also reduce survival in later seasons. For instance, if molt is delayed after a prolonged breeding season, late winter arrival (currently no empirical evidence for this; Marra 2000, Stutchbury et al. 2011) or compromised plumage brightness (Reudink et al. 2009) may result in the acquisition of a poorer quality winter territory and lower overwinter survival. Individual birds operating at an energy deficit after poor weather in temperate breeding areas (Cowley and Siriwardea 2005) may experience reduced body condition, or grow poorer quality feathers after molt, and thus suffer increased mortality during the subsequent fall migration (Nilsson and Svensson 1996, Dawson et al. 2000). Survival over the summer and winter stationary periods appears to be fairly high in Neotropical migrants relative to the spring and fall migratory periods (e.g., Marra and Holmes 2001, Sillett and Holmes 2002, Jones et al. 2004, Johnson et al. 2006), so carry-over effects of stationary period climate that influence survival during migration have the potential to be ecologically important.

Migratory species with restricted ranges may be especially vulnerable to climate change that alters habitat or food availability because they lack alternative breeding and wintering sites. The Kirtland's warbler is one such species, breeding primarily in a limited area of northern Michigan and wintering in the Bahamian archipelago. Though still endangered, its status has improved dramatically in the last 30 years, with the population size increasing from approximately 200 singing males in the 1970s and 1980s to 1800 singing males today (USFWS 2012). However, we

still lack substantial information about their basic ecology throughout the annual cycle. Even though Kirtland's warblers spend six to seven months of the year in the Neotropics, it has previously been thought that availability or quality of winter habitat was not limiting (Mayfield 1992, Bocetti 1994, Sykes 1997, 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 cowbird removal (Shake and Mattsson 1975, Kelly and DeCapita 1982, Walkinshaw 1983) and the creation of new Jack pine (*Pinus banksiana*) plantations (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 breeding and wintering areas affects survivorship.

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. Understanding how climate itself, for example, affects vital rates such as the survival of migratory animals, is an essential first step in our ability to predict how individuals and species may be affected by future climate change. Adult survival rates generally have a stronger influence on population growth than reproductive rates, and thus they represent a critical component of population dynamics (e.g., Newton 1998, Sæther and Bakke 2000). Here we analyze two different mark-recapture datasets (Michigan 2006-2011 and Bahamas 2003-2010) to estimate annual, oversummer, overwinter, and migratory

period survival of the Kirtland's warbler, and to assess the influence of winter and summer climate variables on annual survival rates. We further combined our estimates of the influence of climate variables on survival with data collected in the breeding season (Rockwell et al. 2012) to understand how future climate change may impact population growth. Only through such an approach, taking into account the influence of climate variation throughout the annual cycle, will we be able to make useful predictions of how populations will respond to a changing climate.

Methods

Study species. Kirtland's warblers are small (13.7 ± 1.1 g), sexually dimorphic migratory songbirds that primarily breed in northern lower Michigan and winter in the Bahamian archipelago (Walkinshaw 1983, Mayfield 1992). They are primarily insectivorous during the breeding season, but will also forage on blueberries when ripe (Deloria-Sheffield et al. 2001). These warblers have strict breeding habitat requirements, preferring to nest in large, dense, contiguous stands of young Jack pine on sandy soils located in about 16 counties in northern Michigan, with a few pairs breeding in Wisconsin and Ontario (Mayfield 1960). The Kirtland's warbler is a fire-dependent species, requiring young Jack pine stands approximately 5-15 years post-fire disturbance for nesting habitat (Donner et al. 2009). They spend the non-breeding season primarily in the Bahamian archipelago, where they also occupy disturbance-maintained, early successional habitats (Sykes and Clench 1998; Wunderle et al. 2007, 2010). In the Bahamas, Kirtland's warblers tend to be more omnivorous, consuming a substantial amount of fruit, especially wild sage (*Lantana involucrata*;

Wunderle et al. 2010). Population sizes were very low throughout the 1970s and 1980s (approximately 200 singing males), partially due to their extreme habitat specificity, and the Kirtland's warbler was designated a federally endangered species in 1973 (Byelich et al. 1976). Management efforts on the breeding grounds, including a Brown-headed cowbird (*Molothrus ater*) removal program and the creation of new Jack pine plantation habitat, allowed the population to increase at a rate of about 11.4% per year from 1990 to 2008. Since 2008, the population has stabilized at approximately 1800 singing males (USFWS 2012).

Study Sites. During the breeding season, we used ten 30-ha study plots located in Alcona, Iosco, Oscoda, Ogemaw counties in northern Lower Michigan. Field sites were characterized by fairly homogenous stands of young Jack pine, interspersed with northern pin oak (*Quercus ellipsoidalis*), sand cherry (*Prunus pumila*), and other deciduous trees. Understory vegetation was dominated by Pennsylvania sedge (*Carex pensylvanica*) and lowbush blueberry (*Vaccinium angustifolium*) (see Rockwell et al. 2012 for a full description).

The non-breeding season portion of this study was conducted on Eleuthera, an island in the central Bahamian archipelago. Vegetation on Eleuthera includes evergreen and semi-deciduous broadleaf trees and shrubs, which form a thick brush known as coppice (Correll 1979). Our study was conducted in southern Eleuthera, where Kirtland's warblers occur in early successional habitats 3-28 years after disturbance (Wunderle et al. 2010). Fruiting plants such as wild sage (*Lantana involucrata*), black torch (*Erithalis fruticosa*), and snowberry (*Chiococca alba*) provide important forage (Wunderle et al. 2010). 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 full description).

Marking and resighting efforts. We used resighting of 339 marked individuals to estimate annual and breeding season survival in Michigan from 2006-2011. Male Kirtland's warblers were captured upon spring arrival to breeding territories, banded with one aluminum band and a unique combination of three color bands, and aged as second-year (SY) or after second-year (ASY) individuals as part of a larger ongoing study (Rockwell et al. 2012). Plots were visited every three days from May 1 to June 7 to band new males (2006-2010), and we searched for previously color-banded males every three days until July 31 (2007-2009). In 2011, we resighted color-banded males in the month of May only. In addition, we systematically searched, using playback, areas within 400m of the plot edges once a month, in an attempt to relocate any individuals who moved their territories outside of plot boundaries. Cormack-Jolly-Seber models underestimate survival to some degree if any individuals permanently emigrate from study sites following capture (Lebreton et al. 1992); thus, efforts were made to eliminate floaters from our dataset. We only analyzed capture histories of males that established territories on our study plots (i.e., sang in one area for at least 2 weeks) to minimize this potential bias.

We used capture and resighting of 215 Kirtland's warblers to estimate overwinter survival in the Bahamas from 2003 - 2010. Warblers were captured from 1 October through 30 April, beginning in October 2003 and ending in April 2009, with

additional captures in April 2010. Some birds were captured via target-netting with playback of conspecific songs and chip notes. Others were captured using passive netting (with or without playback). Passive netting, with lines of 11-16 nets, occurred in the early (October-December), mid, (January-February), and late (March-April) winter periods. Nets were operated from sunrise to 0930-1000 EST for at least two mornings and an afternoon (1600 to sunset) at a site before moving the net line. All individuals were given a unique band combination and released at or near the capture site. We classified age at capture as either a returning adult (AHY) or a first-winter juvenile (HY). To resight marked birds, intensive searches of the study sites were conducted during the early, mid, and late winter periods following each netting session to find banded warblers. Searches were conducted primarily from sunrise to 0930-1000 EST during which time solitary observers traversed access trails and roads to locate banded birds. Some searches were also conducted in late afternoon (1600 to sunset), and opportunistically while mist netting and during site visits to collect other data not reported here. As observations of different banded individuals accumulated at a site during each winter period, observers concentrated on locating missing birds previously known from the study site. The effort allocated to searching each study site was related to the size of the study site and the number of warblers on the site. Generally, 5-9 mornings were spent searching a study site during each winter period by 2-5 observers searching independently on a site.

In Michigan, encounter occasions occurred at the beginning of May, June, and July in the years 2007-2009. In 2006, 2010, and 2011, encounter occasions occurred at the beginning of May only. Thus, in some years we estimated 2 months of

oversummer survival and 10 months of overwinter + migration survival, and in some years we estimated annual survival only. In the Bahamas, encounter occasions occurred each month from October – April, to estimate survival over a 6-month long winter period, and a 6-month long oversummer + migration period. Observations of marked individuals from both datasets were recorded monthly, to facilitate comparisons between survival intervals of different lengths.

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 each global model was 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 overdispersion (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 with two model subsets. The first model subset examined the influence of all possible combinations of age, sex, season, and time (year or month) on survivorship, compared to a constant survival model. We also considered models including effects of sex, season, and time (month or year) on recapture probability. We allowed detection probability to vary by sex, season, and year. We did not model p as a

function of age, because behaviors that affect how conspicuous and detectable individuals are did not vary by age (S. Rockwell, pers. obs.). 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 from May – May in Michigan, including many summer and winter climate covariates. We considered models with effects of Bahamas March rain, late winter rain (Feb-Apr), total winter rain (Oct - Apr), mean winter high temperature, number of winter drought days, and a binary variable representing whether there was a hurricane that year. We also considered models with effects of May rain, total summer rain (May – July), May minimum temperatures, number of summer days over 90°F, mean summer minimum temperature, number of May days below freezing, and number of summer days below freezing in Mio, MI. Other models included effects of mean winter North Atlantic Oscillation (NAO) index, monthly mean Southern Oscillation Index (SOI) values of the previous year, and monthly mean SOI values of the concurrent year. All climate data were obtained from the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (Nassau Airport, station GHCND: BF000078073; and Mio WWTP MI, station GHCND: USC00205533). While it is unknown exactly where all subpopulations of Kirtland's warblers overwinter, climate throughout the Bahamas is correlated to that in Nassau (Sealey 2006), including precipitation measured in some years at the Eleuthera field site (J. White and J. Wunderle, unpub. data). Other sources of annual variation we considered were population size in June, obtained from the annual census of singing males (USFWS 2012), and a simple linear trend

over time. These were compared to a constant survival model and a model of survival with random yearly variation, for a total of 20 *a priori* candidate models.

For the 2006-2011 Michigan dataset, we carried over any model from either subset that had a $\Delta\text{QAIC}_c < 2$ into the final model set, a threshold value proposed by Burnham and Anderson (2002). We also added new models containing combinations of the variables found in highly-ranked models of both subsets. The Bahamas dataset was only used to estimate seasonal survival probabilities, and not to compare annual survival to climate covariates, so only one set of models was used (equivalent to the first model subset of the Michigan dataset). We calculated model-averaged estimates of monthly survival from each final model set, and then raised monthly survival to the number of months in each period of interest (oversummer, 4; overwinter, 6; and annual, 12) to determine the cumulative survival rate for each period. Annual survival probability is the product of survival probabilities during each phase of the annual cycle: $\phi_{\text{annual}} = \phi_{\text{overwinter}} \times \phi_{\text{oversummer}} \times \phi_{\text{migration}}$. Direct observation of 5 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. 2009a, Hecksher et al. 2011, Seavy et al. 2012), so we considered fall and spring migration to have a combined length of 2 months. To estimate survival over the 2-month migratory period, we used the equation above and solved for $\phi_{\text{migration}}$. All survival estimates are given as: estimate \pm standard error (SE). Standard errors of monthly survival probabilities were calculated in 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 the effect of March rainfall in the Bahamas, as this was the best-supported survival model (see Results). An estimate of the effect of March rainfall on survival was obtained by plotting annual survival estimates from the top-ranked March rainfall model against March rainfall. Simple least-squares regression yielded a value of 0.034 for the slope of this relationship. We then combined the influence of March rainfall on survival with data collected in the breeding season (Rockwell et al. 2012). For every 1-cm reduction in March rainfall, apparent survival rates are predicted to decrease by 3.4 percentage points (this study), and reproductive success is predicted to decrease by 0.6 fledglings per pair per year (Rockwell et al. 2012). To model the effects of different levels of rainfall declines on population growth rate, we used the equation $\lambda = \phi_{\text{adult}} + (\# \text{ female offspring/female}) * \phi_{\text{juvenile}}$ (Pulliam 1988). We used 0.35 as the baseline estimate of ϕ_{juvenile} for these calculations (C. Bocetti and S. Rockwell, unpub. data), and assumed that it decreased in parallel with ϕ_{adult} . We then modeled the effects of a 5%, 10%, 25%, and 50% decrease in March rainfall on population growth rate (λ).

Results

We gathered capture histories for 339 color-banded Kirtland's warbler males in Michigan from May through the end of July in the years 2006-2011. In the first model subset assessing the effects of age, season, and time (year or month), the seasonal survival model had the most support (QAIC_c weight = 0.25; Table 1). However, models with effects for age, year, age and season (additive), and age and

season (factorial) all had nearly equivalent support in the data ($\Delta\text{QAIC}_c < 2$), suggesting that these variables are also likely to be important. All models with $\Delta\text{QAIC}_c < 10$ included detection probabilities that varied by month. In the second model set examining the effects of annual climate variables on survival, March rain received twice as much support as the second-ranked model, while late winter rain and mean monthly SOI in the prior year were also well-supported compared to the remaining models ($\Delta\text{QAIC}_c < 2$; Table 2).

The final model set, using combinations of variables found in the top-ranked models from the first two subsets, contained 29 candidate models. Because several models were well-supported by the data, we used model-averaging to obtain survival and slope parameter estimates. Mean annual survival for ASY males (0.580 ± 0.11) was slightly higher than for SY males (0.553 ± 0.10), while oversummer survival was more similar across age classes (0.862 ± 0.06 and 0.852 ± 0.05 , respectively; Table 4). These should still be considered minimum survival estimates, as Cormack-Jolly-Seber models cannot fully separate mortality from emigration (Lebreton et al. 1992). March rain was the best supported model of apparent annual survival, found in five out of the seven most highly ranked models, with a variable importance of 0.42 (Table 3). Models including effects of season, age, late winter rain, and SOI also had values of $\Delta\text{QAIC}_c < 2$. March rain ($\beta = 0.269 \pm 0.14$ SE; Figure 8) and late winter rain ($\beta = 0.05 \pm 0.03$ SE) both exerted a positive influence on annual survival in the subsequent year. Because the logit-link function was used for parameter estimation, this means that the logit of survival probability decreases by 0.269 for every 1-cm reduction in Bahamas March rainfall. Mean monthly SOI of the preceding year was

negatively related to survival, but its slope ± 1 SE overlapped zero ($\beta = -0.236 \pm 0.32$ SE), indicating a relatively weak effect.

In the second dataset, we used capture histories of 215 Kirtland's warblers recorded in the Bahamas during the October - April winter stationary periods from 2003-2010. The top two survival models both included effects of age, season, and year (total QAIC_c weight = 0.72; Table 5). Other models including effects of age and season, or sex, age, and season were also moderately supported by the data. Models including effects of sex and season on detection probabilities received the most support, while models including effects of sex, season, and year, or just season and year were also moderately supported. We used model-averaging to obtain survival estimates because multiple models received substantial support in the data. AHY males appeared to survive the winter period at much higher rates than HY males (0.902 ± 0.06 vs. 0.245 ± 0.47 , respectively), though HY estimates suffered from low precision due to small sample sizes. Differences between the sexes were apparent but much smaller in magnitude (males: 0.902 ± 0.06 , females: 0.878 ± 0.10 ; Table 6). The problem of underestimation of survival parameters is likely to be more severe during winter months because of the behavior of Kirtland's warblers in the non-breeding season. Permanent emigrations probably occur often during the winter period, because individuals will readily shift home ranges to track patchy, ephemeral food resources (Wunderle et al. 2010).

Mean annual and oversummer survival estimates for ASY males in 2006-2011 were combined with the mean overwinter survival estimate of AHY males in 2002-2010 to obtain an estimate of survival over the two migratory periods combined

($\phi_{\text{annual}} = \phi_{\text{summer}} * \phi_{\text{winter}} * \phi_{\text{migration}}$). Survivorship of adult male Kirtland's warblers during the migratory phase, considered here to be the 2 combined months of fall and spring migration, was 0.745 ± 0.18 (Figure 9). This means that survival is lower during the migratory periods relative to the stationary periods, with approximately 50% of mortalities occurring during this portion of the annual cycle (Figure 9). Monthly survival probabilities for adult males in each season were: oversummer, 0.963 ± 0.02 ; overwinter, 0.983 ± 0.01 ; and migration, 0.863 ± 0.06 .

Because $\phi_{\text{Marchrain}, p_t}$ was the highest-ranked model of survival, we further modeled the impact of different levels of decline in March rainfall on population growth rate. By regressing annual survival estimates from the $\phi_{\text{Marchrain}, p_t}$ model on March rainfall, we obtained a slope estimate of 0.034. For every 1-cm reduction in March rainfall, apparent survival rates are predicted to decrease by 3.4 percentage points (this study), and reproductive success is predicted to decrease by 0.6 fledglings per pair per year (Rockwell et al. 2012). For example, at the mean level of March rainfall during the years of our study (3.21 cm), we would expect adult survival to be 0.58, juvenile survival to be 0.35 (S. Rockwell and C. Bocetti et al., unpub. data), and the number of female fledglings per pair to be 1.46 (half the number of total fledglings; Rockwell et al. 2012). Using Pulliam's (1988) formula for lambda, population growth rate at the current mean level of March rainfall would be 1.09 ($\lambda_{3.21} = 0.58 + 1.46 * 0.35$). With 5%, 10%, 25%, and 50% reductions in March rainfall, population growth rates are predicted to be 1.06, 1.04, 0.96, and 0.85, respectively.

Discussion

Our study presents the first published estimates of survivorship of the endangered Kirtland's warbler based on Cormack-Jolly-Seber (CJS) models. It is also only the second study to estimate survival in different portions of the annual cycle for a migratory bird species. The quantification of season-specific vital rates is essential for effectively identifying conservation priorities, yet these data do not exist for most migratory animal species. We used a unique opportunity to estimate season-specific survival for an endangered species with marked populations of Kirtland's warblers at both breeding and non-breeding sites. We also found that late winter rainfall in the Bahamas, particularly in March (the month prior to spring migration), was the best predictor of annual survival.

Apparent annual survival probabilities for adult male Kirtland's warblers in this study are similar to published CJS estimates for other, non-endangered warbler species (0.51 for Black-throated blue warblers [*Setophaga caerulescens*], Sillett et al. 2002; 0.41 - 0.74 among warbler species reviewed in Faaborg et al. 2010). Annual estimates of female survival were not available in 2006 - 2011, but data from 1984-2001 (S. Rockwell and C. Bocetti et al., unpub. data) and earlier published estimates based on return rates (Mayfield 1960, Walkinshaw 1983) suggest that they are similar or slightly lower than those of males. CJS estimates are less negatively biased than return rates, because they take detection probabilities into account, and therefore not all missed detections are confounded with mortality (Lebreton et al. 1992). However, CJS methods can still only measure apparent survival because detection is rarely perfect (DeSante et al. 1995, Sandercock and Jaramillo 2002), and permanent

emigration cannot be distinguished from mortality. Thus, our values for apparent annual, oversummer, and overwinter survival should be considered minimum estimates.

A striking result from this study is that March rainfall in the Bahamas explained variation in survivorship better than any other winter or summer climate variable that we included in our model sets (Table 2; see Methods for a full list of variables). March rain explained survival 14 times better than a constant survival model, and 7 times better than a model where survival varied randomly by year. The second and third highest ranked models included the influence of Feb-Apr rainfall, and mean SOI of the previous year, two variables that are also closely related to late winter precipitation in the Bahamas. This result corroborates theoretical (Sherry and Holmes 1995) and empirical research (e.g., Ryel 1981; Peach et al. 1991; Baille and Peach 1992; Szép 1995; Sillett et al. 2000; Saino et al. 2004; Mazerolle et al. 2005; Studds and Marra 2007, 2011; Wilson et al. 2011; Rockwell et al. 2012) suggesting that migratory bird populations may be limited by winter climate. 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). The amount of rainfall 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; J. White and J. Wunderle unpub. data). Reduced rainfall limits food availability, which can lead to reduced body condition (Brown and Sherry 2006; Studds and Marra 2007, 2011) and slower rates of fat deposition (Smith et al. 2010)

in overwintering migratory birds. Birds in poorer condition at the end of the late winter drought season may then be less likely to survive the subsequent spring migration (Sillett et al. 2000, Sillett and Holmes 2002, Studds and Marra 2005).

Survival of male Kirtland's warblers is lower during the migratory period (0.745 ± 0.18) relative to the summer (0.862 ± 0.06) and winter (0.902 ± 0.06) stationary periods. This indicates that 50% of total annual mortality in this species occurs during the estimated 2 months that they spend on migration. Of 100 adult male warblers observed on the breeding grounds on May 1, we would expect 42 of them to perish by the following May. Of these, ~21 would die during spring or fall migration. However, we suggest that this is not solely due to the challenges of migration itself, but may in fact be a carry-over effect that is tightly linked to winter rainfall in the Bahamas. Migratory birds undergo a period of hyperphagy prior to spring departure to gain the fat and muscle mass necessary for an energetically demanding migration. Occupation of drier winter habitats may lead to limited food resources and poor within-winter body condition (Brown and Sherry 2006; Studds and Marra 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 (J. Wunderle et al., unpub. data). During dry winters fewer individuals may be able to gain sufficient body mass to survive the subsequent spring migration. This type of carry-over effect on survival driven by winter conditions could have important consequences for the population dynamics of this species, and has been suggested to occur in other migratory birds as well (Peach et al. 1991, Szép 1995, Sillett et al. 2000, Sillett and Holmes 2002, Mazerolle et al. 2005). If our hypothesis regarding the

carry-over effect of winter rainfall is correct, we would expect to see higher mortality during spring migration than fall migration. Unfortunately, we did not have a sufficient number of marked individuals observed at both the summer and winter field sites, and thus it was not possible to separate apparent survival during spring vs. fall migration.

We found high apparent within-winter survival rates, similar to previous studies of marked populations of parulids, such as Black-throated blue warblers (*S. caerulescens*, 0.93; Sillett and Holmes 2002) and American redstarts (*S. ruticilla*, 0.70-0.97; Johnson et al. 2006) in Jamaica. Our overwinter survival estimates are somewhat lower than those of Sillett and Holmes (2002), perhaps because the males they studied were only those holding winter territories, and we were unable to restrict our analysis in this way. The winter home ranges of Kirtland's warblers are flexible, and can change throughout the winter in response to variation in food resources (Wunderle et al. 2010), which may result in more permanent emigrations from our study sites during the non-breeding season. If so, true within-winter survival may be higher than reported here. Winter survivorship of females was lower than that of males, which is consistent with patterns of social dominance of males over females observed in *S. ruticilla* (Marra 2000, Marra and Holmes 2001), and sexual segregation on wintering grounds observed in other species (Wunderle 1995; Latta and Faaborg 2001, 2002). Some empirical evidence exists for these patterns in Kirtland's warblers as well. Adult males increase pre-migration body condition significantly faster than adult females, and exhibit stronger site fidelity (Wunderle et al., unpubl. data), suggesting that females may be relegated to poorer winter habitats

where survival is slightly lower. Age was better-supported than sex as a factor affecting overwinter survival, but we were unable to obtain precise estimates of within-winter survival of yearling birds due to low sample sizes.

Survival rates of Kirtland's warblers within the breeding season were also fairly high, though somewhat lower than previous studies of Neotropical-Nearctic migratory birds (0.99 ± 0.01 for *S. caerulescens*, Sillett and Holmes 2002; 0.94 ± 0.08 for *S. cerulea*, Jones et al. 2004). This is partly explained by the fact that we used a 4-month summer stationary period while the aforementioned studies used a 3-month summer stationary period. Our monthly summer survival estimate is more similar to, but still lower than, those of these two studies (0.963 ± 0.01 vs. 0.999 ± 0.001 and 0.98 ± 0.01 , respectively). One possibility is that Kirtland's warbler males reduce song rates near the end of the breeding season, making them difficult to detect (Wilson and Bart 1985, S. M. Rockwell pers. obs.). If some of these males disperse to other Jack pine stands for the next year's breeding season, these permanent emigrations from our study plots would be confounded with oversummer mortality.

Survival of Kirtland's warblers during the migratory periods was lower than either the summer or winter stationary phases. To make this calculation, we combined ASY oversummer and annual survival with AHY overwinter survival (which would include both ASY and SY individuals), because estimates of ASY and SY annual and oversummer survival were similar (Table 3). Our estimates of survival during the migratory periods are markedly higher than the only other study to calculate survival during migration in a songbird (0.45-0.54; Sillett and Holmes 2002). In their study of Black-throated blue warblers, more than 85% of apparent annual mortality occurred

during migration, compared to 50% in our study. This may be less surprising in light of the fact that 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. careluscens*, Holmes et al. 1995), and have a slightly shorter migration route. Their relatively shorter passage over open ocean may lower their risk of mortality during migration (Butler 2000).

Factors operating at other times of the year (such as the breeding season), including Jack pine stand age and cowbird parasitism, are known to be important to Kirtland's warbler ecology. For instance, the number of male warblers occupying a habitat patch tends to decrease in Jack pine stands over 14-15 years of age due to declining habitat suitability (Donner et al. 2009). Thus, it is possible that there are factors affecting survival not examined here. We hypothesize that survival probabilities may decline as Jack pine stands age past the optimal range of 5-15 years old. Because individuals are also more likely to permanently emigrate from older stands (Walkinshaw 1983, S. M. Rockwell pers. obs.), the effect of stand age on survival probability is confounded with its effect on the probability of emigration, making it difficult to parse out any real effects on survival. We did not detect a sufficient number of individuals moving between stands of different ages to include transition probabilities (ψ) in a multi-state analysis, so we were unable to examine this hypothesis. An important next step would be to estimate habitat-specific survival, and incorporate this with information about current and future distributions of Jack pine stands of different ages across the Kirtland's warbler breeding area.

Nest parasitism by the Brown-headed cowbird during the breeding season is known to reduce Kirtland's warbler reproductive success. Prior to cowbird control,

productivity was down to 0.8 fledglings per nest in 1957-1971 (Walkinshaw 1972, 1983), compared to the 2007-2009 mean of 3.0 fledglings per nest (S. M. Rockwell, unpub. data). Cowbird parasitism could also potentially affect survival if it increases the stress experienced by adults or their number of nest attempts (reproductive effort). Currently, nearly all Kirtland's warbler breeding sites in the lower peninsula of Michigan have active cowbird traps operating < 1 mile away, and thousands of cowbirds are removed each year (D. Elbert, pers. comm.). Parasitism rates have been reduced to < 1% of all nests (S. M. Rockwell, unpub. data). Without measurable variation in trapping effort or parasitism rates, it is not currently possible to measure the effect of cowbirds on Kirtland's warbler survivorship, although historically nest parasitism may have been a factor.

Our estimates of annual, oversummer, and overwinter survival are likely to be underestimates due to an unknown number of undetected emigrants (DeSante et al. 1995, Sandercock and Jaramillo 2002). Because we used these values to calculate survival during the migratory periods, our estimate of survival during migration should be considered a maximum rate. Several aspects of Kirtland's warbler ecology make the problem of underestimation more likely to be a factor. This warbler does not fit the archetype of a strongly territorial, insectivorous bird in winter like other model species such as the American redstart or Black-throated blue warbler. They exhibit less site-fidelity during the breeding season as well, returning to the same territory while the age of the Jack pine remains suitable, then abandoning it for a younger stand (Donner et al. 2009). Our estimates of ϕ_{summer} and ϕ_{winter} are lower than that of 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 (i.e., larger body size, shorter migration route) and a natural history that causes underestimation of some survival parameters (i.e., less philopatric). Furthermore, Sillett and Holmes (2002) included both the post-breeding period and the period of pre-migratory preparation in winter in their 3-month estimate of the duration of migration. Information from light-level geolocators (e.g., Stutchbury et al. 2009a, Ryder et al. 2011) and direct observation of marked individuals (Ewert et al. 2012) indicates that the time actually spent migrating is shorter than this. We emphasize that the interpretation of mark-recapture analyses relies on good knowledge of the ecology of the study species. Full resolution of survival in different portions of the annual cycle awaits technological advances, such as satellite transmitters light enough to be placed on small songbirds year-round.

It is of vital conservation importance to know when during the annual cycle that migratory bird populations are limited in order to implement effective management plans. Here we have demonstrated that survival of Kirtland's warblers during migration is lower than any other portion of the annual cycle, and that March rainfall on the Bahamian wintering grounds is an important factor influencing annual survival. Our results support other studies suggesting that migratory bird populations can be limited by events that occur during the non-breeding season (Ryel 1981; Marra et al. 1998; Peach et al. 1991; Baille and Peach 1992; Szép 1995; Sillett et al. 2000; Saino et al. 2004; Norris et al. 2004; Studds and Marra 2005, 2007, 2011; Reudink et al. 2009; Smith et al. 2010, Wilson et al. 2011; Rockwell et al. 2012). The Caribbean already experiences a late winter drought period linked to decreased insect

availability (Lefebvre et al. 1994, Parrish and Sherry 1994, Brown and Sherry 2006, Smith et al. 2010). The Bahamas archipelago has also experienced a general decline in rainfall from 1959 – 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 lower Kirtland's warbler survival, and is also predicted to reduce productivity (Rockwell et al. 2012), causing a two-fold negative impact on population dynamics. Our population growth rate model revealed that with 5%, 10%, 25%, and 50% reductions in Bahamas March rainfall, values of λ are predicted to be 1.06, 1.04, 0.96, and 0.85, respectively. Thus, if March rainfall falls below 18% of current mean levels, the population size of Kirtland's warblers may begin to decrease. More detailed predictions of future variation in winter rainfall and how it will impact the population dynamics of multiple migratory bird species will enhance conservation efforts.

Our study emphasizes the importance of conserving high-quality, drought-resistant habitats for migrants wintering in the Caribbean. In addition, any actions taken now to mitigate global climate change will help reduce potential negative impacts on migratory bird populations. Because birds may be departing from drought-stressed winter habitats, and struggling to maintain sufficient body condition during a strenuous migratory period, survival during migration may also be a limiting factor. Thus, management actions that alleviate migration mortality, such as reducing collisions with manmade structures and protecting high-quality stopover sites, could also benefit many migratory bird species. While the status of the endangered

Kirtland's warbler has improved greatly in recent years, emerging threats such as climate change, and unknowns such as the location and importance of stopover sites used during migration, must now also be taken into consideration.

Enhanced knowledge of season-specific mortality and its causes are of vital conservation importance for all taxa of migratory animals, from Monarch butterflies to Gray whales, yet these data are virtually unknown for most species (Calvert et al. 2009, Hedenstrøm et al. 2011). Such information is crucial for recognizing and mitigating potential threats that occur throughout the annual cycle, as well as identifying conservation priorities. Climate change is one such threat that has the potential to impact migratory animals in different ways during the breeding, non-breeding, and migratory periods, depending on the ecology of the organism in question. Estimates of future climate change and its effect on vital rates can be combined with data from the breeding season to predict effects on population sizes or growth rates. Using full annual cycle biology to understand how populations are limited throughout the year should be a conservation research priority for migratory animals.

Table 1. First model subset of monthly survival (ϕ) and recapture probabilities (p) for male *S. kirtlandii* in Michigan from 2006-2011. Includes number of estimable parameters (K), QAIC_c values, differences between current QAIC_c and QAIC_c value for the best model (Δ QAIC_c), and QAIC_c weights (w_i). Subscripts give parameterization for ϕ and p : age = two age classes (SY or ASY), year = annual variation, t = monthly variation, and season = oversummer (May - Aug) or winter + migration (Sept - Apr) periods. Goodness of fit test for the global model (ϕ_{age^*t} , p_t) indicated a minor lack of fit to the data, so a \hat{c} adjustment was used ($\hat{c} = 1.40$). Models with Δ QAIC_c values > 10 are not shown.

Model	K	QAIC _c	Δ QAIC _c	w_i
$\phi_{\text{season}}, p_t$	13	1377.41	0.00	0.25
ϕ_{age}, p_t	13	1378.08	0.67	0.18
ϕ_{year}, p_t	15	1378.34	0.93	0.16
$\phi_{\text{age}+\text{season}}, p_t$	14	1378.59	1.18	0.14
$\phi_{\text{age}^*\text{season}}, p_t$	14	1379.26	1.85	0.10
ϕ_{\cdot}, p_t	11	1379.73	2.32	0.08
$\phi_{\text{age}^*\text{year}}, p_t$	20	1379.79	2.38	0.08
$\phi_{\text{season}^*\text{year}}, p_t$	18	1382.26	4.86	0.02
$\phi_{\text{age}^*\text{season}^*\text{year}}, p_t$	25	1386.72	9.31	0.00
ϕ_t, p_t	21	1387.07	9.66	0.00

Table 2. Second model subset of monthly survival (ϕ) and recapture probabilities (p) for male *S. kirtlandii* in Michigan from 2006-2011. This subset includes climate variables and all other annual covariates. The number of estimable parameters (K), QAIC_c values, differences between current QAIC_c and QAIC_c value for the best model (Δ QAIC_c), and QAIC_c weights (w_i) are shown. Subscripts give parameterization for ϕ and p , where t = monthly variation. Goodness of fit test for the global model ($\phi_{\text{age}^*t}, p_t$) indicated a minor lack of fit to the data, so a \hat{c} adjustment was used ($\hat{c} = 1.40$). Models with QAIC_c values > 10 are not shown.

Model	K	QAIC _c	Δ QAIC _c	w_i
$\phi_{\text{Marchrain}}, p_t^a$	13	1374.40	0.00	0.24
$\phi_{\text{late winter rain}}, p_t^b$	13	1376.19	1.78	0.10
$\phi_{\text{ENSO}_{n-1}}, p_t^c$	13	1376.23	1.83	0.10
$\phi_{\text{summer rain}}, p_t^d$	13	1376.75	2.34	0.08
$\phi_{\text{hurricane}}, p_t^e$	13	1377.61	3.20	0.05
$\phi_{\text{Maymintemp}}, p_t^f$	13	1377.94	3.54	0.04
$\phi_{\text{wintermaxtemp}}, p_t^g$	13	1378.13	3.72	0.04
$\phi_{\text{Mayfreeze}}, p_t^h$	13	1378.19	3.78	0.04
$\phi_{\text{year}}, p_t^i$	15	1378.34	3.93	0.03
$\phi_{\text{winter90deg}}, p_t^j$	13	1378.34	3.94	0.03
$\phi_{\text{linear}}, p_t^k$	13	1378.82	4.42	0.03
$\phi_{\text{popsize}}, p_t^l$	13	1378.87	4.47	0.03
$\phi_{\text{Mayrain}}, p_t^m$	13	1378.94	4.53	0.03
$\phi_{\text{winter rain}}, p_t^n$	13	1378.97	4.57	0.02
$\phi_{\text{winterNAO}}, p_t^o$	13	1379.00	4.60	0.02
$\phi_{\text{ENSOconcurrent}}, p_t^p$	13	1379.01	4.60	0.02
ϕ_{\cdot}, p_t^q	11	1379.73	5.33	0.02

^aMarchrain = total March rainfall in Bahamas; ^blate winter rain = total late winter (Feb-Apr) rainfall in the Bahamas; ^cENSO_{n-1} = mean monthly SOI value in the preceding year; ^dsummer rain = May-July rain in Mio, MI; ^ehurricane = binary variable representing whether there was a hurricane that year in the Bahamas; ^fMaymintemp = mean minimum May temperature in Mio, MI; ^gwintermaxtemp = mean maximum Oct – Apr temperature in the Bahamas; ^hMayfreeze = number of days with minimum temperatures below freezing in May in Mio, MI; ⁱyear = random yearly variation; ^jwinter90deg = number of days from Oct-Apr with maximum temperatures above 90°F in the Bahamas; ^klinear = linear trend in annual survival; ^lpopsize = estimated population size in June, from the annual census of singing males; ^mMayrain = total May rainfall in Mio, MI; ⁿwinter rain = total Oct – Apr rainfall in the Bahamas; ^owinterNAO = mean Oct - Apr value of the North Atlantic Oscillation Index; ^pENSOconcurrent = mean monthly SOI value in the concurrent year; ^q. = constant survival model

Table 3. Final model set of monthly survival (ϕ) and recapture probabilities (p) for male *S. kirtlandii* in Michigan from 2006-2011. Includes number of estimable parameters (K), QAIC_c values, differences between current QAIC_c and QAIC_c value for the best model (Δ QAIC_c), and QAIC_c weights (w_i). Subscripts give parameterization for ϕ and p : age = two age classes (SY or ASY), t = monthly variation, season = oversummer (May - Aug) or winter + migration (Sept - Apr) periods, Marchrain = total March rainfall in Bahamas, late winter rain (lwr) = Feb-Apr rain in Bahamas, and ENSO_{n-1} = mean monthly SOI value in year n-1. Goodness of fit test for the global model ($\phi_{\text{age}^*\text{t}}$, p_t) indicated a minor lack of fit to the data, so a \hat{c} adjustment was used ($\hat{c} = 1.40$). Models with QAIC_c values > 3 are not shown.

Model	K	QAIC _c	Δ QAIC _c	w_i
$\phi_{\text{Marchrain}}$, p_t	13	1374.40	0.00	0.14
$\phi_{\text{Marchrain+season}}$, p_t	14	1375.14	0.74	0.10
$\phi_{\text{Marchrain+age}}$, p_t	14	1375.62	1.22	0.08
$\phi_{\text{late winter rain}}$, p_t	13	1376.19	1.78	0.06
$\phi_{\text{ENSO}_{n-1}}$, p_t	13	1376.23	1.83	0.06
$\phi_{\text{Marchrain*season}}$, p_t	15	1376.44	2.04	0.05
$\phi_{\text{Marchrain+age+season}}$, p_t	15	1376.48	2.08	0.05
$\phi_{\text{lwr+season}}$, p_t	14	1376.54	2.13	0.05
$\phi_{\text{ENSO}_{n-1+season}}$, p_t	14	1376.55	2.14	0.05
$\phi_{\text{ENSO}_{n-1+age}}$, p_t	14	1376.74	2.33	0.04
$\phi_{\text{lwr+age}}$, p_t	14	1376.77	2.36	0.04
$\phi_{\text{ENSO}_{n-1+age+season}}$, p_t	15	1377.22	2.82	0.03
$\phi_{\text{lwr+age+season}}$, p_t	15	1377.29	2.89	0.03

Table 4. Model-averaged estimates of annual and oversummer survival for male *S. kirtlandii* in Michigan from 2006-2011, using the final model set. The oversummer stationary period is considered to be May – August (summer monthly estimate⁴). Annual survival estimates (May – May) were calculated as the product of all monthly survival estimates in a given year. Standard errors were calculated using the Delta method.

	Annual		Oversummer	
	ASY	SY	ASY	SY
2006-2007	0.554 ± 0.04	0.526 ± 0.05	--	--
2007-2008	0.646 ± 0.07	0.623 ± 0.07	0.890 ± 0.05	0.883 ± 0.05
2008-2009	0.531 ± 0.06	0.502 ± 0.06	0.836 ± 0.06	0.827 ± 0.07
2009-2010	0.574 ± 0.06	0.542 ± 0.07	0.859 ± 0.06	0.846 ± 0.07
2010-2011	0.596 ± 0.24	0.572 ± 0.24	--	--
Mean	0.580 ± 0.11	0.553 ± 0.10	0.862 ± 0.06	0.852 ± 0.05

Table 5. Models of monthly survival (ϕ) and recapture probabilities (p) for *S. kirtlandii* in the Bahamas from 2003-2010. Includes 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 (HY or AHY), sex = male or female, year = annual variation, t = monthly variation, and season = overwinter (Oct - Mar) or summer + migration (Apr - Sept). The global model ($\phi_{\text{sex*age*t}}, p_{\text{sex*t}}$) provided a good fit to the data. Models with AIC_c values > 10 are not shown.

Model	K	AIC_c	ΔAIC_c	w_i
$\phi_{\text{age*season*year}}, p_{\text{sex*season}}$	22	1856.96	0.00	0.51
$\phi_{\text{age*season*year}}, p_{\text{sex*season*year}}$	41	1858.87	1.91	0.19
$\phi_{\text{age*season}}, p_{\text{sex*season}}$	8	1860.43	3.47	0.09
$\phi_{\text{sex*age*season}}, p_{\text{season*year}}$	22	1861.15	4.19	0.06
$\phi_{\text{age*season}}, p_{\text{sex*season*year}}$	29	1861.81	4.86	0.04
$\phi_{\text{sex*age*season}}, p_{\text{sex*season}}$	11	1862.40	5.44	0.03
$\phi_{\text{age*season}}, p_{\text{season*year}}$	19	1863.36	6.40	0.02
$\phi_{\text{age*season*year}}, p_{\text{season*year}}$	33	1863.64	6.68	0.02
$\phi_{\text{sex*age*season}}, p_{\text{sex*season*year}}$	32	1864.93	7.97	0.01

Table 6. Model-averaged estimates of overwinter survival for adult male and female *S. kirtlandii* in the Bahamas from 2003-2010. The overwinter stationary period was considered to be October – March (winter monthly estimate⁶). Standard errors were calculated using the Delta method.

	AHY male	AHY female
2003-2004	0.817 ± 0.14	0.797 ± 0.14
2004-2005	0.763 ± 0.16	0.739 ± 0.16
2005-2006	0.972 ± 0.06	0.946 ± 0.12
2006-2007	0.935 ± 0.14	0.908 ± 0.17
2007-2008	0.972 ± 0.07	0.947 ± 0.12
2008-2009	0.889 ± 0.17	0.859 ± 0.20
2009-2010	0.972 ± 0.06	0.947 ± 0.12
Mean	0.902 ± 0.06	0.878 ± 0.10

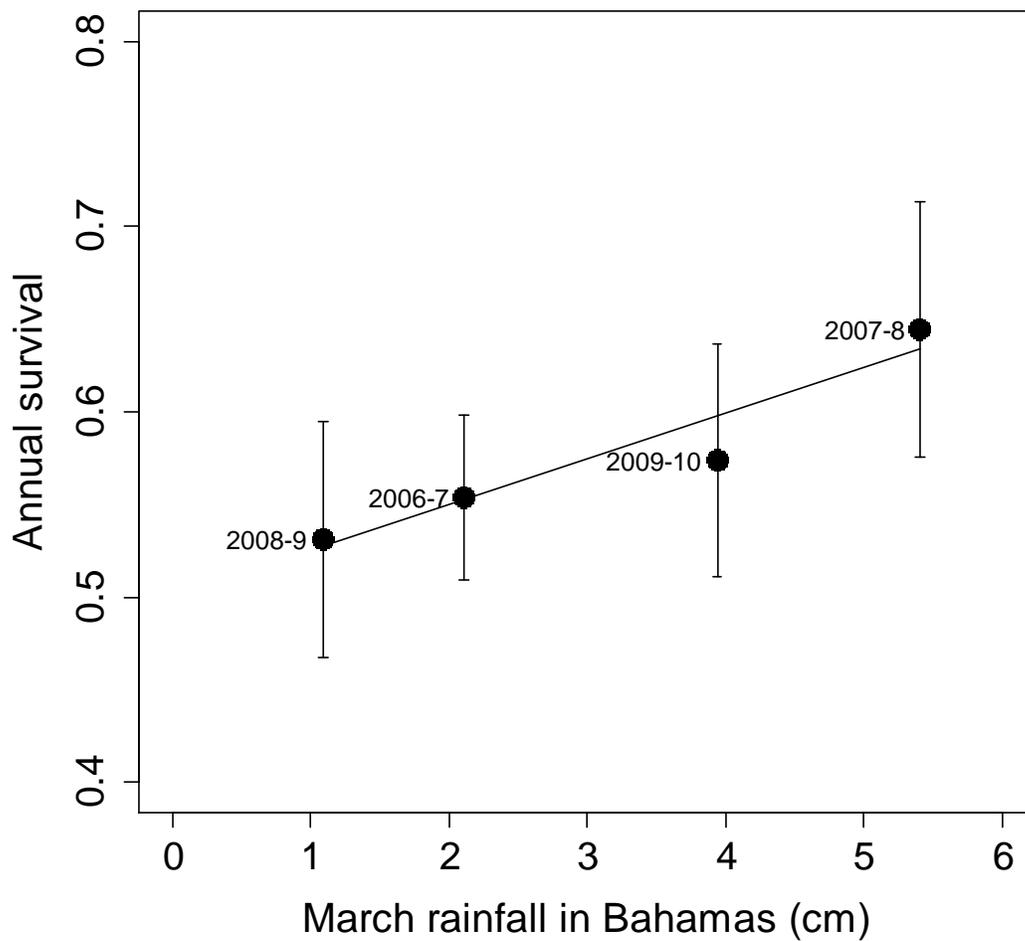


Figure 8. Total March precipitation in the Bahamas predicts annual survival probability of adult male Kirtland's warblers in the subsequent year. Data points are model-averaged annual survival estimates from the final model set for mark-recapture data collected in Michigan, 2006-2011 (see Table 2 for AIC results). Data labels show the intervals over which apparent survival was estimated. Error bars represent ± 1 SE, which were calculated using the Delta method. The linear trend is a simple least-squares regression line, meant for illustration only.

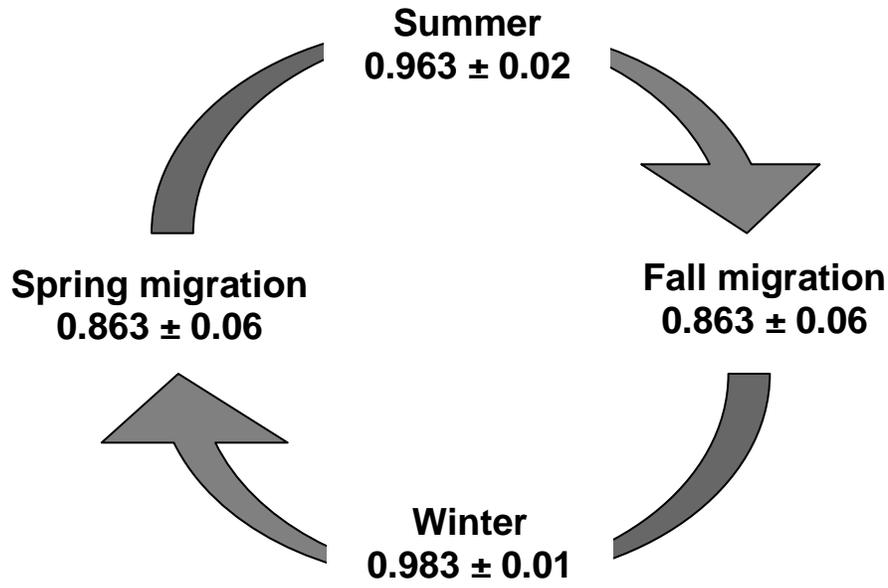


Figure 9. Monthly survival probabilities during four seasonal intervals in the annual cycle of adult male *S. kirtlandii*. Summer = May - Aug survival (4 months), Winter = October - March survival (6 months), Spring migration = April survival, and Fall migration = September survival. Monthly summer survival estimate is the mean \pm SE of years 2006 - 2011, while monthly winter survival estimate is the mean \pm SE of years 2003-2010. Survival estimates during the two migratory months are the square roots of the overall migration estimate (0.745 ± 0.18). Standard errors were calculated using the Delta method.

Appendix A: Isotope data

Table A1. Results of repeated measures linear mixed models for all combinations of isotopes and response variables tested. Tissue samples were collected from male Kirtland's warblers upon spring arrival to breeding grounds, but should reflect isotope signatures of winter habitat and diet. If significant, the p-value and direction of the relationship (+ or -) is given. NS = not significant.

	Arrival date	Body condition	Reproductive success
$\delta^{13}\text{C}$ in blood	p<0.001; +	NS	NS
$\delta^{13}\text{C}$ in toenail	p=0.002; +	NS	NS
$\delta^{15}\text{N}$ in blood	p<0.001; -	NS	NS
$\delta^{15}\text{N}$ in toenail	NS	NS	NS
δD in crown feather	p <0 .001; -	NS	p = 0.02; -

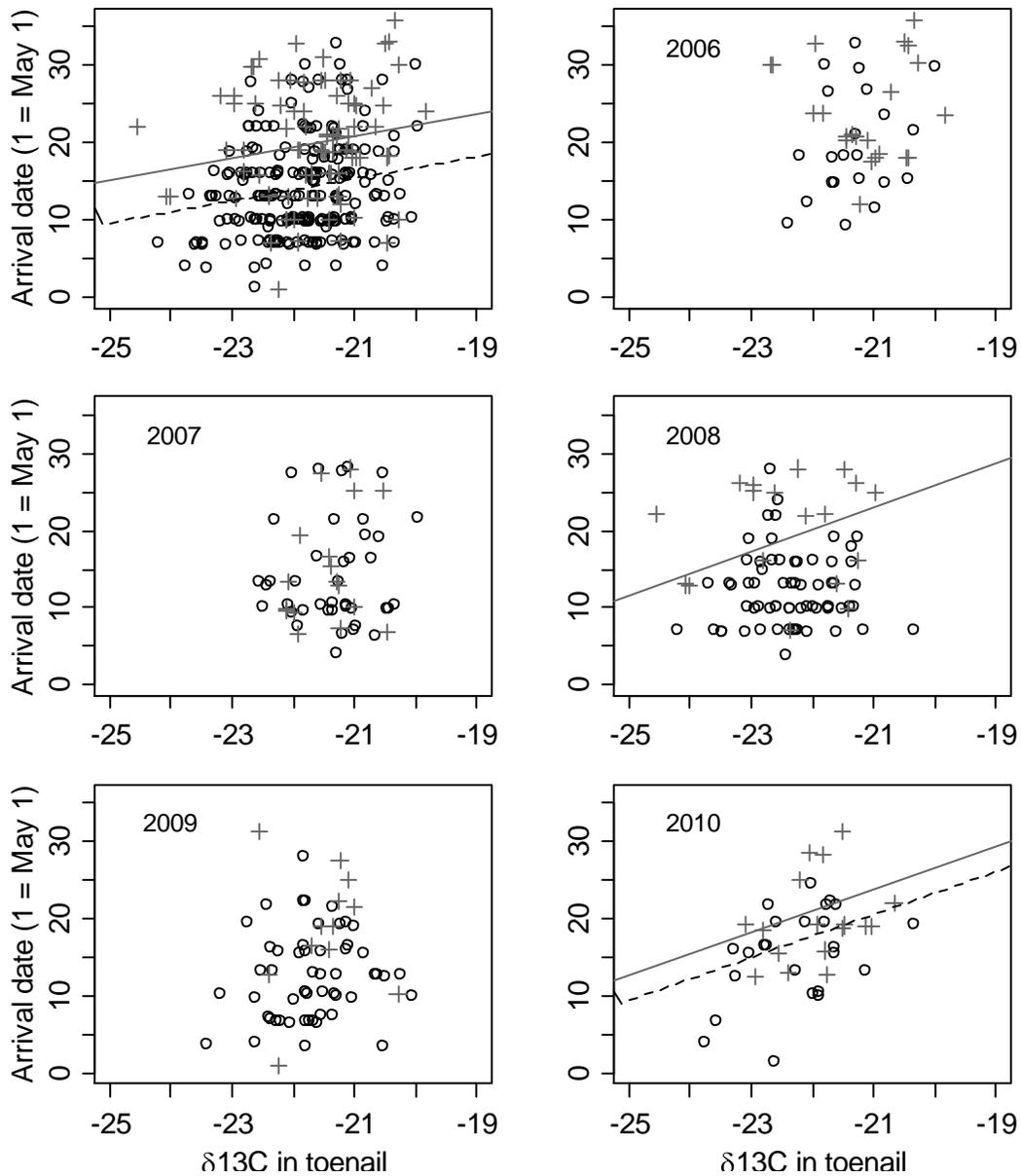


Figure A1. Relationships between $\delta^{13}\text{C}$ in toenail material and spring arrival timing for male Kirtland's warblers sampled upon arrival to Michigan breeding grounds from 2006 – 2010. Each data point represents an individual bird, with ASY males as open circles and SY males as gray crosshatches. Top left panel shows data from all years combined; other panels show data from individual years. Fitted lines are from general linear mixed models including $\delta^{13}\text{C}$ and age as fixed effects, and breeding site (all panels) and individual bird ID (top left panel only) as random effects. Fitted lines are only shown where relationships are significant. ASY males are fitted with dashed black lines and SY males are fitted with solid gray lines.

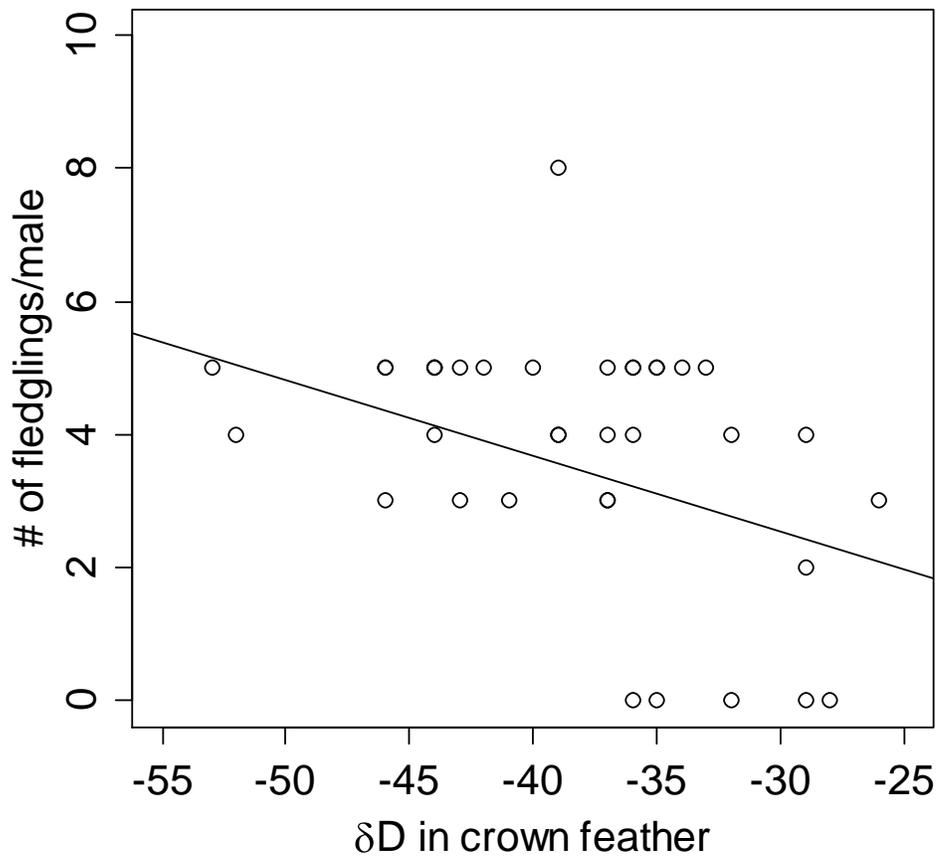


Figure A2. Relationship between δD in crown feathers and spring arrival timing for male Kirtland’s warblers sampled upon arrival to Michigan breeding grounds. Data points represent individual birds in sampled 2007, the only year in which both isotopes in crown feathers and reproductive success were recorded. Fitted line is from a general linear mixed model including δD and age as fixed effects, and breeding site as a random effect. Age was not a significant factor, so males of all ages are pooled.

Appendix B: Reproductive data

Table B1. Summary of reproductive data for Kirtland's warbler males of all ages combined.

	2007	2008	2009	Total	% of total nests	Mean
# of nests found	63	111	105	279	.	.
# of individual males	55	81	85	221	.	.
#depredated	14	34	24	72	0.258	.
#abandoned	1	2	0	3	0.011	.
#parasitized	0	2	0	2	0.007	.
#infertile	2	2	3	7	0.025	.
#successful	44	70	76	190	0.681	.
#undetermined	2	1	2	5	0.018	.
# of renests	5	18	12	35	0.125	.
# of 2nd nests	4	8	13	25	0.090	.
# of nests by 2nd female	1	4	1	6	0.022	.
mean fledglings per male	3.54	2.58	3.76	.	.	3.27
mean fledglings per nest	2.76	2.36	3.04	.	.	2.71

Appendix C: Full AIC tables for survival models

Table C1. Full first model subset of monthly survival (ϕ) and recapture probabilities (p) for male *S. kirtlandii* in Michigan from 2006-2011. Includes number of estimable parameters (K), QAIC_c values, differences between current QAIC_c and QAIC_c value for the best model (Δ QAIC_c), and QAIC_c weights (w_i). Goodness of fit test for the global model (ϕ_{age^*t} , p_t) indicated a minor lack of fit to the data, so a \hat{c} adjustment was used ($\hat{c} = 1.40$).

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	K
{Phi(season)p(t)}	1377.408	0	0.2487	1	13
{Phi(age)p(t)}	1378.077	0.6687	0.17802	0.7158	13
{Phi(year) p(t)}	1378.336	0.9281	0.15637	0.6288	15
{Phi(age+season)p(t)}	1378.589	1.1807	0.13781	0.5541	14
{Phi(age*season)p(t)}	1379.258	1.85	0.09862	0.3965	14
{Phi(.)p(t)}	1379.732	2.3232	0.07784	0.313	11
{Phi(age*year)p(t)}	1379.791	2.3825	0.07557	0.3039	20
{Phi(season*yr) p(t)}	1382.264	4.8553	0.02195	0.0883	18
{Phi(age*season*year) p(t)}	1386.177	8.7687	0.0031	0.0125	25
{Phi(t)p(t)}	1387.067	9.6587	0.00199	0.008	21
{Phi(t*age)p(t)}	1394.529	17.1205	0.00005	0.0002	30
{Phi(t)p(season*yr)}	1420.51	43.102	0	0	18
{Phi(t*age)p(season*yr)}	1425.84	48.4314	0	0	26
{Phi(.)p(season*yr)}	1426.525	49.1165	0	0	9
{Phi(age)p(season*yr)}	1427.679	50.2705	0	0	10
{Phi(year)p(season*yr)}	1427.949	50.5402	0	0	12
{Phi(season)p(season*yr)}	1428.241	50.8328	0	0	10
{Phi(age+season)p(season*yr)}	1429.097	51.6887	0	0	9
{Phi(age*year)p(season*yr)}	1429.238	51.8301	0	0	17
{Phi(age*season)p(season*yr)}	1430.838	53.4293	0	0	12
{Phi(year) p(year)}	1433.283	55.8746	0	0	9
{Phi(season*yr) p(season*yr)}	1433.513	56.1049	0	0	15
{Phi(season)p(year)}	1433.908	56.4993	0	0	7
{Phi(age)p(year)}	1435.955	58.5463	0	0	6
{Phi(age*season)p(year)}	1436.59	59.1821	0	0	9
{Phi(t)p(season)}	1437.137	59.7288	0	0	11
{Phi(t)p(.)}	1438.736	61.328	0	0	10
{Phi(t*age)p(season)}	1439.858	62.4492	0	0	18
{Phi(age*season*yr)p(season*yr)}	1439.899	62.4911	0	0	23
{Phi(t*age)p(.)}	1441.733	64.3245	0	0	17
{Phi(.)p(.)}	1449.998	72.5901	0	0	2
{Phi(.)p(season)}	1450.026	72.6179	0	0	3
{Phi(year)p(season)}	1450.44	73.0317	0	0	7
{Phi(year)p(.)}	1450.813	73.4045	0	0	6
{Phi(age)p(season)}	1450.919	73.5106	0	0	4
{Phi(age)p(.)}	1450.925	73.5166	0	0	3

{Phi(age*year)p(season)}	1451.424	74.016	0	0	12
{Phi(age*year)p(.)}	1451.89	74.4821	0	0	11
{Phi(season)p(season)}	1451.926	74.5181	0	0	4
{Phi(season)p(.)}	1451.968	74.5594	0	0	3
{Phi(age+season)p(.)}	1452.918	75.51	0	0	4
{Phi(age*season)p(season)}	1454.224	76.8153	0	0	6
{Phi(age*season)p(.)}	1454.513	77.1049	0	0	5
{Phi(season*yr) p(season)}	1455.335	77.9263	0	0	10
{Phi(season*yr) p(.)}	1456.082	78.6735	0	0	9
{Phi(age*season*yr)p(season)}	1461.579	84.1711	0	0	18
{Phi(age*season*yr)p(.)}	1462.343	84.9346	0	0	17
{Phi(age+season)p(season)}	1492.972	115.564	0	0	4
{Phi(age*season*yr)p(season)}	1461.579	84.1711	0	0	18
{Phi(age*season*yr)p(.)}	1462.343	84.9346	0	0	17
{Phi(age+season)p(season)}	1492.972	115.564	0	0	4

Table C2. Final model set of monthly survival (ϕ) and recapture probabilities (p) for male *S. kirtlandii* in Michigan from 2006-2011. Includes number of estimable parameters (K), QAIC_c values, differences between current QAIC_c and QAIC_c value for the best model (Δ QAIC_c), and QAIC_c weights (w_i). Goodness of fit test for the global model (ϕ_{age^*t} , p_t) indicated a minor lack of fit to the data, so a \hat{c} adjustment was used ($\hat{c} = 1.40$).

Model	QAIC _c	Delta QAIC _c	QAIC _c Weights	Model Likelihood	K
{Phi(Marchrain)p(t)}	1374.405	0	0.13799	1.00000	13
{Phi(Marchrain+season)p(t)}	1375.142	0.7367	0.09547	0.69190	14
{Phi(Marchrain+age)p(t)}	1375.623	1.2177	0.07506	0.54400	14
{Phi(lwrain)p(t)}	1376.185	1.7805	0.05665	0.41050	13
{Phi(ENSON-1)p(t)}	1376.234	1.8293	0.05529	0.40070	13
{Phi(Marchrain*season)p(t)}	1376.441	2.0356	0.04987	0.36140	15
{Phi(Marchrain+age+season)p(t)}	1376.483	2.0779	0.04882	0.35380	15
{Phi(lwr+season)p(t)}	1376.539	2.1342	0.04747	0.34400	14
{Phi(ENSON-1+season)p(t)}	1376.548	2.1432	0.04726	0.34250	14
{Phi(ENSON-1+age)p(t)}	1376.736	2.3306	0.04303	0.31180	14
{Phi(lwr+age)p(t)}	1376.767	2.3621	0.04236	0.30700	14
{Phi(ENSON-1+age+season)p(t)}	1377.221	2.8157	0.03376	0.24470	15
{Phi(lwr+age+season)p(t)}	1377.294	2.8894	0.03254	0.23580	15
{Phi(season)p(t)}	1377.408	3.0034	0.03074	0.22280	13
{Phi(Marchrain*age)p(t)}	1377.504	3.0993	0.0293	0.21230	15
{Phi(age)p(t)}	1378.077	3.6721	0.022	0.15940	13
{Phi(ENSON-1*age)p(t)}	1378.136	3.7313	0.02136	0.15480	15
{Phi(lwr*age)p(t)}	1378.182	3.7766	0.02088	0.15130	15
{Phi(year)p(t)}	1378.336	3.9315	0.01933	0.14010	15
{Phi(lwr*season)p(t)}	1378.4	3.9949	0.01872	0.13570	15
{Phi(ENSON-1*season)p(t)}	1378.414	4.0095	0.01859	0.13470	15

{Phi(age+season)p(t) - DM}	1378.589	4.1841	0.01703	0.12340	14
{Phi(age*season)p(t)}	1379.258	4.8534	0.01219	0.08830	14
{Phi(.)p(t)}	1379.732	5.3266	0.00962	0.06970	11
{Phi(ENSO _{t-1} *age*season)p(t)}	1380.247	5.8422	0.00743	0.05380	18
{Phi(Marchrain*age*season)p(t)}	1380.742	6.3375	0.0058	0.04200	19
{Phi(lwr*age*season)p(t)}	1383.897	9.4918	0.0012	0.00870	19
{Phi(t)p(t)}	1387.067	12.6621	0.00025	0.00180	21
{Phi(t)p(.)}	1438.736	64.3314	0	0.00000	10
{Phi(.)p(.)}	1449.998	75.5935	0	0.00000	2

Table C3. Full set of models of monthly survival (ϕ) and recapture probabilities (p) for *S. kirtlandii* in the Bahamas from 2003-2010. Includes 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). The global model ($\phi_{sex*age*t}$, p_{sex*t}) provided a good fit to the data.

Model	AIC_c	Delta AIC_c	AIC_c Weights	Model Likelihood	K
{Phi(age*season*year)p(sex*season)}	1856.956	0	0.50943	1	22
{Phi(age*season*year)p(sex*season*year)}	1858.871	1.9147	0.19557	0.3839	41
{Phi(age*season)p(sex*season)}	1860.427	3.4703	0.08985	0.1764	8
{Phi(sex*age*season)p(season*year)}	1861.147	4.1904	0.06268	0.123	22
{Phi(age*season)p(sex*season*year)}	1861.814	4.8575	0.0449	0.0881	29
{Phi(sex*age*season)p(sex*season)}	1862.399	5.4429	0.03351	0.0658	11
{Phi(age*season)p(season*year)}	1863.356	6.3997	0.02077	0.0408	19
{Phi(age*season*year)p(season)}	1864.305	7.3486	0.01292	0.0254	20
{Phi(sex*age*season)p(sex*season*year)}	1864.929	7.9731	0.00946	0.0186	32
{Phi(sex*age*season)p(season) - fixed}	1867.342	10.386	0.00283	0.0056	9
{Phi(sex*age*season*year)p(season*year)}	1868.201	11.245	0.00184	0.0036	43
{Phi(sex*age*season*year)p(sex*season)}	1868.22	11.2641	0.00182	0.0036	34
{Phi(sex*age)p(season*year)}	1868.292	11.3356	0.00176	0.0035	19
{Phi(sex*age*season*year)p(sex*season*year)}	1868.371	11.4146	0.00169	0.0033	50
{Phi(sex*age*season)p(t) - fixed}	1868.565	11.6085	0.00154	0.003	52
{Phi(age)p(sex*season*year)}	1868.584	11.6274	0.00152	0.003	27
{Phi(age)p(season*year)}	1868.729	11.7727	0.00141	0.0028	17
{Phi(age*season)p(season) - fixed}	1869.559	12.6028	0.00093	0.0018	6
{Phi(sex*season)p(season*year)}	1869.724	12.7678	0.00086	0.0017	19
{Phi(age*season)p(t) - fixed}	1869.788	12.8318	0.00083	0.0016	49
{Phi(sex*age*season*year)p(season)}	1869.989	13.0328	0.00075	0.0015	31
{Phi(sex*season)p(sex*season)}	1870.155	13.1989	0.00069	0.0014	8
{Phi(age)p(sex*season)}	1870.571	13.6152	0.00056	0.0011	6
{Phi(sex*age)p(t) - fixed}	1871.487	14.5305	0.00036	0.0007	49
{Phi(sex*season*year)p(sex*season)}	1872.027	15.0703	0.00027	0.0005	26

{Phi(sex*age)p(sex*season*year)}	1872.046	15.0902	0.00027	0.0005	29
{Phi(sex*age)p(sex*season)}	1872.627	15.671	0.0002	0.0004	8
{Phi(sex*season)p(sex*season*year)}	1872.662	15.7062	0.0002	0.0004	29
{Phi(sex*season*year)p(sex*season*year)}	1874.084	17.1279	0.0001	0.0002	44
{Phi(season*year)p(sex*season)}	1874.621	17.665	0.00007	0.0001	17
{Phi(t) p(sex*season)}	1875.244	18.2873	0.00005	0.0001	26
{Phi(season)p(sex*season)}	1875.567	18.6107	0.00005	0.0001	6
{Phi(sex)p(season*year)}	1875.575	18.6184	0.00005	0.0001	17
{Phi(sex*t) p(season)}	1876.308	19.3521	0.00003	0.0001	41
{Phi(age*season*year)p(sex)}	1876.531	19.5752	0.00003	0.0001	19
{Phi(sex*season*year)p(season*year)}	1876.648	19.6913	0.00003	0.0001	37
{Phi(season*year)p(sex*season*year)}	1876.676	19.7197	0.00003	0.0001	37
{Phi(sex*season)p(season)}	1876.735	19.7788	0.00003	0.0001	6
{Phi(sex)p(sex*season)}	1877.702	20.7456	0.00002	0	6
{Phi(season)p(sex*season*year)}	1877.735	20.7783	0.00002	0	27
{Phi(sex*age)p(season) - fixed}	1878.165	21.2088	0.00001	0	6
{Phi(sex*season)p(t)}	1878.299	21.3432	0.00001	0	50
{Phi(sex)p(sex*season*year)}	1878.443	21.4863	0.00001	0	27
{Phi(t) p(season)}	1880.083	23.1271	0	0	23
{Phi(sex*season*year)p(season)}	1880.171	23.2146	0	0	25
{phi(.)p(sex*season*year)}	1880.309	23.3528	0	0	26
{Phi(age*season)p(sex)}	1881.145	24.1889	0	0	6
{phi(.)p(sex*season)}	1881.284	24.3279	0	0	5
{Phi(t) p(sex*season*year)}	1881.518	24.5621	0	0	46
{Phi(sex*age*season)p(sex)}	1883.144	26.1882	0	0	9
{Phi(t) p(season*year)}	1883.319	26.3623	0	0	38
{Phi(sex*age*season)p(.)}	1884.48	27.5241	0	0	6
{Phi(year)p(sex*season)}	1884.835	27.8789	0	0	11
{Phi(sex)p(season)}	1884.864	27.9075	0	0	4
{phi(.)p(season*year)}	1884.927	27.971	0	0	16
{Phi(season)p(season*year)}	1884.927	27.971	0	0	17
{Phi(sex*year)p(sex*season)}	1886.597	29.6406	0	0	19
{Phi(sex*year)p(season*year)}	1887.323	30.367	0	0	30
{Phi(sex*year)p(sex*season*year)}	1887.356	30.3996	0	0	38
{Phi(season*year)p(season)}	1887.405	30.4486	0	0	15
{Phi(age*season*year)p(t)}	1887.42	30.4641	0	0	66
{Phi(age*season*year)p(sex*year)}	1888.304	31.348	0	0	32
{Phi(season*year)p(season*year)}	1888.534	31.5777	0	0	29
{Phi(year)p(sex*season*year)}	1888.736	31.7796	0	0	32
{Phi(age*season*year)p(.)}	1889.063	32.107	0	0	20
{Phi(age*season)p(.)}	1890.63	33.6733	0	0	5
{Phi(age*season*year)p(year)}	1891.327	34.371	0	0	25
{Phi(season)p(season)}	1891.641	34.6844	0	0	4

{Phi(.) p(t) PIM}	1892.209	35.2526	0	0	48
{Phi(year)p(season*year)}	1892.382	35.4257	0	0	22
{Phi(sex*year)p(season)}	1892.953	35.9965	0	0	17
{Phi(sex*age*season)p(year)}	1893.312	36.3558	0	0	15
{Phi(age*season)p(sex*year)}	1894.749	37.7923	0	0	21
{Phi(sex*age*season)p(sex*year)}	1895.944	38.9874	0	0	23
{Phi(year)p(season)}	1896.189	39.2332	0	0	9
{Phi(age*season)p(year)}	1897.378	40.4218	0	0	13
{Phi(sex*season)p(.)}	1897.416	40.4602	0	0	4
{Phi(season*year)p(t)}	1907.523	50.5665	0	0	60
{Phi(age*season)p(sex*t)}	1908.563	51.6069	0	0	85
{Phi(t) p(t) PIM}	1909.002	52.0458	0	0	70
{Phi(t) p(.) PIM}	1909.742	52.7862	0	0	22
{Phi(sex*age*season)p(sex*t)}	1911.441	54.4847	0	0	88
{Phi(sex*age)p(.) - fixed}	1911.468	54.512	0	0	5
{Phi(age)p(.) - fixed}	1911.881	54.9246	0	0	3
{Phi(season)p(.)}	1915.391	58.4351	0	0	3
{Phi(sex)p(.)}	1917.541	60.5852	0	0	3
{Phi(sex*age*t) p(sex*t)}	1922.179	65.2231	0	0	117
{Phi(age*season*year)p(sex*t)}	1922.285	65.3288	0	0	98
{Phi(.)p(.)}	1926.146	69.1895	0	0	2
{Phi(.) p(.) PIM}	1926.146	69.1895	0	0	2
{Phi(year)p(year)}	1936.382	79.4254	0	0	16

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