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Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's Warbler (*Setophaga kirtlandii*) (Efectos Diferidos del Clima Invernal en la Fecha de Llegada en Primavera y en el Éxito Reproductivo de *Setophaga kirtlandii*, un Ave Migratoria Amenazada)

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Reviewed work(s):

Source: *The Auk*, Vol. 129, No. 4 (October 2012), pp. 744-752

Published by: [University of California Press](#) on behalf of the [American Ornithologists' Union](#)

Stable URL: <http://www.jstor.org/stable/10.1525/auk.2012.12003>

Accessed: 11/12/2012 15:59

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CARRY-OVER EFFECTS OF WINTER CLIMATE ON SPRING ARRIVAL DATE AND REPRODUCTIVE SUCCESS IN AN ENDANGERED MIGRATORY BIRD, KIRTLAND'S WARBLER (*SETOPHAGA KIRTLANDII*)

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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 because of the wide range of geographic areas that they depend on throughout the annual cycle. We examined the potential effects of non-breeding season climate change on the breeding biology of Kirtland's Warbler (*Setophaga kirtlandii*, formerly *Dendroica kirtlandii*), an endangered songbird that breeds in the Northern Lower Peninsula of Michigan and winters in the Bahamas. Our objectives were to determine whether spring arrival dates on the breeding grounds correlate 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 * rainfall interaction, which indicates 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. *Received 6 January 2012, accepted 30 March 2012.*

Key words: arrival dates, climate change, Kirtland's Warbler, migratory birds, reproductive success, *Setophaga kirtlandii*, winter rainfall.

Efectos Diferidos del Clima Invernal en la Fecha de Llegada en Primavera y en el Éxito Reproductivo de *Setophaga kirtlandii*, un Ave Migratoria Amenazada

RESUMEN.—Comprender cómo los animales se adaptan al cambio climático requiere entender cómo las variables climáticas afectan su biología a lo largo del año, y cómo interactúan los eventos sucedidos en diferentes temporadas. Las aves migratorias pueden ser especialmente vulnerables dado el amplio espectro de áreas geográficas de las que ellas dependen a lo largo del ciclo anual. Examinamos los efectos potenciales del cambio climático en las temporadas no reproductivas sobre la biología reproductiva de *Setophaga kirtlandii* (antes *Dendroica kirtlandii*), un ave canora amenazada que se reproduce en el norte de la península inferior de Michigan y pasa el invierno en las Bahamas. Nuestros objetivos fueron determinar si las fechas de llegada a las áreas de reproducción en primavera se correlacionan con la precipitación del final del invierno en las áreas no reproductivas, y si lo anterior tiene consecuencias sobre el éxito reproductivo. Usamos datos de las fechas de llegada en primavera y el número de volantones por año, muestreando múltiples individuos a lo largo de múltiples años, y logramos demostrar que los machos llegan a las áreas de reproducción más tarde luego de inviernos más secos. Hubo una interacción fuerte entre la edad de los machos y la precipitación, de modo que los que se reproducían por primera vez fueron mucho más sensibles a los cambios en la precipitación que los adultos más experimentados. Sin embargo, independientemente de la edad, los inviernos más secos y la llegada e iniciación tardía de la nidación estuvieron significativamente asociados con un menor número de crías emplumadas. Estos resultados son importantes porque la región Caribe actualmente está experimentando una tendencia hacia la aridez y los modelos de cambio climático predicen que la severidad de la sequía continuará incrementándose. Cualquier desajuste en la sincronización de la migración que se produzca como consecuencia de lo anterior podría restringir las fechas de arribo en la primavera y limitar el éxito reproductivo de *S. kirtlandii*, así como de otros migrantes neotropicales que pasan el invierno en el Caribe.

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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 proved difficult, yet this information is critical for developing adaptive management plans. 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, Marra et al. 2005, Sparks et al. 2005) and the potential negative consequences for productivity (Visser et al. 1998, Both and Visser 2001, Both et al. 2010), but researchers have only recently begun to recognize the importance of winter climate on migratory bird ecology (Sillert 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, which suggests 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, Johnson and Sherry 2001, 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 bird's 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 American Redstarts shows that spatial variation in rainfall across their winter range explains spring arrival dates in different breeding populations (A. E. McKellar et al. unpubl. data).

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 the present study, Kirtland's Warbler (*S. kirtlandii*), showed a positive relationship between winter rainfall and number of singing males observed on the breeding grounds in the subsequent spring from 1971 to 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 (Sillert 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, whether 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.

Here, we examine the effects of winter climate on spring arrival dates, body condition, and reproductive success in Kirtland's Warbler, an endangered songbird that breeds in the Northern Lower Peninsula of Michigan and winters primarily in the Bahamas. Management of breeding habitat has led to a substantial increase in its 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 of Kirtland's Warblers are correlated with late winter rainfall in the Bahamas. Kirtland's Warbler is an excellent study species for these questions. Their 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.—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). It is a disturbance-adapted species, specializing in Jack Pine (*Pinus banksiana*) barrens that were historically maintained by wildfires. Kirtland's Warblers prefer large (>32 ha), fairly homogeneous stands of Jack Pine that grow on well-drained, sandy soils. Stands must be relatively young (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, and low coppice, which are maintained by anthropogenic disturbance, fire, and hurricanes (Sykes and Clench 1998, Wunderle et al. 2007). Unlike most other warbler species, they 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 because of modern fire suppression practices led to a precipitous decline in Kirtland's Warbler numbers. The species was listed as federally endangered in 1973 (Byelich et al. 1976). Currently, 76,900 ha are designated Kirtland's Warbler Management Areas, and these are managed on a 50-year rotation so that 15,380 ha 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). The Kirtland's Warbler population has since increased steadily from an estimated 200 singing males in the 1970s and 1980s to ~1,800 in 2011 (U.S. Fish and Wildlife Service 2011).

Field sites.—Our study sites included ten 30-ha plots located in Alcona, Crawford, Iosco, Ogemaw, and Oscoda counties in the Northern Lower Peninsula of Michigan (Fig. 1). Each plot was established using a global positioning system, 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 Sandcherry (*Prunus pumila*). Groundcover 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*

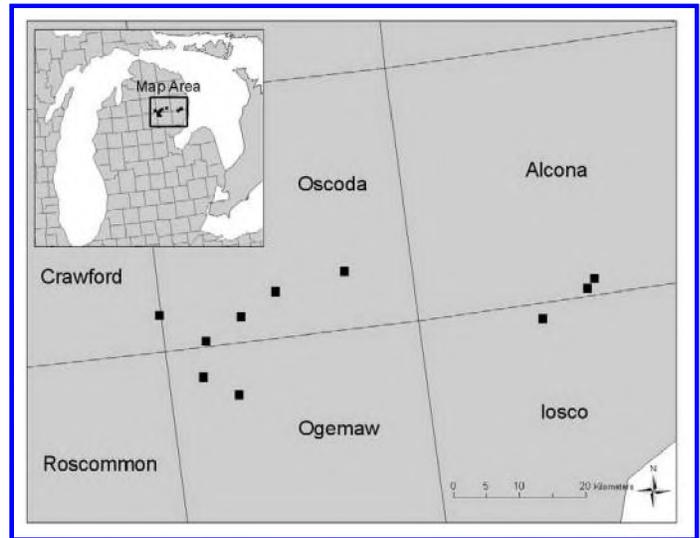


FIG. 1. Distribution of ten 30-ha study sites located within Kirtland's Warbler Management Areas in the Northern Lower Peninsula of Michigan, 2006–2010. Inset shows location of the study area within Michigan, USA.

pennsylvanica) 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 3 days, beginning on 1 May, for the arrival of new males from 2006 to 2010. Plots were surveyed by multiple observers walking along transects 200–300 m 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 1, 2, or 3 May were recorded as arrival date 1). Numbered days starting with 1 May are used throughout (1 = 1 May). 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 aluminum band. Males were aged as either first-time breeders (second-year [SY]) or adults returning to breed (after-second-year [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 to 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, thus, 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 parental behaviors indicative of the presence of dependent young (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 renests 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 (see Acknowledgments). 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 non-breeding 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 it 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-square likelihood ratio test with one degree of freedom. Nonsignificant 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 nonsignificant interactions were removed from final models. All analyses were performed in R (R Foundation for Statistical Computing, Vienna). Results are presented as means \pm SE.

RESULTS

Arrival dates and reproductive success.—Male Kirtland's Warblers returning to northern breeding areas had arrival dates ranging from 2 May to 5 June, with a global mean of day 14.6 ± 0.36 days. 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 3 years, 66 in 2 years, and the remaining 191 individuals were observed in only 1 year. Males that arrived earlier on spring breeding grounds had mates that initiated clutches earlier (arrival date: $\chi^2 = 89.8$, $df = 1$, $P < 0.001$; Fig. 2A). Early-arriving males also fledged more offspring (arrival date: $\chi^2 = 89.5$, $df = 1$, $P < 0.001$; Fig. 2B), and the slope of this relationship did not vary with age (arrival date * age: $\chi^2 = 0.15$, $df = 1$, $P = 0.70$). A 10-day delay

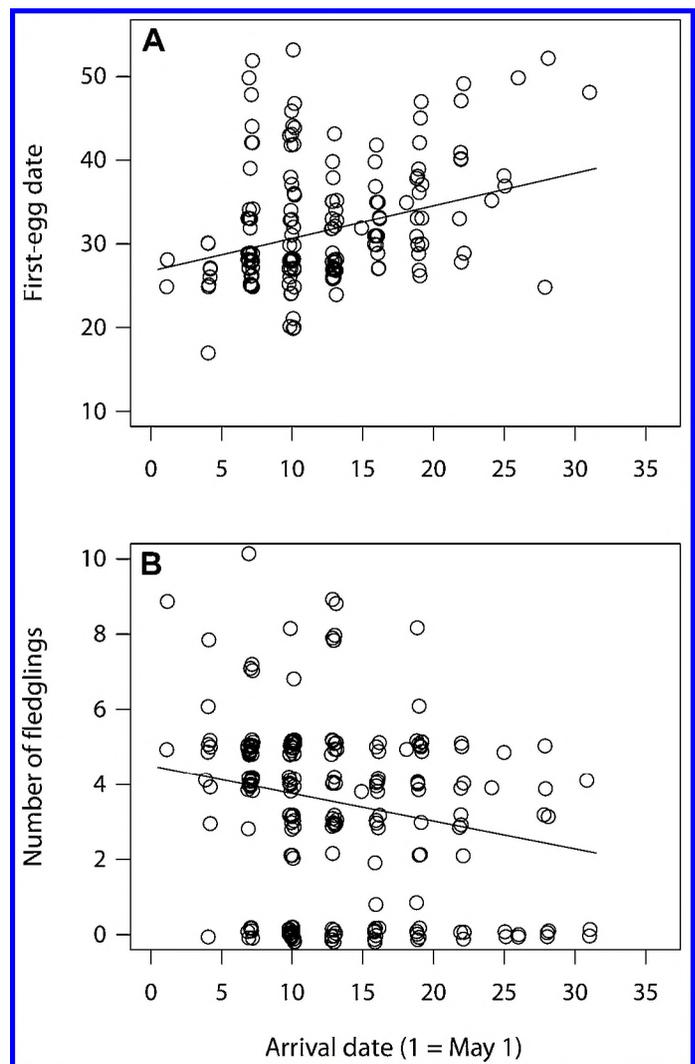


FIG. 2. Spring arrival dates at breeding grounds explain (A) first-egg dates and (B) yearly reproductive success (number of fledglings per male per season) of male Kirtland's Warblers of all age classes. Data were collected in the Northern Lower Peninsula of Michigan in 2007–2009. Each data point represents 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.

in arrival was associated with 0.74 fewer fledglings raised, on average; this is equivalent to a difference in reproductive success of >2.5 fledglings year⁻¹ across the range of spring arrival dates in our study ($\beta = -0.074 \pm 0.03$; Fig. 2B). 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 males arrived at spring breeding grounds in advance of SY 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 * age interaction (rainfall * 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: $\beta = -1.42 \pm 0.40$; Fig. 3A), whereas arrival dates of adult males remained relatively constant (ASY males: $\beta = -0.12 \pm 0.19$; Fig. 3A). The random effect of 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, but the effect size was small ($\beta = 0.02 \pm 0.02$) and not significant (rainfall: $\chi^2 = 1.09$, $df = 1$, $P = 0.30$). Adult males arrived in significantly better body condition than SY 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 test for an association between winter rainfall and the number of young fledged, we recorded annual reproductive success 232 times for 169 individuals, including 50 SY and 182 ASY males. Reproductive success of 5 males was recorded in all 3 years, 53 were recorded in 2 years, and the remaining 111 individuals were recorded in 1 year. Male annual reproductive success ranged from zero to 10 offspring, with a global mean of 3.3 ± 0.16 fledglings year⁻¹. No males had >2 successful nests, and only 1 male attempted 3 nests, within a single breeding season. Adult males raised significantly more fledglings than SY 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, males raised 0.23 additional fledglings for every 1-cm increase in March rainfall ($\beta = 0.23 \pm 0.09$; Fig. 3B), and this pattern did not vary between age classes (rainfall * 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 males of all ages experienced 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

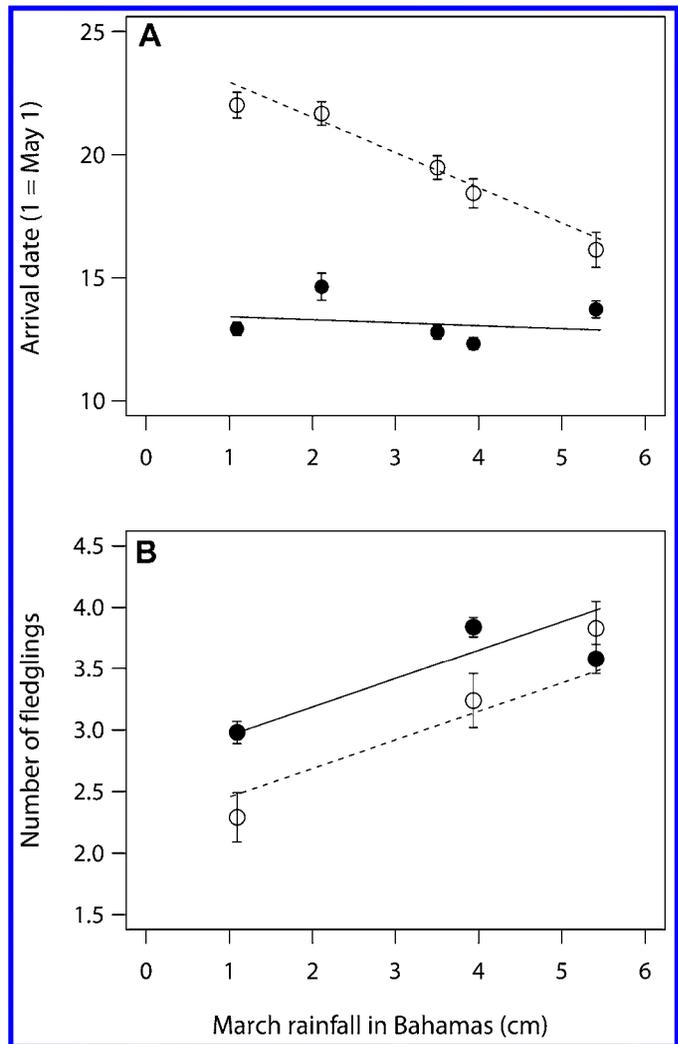


FIG. 3. Total March rainfall in the Bahamas predicts (A) spring arrival dates in 2006–2010 and (B) yearly reproductive success (number of fledglings per male per season) in 2007–2009 for male Kirtland's Warblers in the Northern Lower Peninsula of Michigan. Data points are predicted values (means \pm 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. After-second-year males are represented by filled circles with a solid fitted line, and second-year males are represented by open circles with a dashed fitted line.

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 for ASY males (Fig. 3A), with younger males delaying arrival by 1.4 days for every 1-cm reduction in precipitation. Two non-mutually exclusive explanations for this pattern are possible. First, ASY males may be socially dominant, and

they may 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 exhibit higher overwinter site persistence and increase premigration body condition faster than SY males and females, which suggests 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). 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 fruits 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, therefore, cannot maintain body condition and advance migratory fattening as well as ASY males in dry conditions (Smith et al. 2010). Adult male Kirtland's Warblers increase premigration 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, whereas the arrival schedules of older males are less affected by winter drought conditions.

We found that male Kirtland's Warblers of all age classes were able to increase productivity by an average of 0.23 fledglings year⁻¹ for every 1-cm increase in March rainfall (Fig. 3B). Within the observed range of precipitation during our study (1.09–5.41 cm), this could account for a difference of 1 fledgling male⁻¹ year⁻¹. 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, which maintained 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. Female Kirtland's Warblers 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) have been documented in other migratory bird species. The fact that adult male Kirtland's Warblers increase premigration 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 in the Bahamas 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 Kirtland's Warblers in poor condition prior to spring departure may be forced to stay longer in the Bahamas or migrate more slowly to compensate for a body-condition deficit after dry winters. This would result in later arrival for some males but relatively equal postmigration 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, we would expect to see the differences we observed in spring arrival dates without corresponding variation in body condition upon arrival.

Male Kirtland's Warblers had mates that delayed clutch initiation by 0.39 days for each day of later male arrival on spring breeding grounds (Fig. 2A). 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 (Fig. 2B). This difference is likely to be biologically important, because the range of arrival dates of males in our study was >30 days, leading to a difference in male annual reproduction of >2 whole fledglings (Fig. 2B). 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, Cooper et al. 2011), which would exacerbate differences due to arrival dates. This likely only made our test more conservative, rather than changing 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 that have reported 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, Cooper et al. 2011). 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 renests and second clutches (Marra et al. 1998, Visser et al. 2003, Norris et al. 2004, Cooper et al. 2011). 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 the hatching failure of some species may be greater (Perrins 1970, Martin 1987, Rowe et al. 1994). The clutch size of first nest attempts in Kirtland's Warblers decreases significantly with first-egg date, even among the same individual males (see above). In fact, there appears to be a threshold effect: males that arrive after a certain date are unable to complete more than one successful nest per season. No males that arrived after 19 May were able to raise >5 fledglings year⁻¹, the clutch size of a typical nest (Fig. 2B), or to complete two successful nesting cycles in a season (S. M. Rockwell unpubl. data).

Our findings support those of other studies in 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 SOI, are associated with increased numbers of young in the subsequent breeding season (Nott et al. 2002, Mazerolle et al. 2005). Winters with more rainfall are also correlated with greater population sizes of migratory birds in the following year (Ryel 1981, Peach et al. 1991, Baillie and Peach 1992, Wilson et al. 2011). Our findings that winter rainfall is correlated with arrival dates on breeding areas and with reproductive success augment existing evidence that winter weather can carry over to affect population processes during the subsequent breeding season (Peach et al. 1991, Baillie and Peach 1992, Szép 1995, Saino et al. 2004, Reudink et al. 2009, Wilson et al. 2011, A. E. McKellar et al. unpubl. data). 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). Evidence from current field studies shows that (1) winter home ranges of Kirtland's Warblers in the Bahamas must overlap as the drought season progresses (Wunderle et al. 2010) and (2) adult males may competitively exclude others from accessing resources (J. M. Wunderle unpubl. data). Taken together with our results, these lines of evidence indicate 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. Although the duration of the present study (5 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 to 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 premigratory 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 winter in the Caribbean, and these species also have the potential to be negatively affected by prolonged drying trends in overwintering habitats. Our study highlights the importance of creating conservation partnerships to protect high-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 such a comprehensive and integrated approach will lead to accurate predictions of how populations will respond, and possibly adapt, to a changing climate.

ACKNOWLEDGMENTS

This research was supported by funding from the American Ornithologists' Union, Cooper Ornithological Society, Manomet Center for Conservation Science, Smithsonian Institution,

University of Maryland, U.S. Fish and Wildlife Service, and U.S. Forest Service. We thank M. Thomas, E. Joseph, R. Badia, R. Slebodnik, A. Frazee, S. Brounce, A. Demko, P. Falatek, E. Banfield, L. Williams, M. Thomas, A. Rogers, B. Kaimal, V. Shevade, and D. Wloch for their hard work in the field. We are grateful to J. Wunderle for sharing his findings, D. Ewert for assistance in the field, C. Studds for help with field work and statistical analyses, and P. Blank for GIS assistance. This work was done in cooperation with the Kirtland's Warbler Recovery Team, who granted their support and access to field sites. D. Inouye, T. S. Sillett, and two anonymous reviewers provided comments that helped improve the manuscript. The National Climatic Data Center of the National Oceanic and Atmospheric Association is available online at www7.ncdc.noaa.gov/IPSMCDW/mcdw.html.

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Associate Editor: J. Jones