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DURATION AND RATE OF SPRING MIGRATION OF KIRTLAND'S WARBLERS

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ABSTRACT.—The duration of migration of the endangered Kirtland's Warbler (*Setophaga kirtlandii*) has not been previously documented. We estimated the average duration of spring migration for five male Kirtland's Warblers by observing uniquely color-banded individuals at or near both the beginning and end of spring migration in Eleuthera, The Bahamas, and Michigan, respectively. We estimated the average duration of spring migration for these five individuals to have been no more than 15.8 days (range 13–23 days) and the average distance traveled to have been 144.5 km/day (96.1–169.1 km/day). *Received 12 April 2011. Accepted 11 November 2011.*

The migratory period is typically the most poorly understood aspect of a migratory species' life history (Faaborg et al. 2010a, b) because of difficulties in studying birds during migration. This information gap constrains our ability to comprehensively describe population demographics, and reduces our ability to effectively implement conservation measures (Faaborg et al. 2010a, b) as mortality of adult migratory songbirds is apparently high during migration (Sillett and Holmes 2002). Lack of information on duration of migration, and its relationship to breeding and wintering season conditions, limits our ability to infer sensitivity of populations to changes in the amount and distribution of habitat required by migrating birds (Faaborg et al. 2010b). The challenge of understanding duration of migration, and integrating this information into models of avian population dynamics, is pressing for rare migratory landbirds that are infrequently observed during migration.

Models that help explain duration of migration are complex, as many possible intrinsic (e.g., body condition, experience) and extrinsic (e.g., weather, habitat distribution, stopover site conditions) factors influence rates and total duration of migration. For example, Cochran and Wikelski (2005) developed a model for *Catharus* thrushes based on the condition of an individual, weather conditions, orientation of flight, and flight duration on any given night; they predicted it could take up to 40 days for an individual to travel between the Gulf Coast of Louisiana and its Canadian breeding areas.

Estimates of migration duration for passerines have largely been based on extrapolations from banding recoveries of birds *en route* (Ellegren 1993, Fransson 1995, Newton 2008, Yohannes et al. 2009) rather than documented departure and arrival dates of individual birds from wintering and breeding areas. However, given potential differences in rates of migration along different portions of the route (Stutchbury et al. 2011), duration estimates for banded birds are best obtained over the complete migration (Fransson 1995, Yohannes et al. 2009). New technologies, such as geolocators, now enable researchers to describe the location and duration of migration for individual birds (Stutchbury et al. 2009, 2011; Bächler et al. 2010, Robinson et al. 2010, Bridge et al. 2011, Heckscher et al. 2011, Ryder et al. 2011). Use of these techniques is currently limited to species larger than small passerines and, even as the weight of geolocators continues to decrease, their use must be carefully evaluated for imperiled species. Only in rare cases can we estimate duration of an individual's migration based on observations of birds with unique color-band combinations at the beginning and ending of migration.

We report empirical estimates of the duration of spring migration for uniquely color-banded individual Kirtland's Warblers (*Setophaga kirtlandii*) observed in the field at the beginning and ending

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of migration. The Kirtland's Warbler, a species designated as federally endangered in the United States and Canada, has a small core breeding range (~716 km^2), and breeds almost exclusively in one distinct habitat type, young stands of jack pine (*Pinus banksiana*) on sandy outwash soils in the northern Lower Peninsula of Michigan (Mayfield 1960, Donner et al. 2008). Small numbers of birds also breed in similar habitat in Michigan's Upper Peninsula, Wisconsin (Probst et al. 2003, Trick et al. 2008), and southern Ontario (Richard 2008). The total number of singing male Kirtland's Warblers was estimated to be 1,750 in 2010 (Elaine Carlson, pers. comm.). This warbler is one of a few passerine species for which it is feasible to search breeding areas for individuals color-banded in wintering areas because locations of all singing males are mapped during an annual population survey (Probst et al. 2005); there are a relatively small number of birds and sites to check for arriving color-banded individuals.

Our objective was to document the duration of spring migration for individual Kirtland's Warblers based on field observations of departure and arrival times of uniquely color-banded birds. To our knowledge, these estimates of spring migration duration of Kirtland's Warblers are the first derived from observations of the same color-banded individuals in wintering and breeding areas. They also provide comparative data for estimates of migration rates and duration generated from other methods.

METHODS

Teams based in The Bahamas, Michigan, Wisconsin, and Ontario searched the Kirtland's Warbler winter and breeding habitat to estimate duration of migration as part of a coordinated effort to study linkages between winter and summer ranges. We captured 232 Kirtland's Warblers from 2002 to 2010 in mist nets and color-banded birds at several sites (Wunderle et al. 2010) within 30 km of each other on southern Eleuthera, The Bahamas (~25° N, 76° W; Fig. 1). Many of the banded individuals were observed repeatedly during a given wintering season. We visited Eleuthera sites with several color-banded Kirtland's Warblers three to 15 times/season from mid-April through 1 May 2003–2010 to document a date as close to departure as possible. Many of these warblers show winter site fidelity (Sykes and Clench 1998, Wunderle et al. 2010), but relocating birds in winter is challenging because some individuals move to different sites, and are difficult to locate and identify in the thick shrubby habitats.

The Kirtland's Warbler breeding habitat was searched for color-banded birds from 2003 to 2010. This species often shows breeding site fidelity (Walkinshaw 1983, Mayfield 1992, Bocetti 1994; SMR, unpubl. data), like many territorial migrant landbirds, although a few birds disperse to new sites between years (Walkinshaw 1983; DNE and KRH, unpubl. data). We could often estimate arrival dates of individuals returning to their territories the following spring by checking sites occupied by banded warblers in previous years. Our searches focused on a subset of banded birds that we were able to relocate between mid-to-late April in The Bahamas, for which we had georeferenced their breeding territories in the Lower Peninsula of Michigan in previous years.

We monitored territories for a minimum of 30 min/day every 1 to 3 days from early May through 30 May or until the bird was found. Observers walked through an area encompassing roughly a 200–400 m radius around the georeferenced site during these visits, searching for color-banded birds. Data for birds with known territories were supplemented with records of individuals for which we had recorded last observation dates from Eleuthera in mid-to-late April and then opportunistically observed the same bird in Michigan while systematically searching for returning territory holders. Field work was initiated each spring, soon after the first confirmed arrival date of a Kirtland's Warbler in the breeding areas.

We calculated each individual's duration of migration, and average distance covered per day from these departure and arrival date estimates. Duration was estimated by calculating the number of nights between the last observation date in The Bahamas (assuming the bird left on the night of the last date it was observed) and the night previous to the first observation in Michigan. The interval between these dates represents the maximum duration of migration. Actual times of migration could be less than the durations reported here because an individual may not have departed immediately following the last Bahamas observation. In addition, individuals may not have been observed on their first day of arrival in Michigan, especially males that did not sing within our sampling period or females. Average

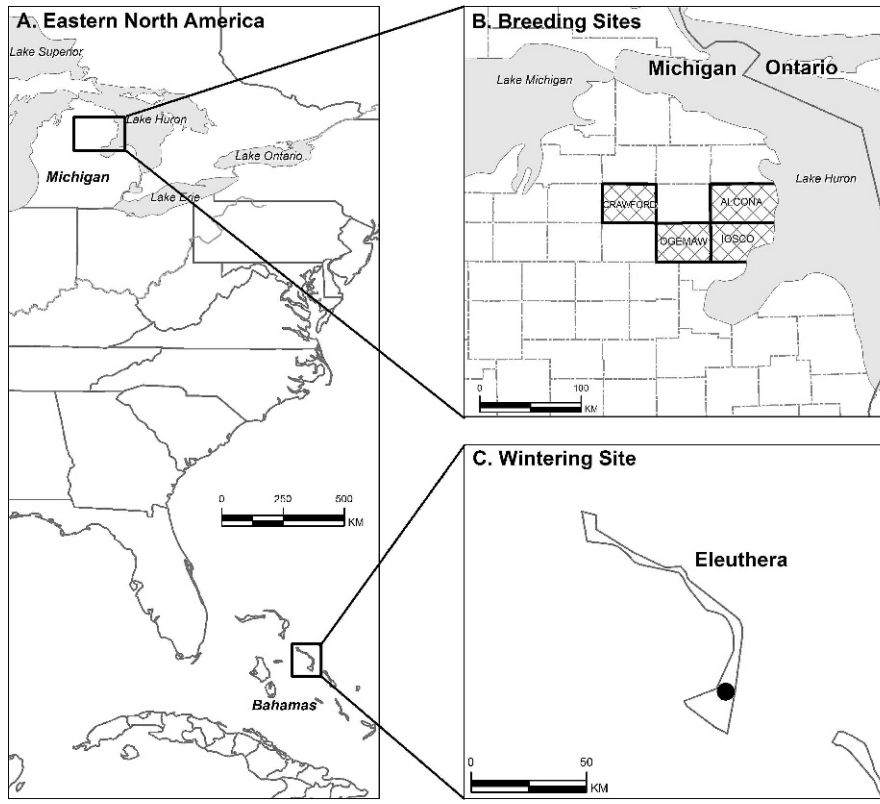

FIG. 1. (A) Approximate breeding and wintering locations of color-banded Kirtland's Warblers for which we estimated duration and distance of spring migration. (B) Breeding locations of color-banded Kirtland's Warblers in the Lower Peninsula of Michigan by county. (C) Approximate location of wintering sites sampled on southern Eleuthera, The Bahamas (described in Wunderle et al. 2010).

distance traveled/day was calculated by dividing the linear distance traveled between wintering and breeding areas by the number of nights between the last observation of an individual on Eleuthera and the first observation of the same bird in Michigan. Values for both the maximum duration of migration and average distance traveled/day are presented as means ± SD.

RESULTS

Kirtland's Warblers were consistently seen on Eleuthera through late April 2003–2010 (Wunderle et al., unpubl. data) with the latest date in any year being 2 May 2006. First arrival dates of males reported anywhere in the Lower Peninsula of Michigan ranged from 2 to 7 May during our study and the total number of Bahamas-banded Kirtland's Warblers observed in breeding areas during the study period in any given year was 7 to 23 (Table 1). In comparison, mean arrival dates of males from 2006 to 2010 ranged from 13 to 22 May for the warblers at a subset of Kirtland's Warbler sites in Michigan's Lower Peninsula (SMR, unpubl. data).

The estimated mean duration of migration for five uniquely color-banded male Kirtland's Warblers observed in breeding areas (Fig. 1) was 15.8 ± 4.2 days (Table 2). Four of these five birds were observed on the first day the territory was checked and the fifth (band # 2221-08906) was observed 3 days after the territory was last visited. Thus, it is likely the actual mean duration of spring migration for these five individuals was less than the calculated mean of 15.8 days. The mean distance traveled/day, based on this estimated duration, was 144.5 ± 31.2 km.

Some observations were not included in our calculations of mean duration of migration because the birds were found opportunistically, and were not detected until relatively late in May,

TABLE 1. Number of color-banded Kirtland's Warblers from southern Eleuthera, The Bahamas found in breeding areas and dates of first observation of males in the Lower Peninsula of Michigan.

Year	Number found in breeding areas	First observation
2005	8	7 May
2006	12	4 May
2007	23	5 May
2008	14	4 May
2009	16	3 May
2010	7	2 May

after the arrival date for most individuals. For example, the range of maximum duration of migration observed for an additional subset of birds, last seen on Eleuthera in mid-to-late April, that were found relatively late in the breeding season in Michigan, was 27–48 days. We also documented that one female, last seen on 27 April 2006 on Eleuthera and first seen in Michigan on 24 May 2006, had a maximum migration duration of 27 days. Estimating arrival dates of females is particularly difficult, even with systematic searches, as they do not sing and may escape detection.

DISCUSSION

The maximum duration of spring migration for male Kirtland's Warblers from Eleuthera (range = 13–23 days) was shorter than predicted based on models developed for thrushes by Cochran and Wikelski (2005), but similar to the 13–14 day period for four trans-Gulf spring migrating Wood Thrushes (*Hylocichla mustelina*) (Stuchbury et al. 2009). However, Wood Thrushes migrate a longer distance of ~3,700 km, compared to ~2,200 km by Kirtland's Warblers.

The mean distance traveled/day by male Kirtland's Warblers, 144.5 km, was similar to the spring migration rate of two female Eurasian Hoopoes (*Upupa epops*) (122 km/day and 163 km/day) between the Sahel of western Africa and Switzerland (Bächler et al. 2010) that were tracked with geolocators and within the range of 105–375 km/day traveled during spring migration by a Swainson's Thrush (*Catharus ustulatus*) that was studied by radiotelemetry between Illinois and Manitoba (Cochran 1987). Daily rates were also within the range of estimates for spring migration of five *Sylvia* warbler species to Great Britain (range = 97–232 km/day) and Scandinavia (range = 98–163 km/day), based on median capture and recovery dates in the Mediterranean region (Fransson 1995), and for 11 European passerine species on the European (50–260 km/day) and desert (120–150 km/day) portions of the migration route, estimated from median passage rates between Africa and northern Europe (Yohannes et al. 2009). One individual fall-migrating Willow Warbler (*Phylloscopus trochilus*) traveled 145 km/day (Hildén and Saurola 1982) and another 218 km/day (Hedenström and Pettersson

TABLE 2. Estimated duration of migration for color-banded male Kirtland's Warblers from southern Eleuthera, The Bahamas to known breeding territory locations in the Lower Peninsula of Michigan. Locations are given in decimal degree coordinates.

Individual	Last Bahamas observation and location	First Michigan observation and location	Migration distance (km)	Max duration (days)	Migration rate (km/day)
1821-91208	25 Apr 2008 24.90787 N 76.17171 W	8 May 2008 44.4629 N 84.1809 W	2,199	13	169.1
2221-08944	25 Apr 2008 24.97589 N 76.15257 W	9 May 2008 44.4998 N 83.5794 W	2,212	14	158.0
2131-75811	25 Apr 2007 24.90010 N 76.14831 W	11 May 2007 44.53544 N 83.53937 W	2,222	16	130.7
2221-08906	24 Apr 2007 24.90091 N 76.15911 W	17 May 2007 44.58206 N 84.60934 W	2,211	23	96.1
2221-08922	27 Apr 2007 24.96263 N 76.17809 W	10 May 2007 44.46725 N 84.29917 W	2,192	13	168.6

1987), comparable to the migration rates of Kirtland's Warblers sampled.

Daily rates of migration by male Kirtland's Warblers were similar to some species, but other species travel at faster rates during spring migration. For instance, four Wood Thrushes migrating from Honduras and Nicaragua to Pennsylvania across the Gulf of Mexico in spring averaged 263 km/day (Stutchbury et al. 2009) and two Purple Martins (*Progne subis*) averaged 281 and 577 km/day during their spring migration from Brazil to Pennsylvania, a distance of ~7,550 km. Similarly, five spring migrating Veeries (*Catharus fuscescens*) tracked with geolocators, whose estimated migration distance ranged from 5,950 to 10,290 km, migrated faster (209–350 km/day) than Kirtland's Warblers (Heckscher et al. 2011), and an Aquatic Warbler (*Acrocephalus paludicola*) averaged 280 km/day within Africa during fall migration (Cramp 1992). Overall, however, daily rates of spring migration by these species and our estimates for male Kirtland's Warblers indicate that many near-passerines and passerines migrate at rates close to the upper range of migration rates reported in Newton (2008).

We obtained estimates of the duration of migration for a small number of males during two spring migration seasons. Ecological, meteorological, physiological, and other factors that affect duration and rate of migration will be better understood (Fransson 1995, Raess 2008, Tøttrup et al. 2008, Yohannes et al. 2009, Stutchbury et al. 2011) as geolocators and other techniques become available to follow larger numbers of individual birds throughout migration (Robinson et al. 2010, Bridge et al. 2011). It may then be possible to describe other aspects of Kirtland's Warbler migration and connectivity such as distribution of frequently used stopover areas, when and where along the migratory route Kirtland's Warbler are most vulnerable, and inter-seasonal interactions, important but missing information needed to develop a comprehensive conservation program for the species.

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