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RRH: North AmericanFlycatcher Migration

Migratory patterns and wintering areas of individual *Tyrannus* flycatchers breeding in the Great Plains of North America

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Abstract.―Descriptions of intra- and interspecific variation in migratory patterns of closely related species are rare yet valuable because they can help assess the degree to which migratory behaviors are fixed or flexible. We report data on timing and location of migratory routes and wintering areas, and on migratory speed and phenology of Eastern Kingbirds (EAKI ; *Tyrannus tyrannus*) from Nebraska and Oklahoma, and Western Kingbirds (WEKI ; *T. verticalis*),and Scissor-tailed Flycatchers (STFL; *T. forficatus*) from Oklahoma. Across these species, fall departures were highly asynchronous; WEKIs left in late July, EAKIs primarily in September, and STFLs mainly in mid-October. WEKIs migrated >1,400 km to the Sonoran Desert in northwestern Mexico, while most EAKIs migrated to the Amazon Basin (Bolivia and Brazil), >6,400 km from their breeding site. STFLs flew directly to Central America (El Salvador, Guatemala, Honduras and Nicaragua), ~2,600 km from the breeding site, and remained until early April before returning to Oklahoma. WEKIs and EAKIs used two (central Mexico and Central America [Guatemala to Nicaragua]) and one (northwestern South America [Colombia, Ecuador, and Peru]) additional site for extended periods, respectively, before returning to the United States in April. Timing of migration appears tightly linked to molt. Early departure of WEKIs from the breeding site appears timed so that they molt in Sonora during the Mexican monsoon, whereas STFLs remain at their breeding site to complete molt in late summer when insect prey are abundant. EAKIs delay their molt until reaching South America where, possibly, abundant fruit supports molt.

Key words:Eastern Kingbird, light-level geologger, migration speed, Nebraska, Neotropics, Oklahoma, Scissor-tailed Flycatcher, Western Kingbird, wintering area

Until recent years it has been nearly impossible to track movements of individual migrant songbirds, but this changed with the application of miniature solar geologger technology (Stutchbury et al. 2009, Bridge et al. 2011). In just a single year, geologgers can yield data comparable to banding tens of thousands of birds over decades (e.g., Ryder et al. 2011). Geologger technology has revolutionized our understanding of the migratory and overwintering strategies of songbirds worldwide, as demonstrated by many recent papers (e.g., Delmore et al. 2012, Schmaljohann et al. 2012, Seavy et al. 2012, Stach et al. 2012, Tøttrup et al. 2012), including those in this special feature of *The Auk*. Geologgers provide spatial and temporal data from across the annual cycle of migratory birds that, when combined with information on timing of reproduction and molt, produce an integrated view of annual events in a bird’s life. Such data are vital for understanding the evolution of life history diversity, and on a more practical level, for developing robust migratory connectivity (e.g., Fraser et al. 2012) and migratory network models (Taylor and Norris 2010). Data on migratory movements, including the identification of migratory stopover locations (e.g., Bayly et al. 2012), is vital for comprehensive species management strategies (Peterjohn and Sauer 1999, Leu and Thomposon 2002, Faaborg et al. 2007, Møller et al. 2008). The potential contribution of geologgers to these goals cannot be overstated.

Indeed, our understanding of migratory bird biology in the nonbreeding season evolves with technological advances. For instance, Schwartz (1964) used band returns to document high site fidelity and territoriality for some species of wintering migrant birds (see also Bates 1992), while later studies used radio telemetry to reveal that sizeable floater populations sometimes exist in otherwise territorial species (Rappole and Warner 1980, Winker et al. 1990). Regardless, our perception was that migrants overwintered at a single geographic site. Geologgers have shown this to be true of some species (e.g., Wood Thrushes [*Hylocichla mustelina*]; Stutchbury et al. 2009), but they have also yielded the surprising result that a phylogenetically diverse group of species, including Veeries (*Catharus fuscescens*, Heckscher et al. 2011), Swainson’s Thrushes (*C. ustulatus*, Delmore et al. 2012), Red-backed Shrikes (*Lanius corullio,* Tøttrup et al. 2012), and Fork-tailed Flycatchers (*T. savana*, Jahn et al., this issue) utilize multiple wintering sites, the significance of which has yet to be elucidated. Geologgers have also yielded data to describe individual variability and year-to-year variation in the movements of individuals (Stanley et al. 2012).

Of the 34 species of tyrant flycatchers (Tyrannidae) breeding north of Mexico, 28 (82%) overwinter in the Neotropics (Sibley 2000). Although widely distributed across North America, details of their life cycle remain rudimentary because previous migration research on flycatchers has relied solely on banding and specimen collections to infer migratory routes, timing of migration, and migratory tendency (e.g., Chesser 2005, Cooper et al. 2009, Colorado 2010, Capllonch et al. 2011, Jahn et al. 2012). Most appear to complete their annual molt away from the breeding grounds (Leu and Thompson 2002), but the degree to which tyrannids overlap molt and migration, or complete the entire process on the wintering grounds is not known. The exception to this generalization is the Western Kingbird (*Tyrannus verticalis*); studies of museum specimens found adults vacate the breeding grounds for the region of the Mexican monsoon to complete their molt in late summer (Barry et al. 2009). Such details are lacking in other species, but even more pressing is our need to delineate migratory phenology and pathways as well as the location of tropical wintering grounds, which remain unknown for even well-studied species such as the Western Kingbird.

Large tyrannids such as kingbirds (*Tyrannus* spp.) are ideal subjects for the application of geologgers because their body mass (>30 g) allows them to carry geologgers relatively easily. High annual survival and high site fidelity (Murphy 1996), and their use of open habitats are also desirable qualities for geologger use. Here we use geologgers to describe variation in the timing of migration, distance and speed of migration, and the location and number of sequential wintering areas occupied by individual Eastern Kingbirds (*T. tyrannus*), Western Kingbirds (*T. verticalis*), and Scissor-tailed Flycatchers (*T. forficatus*), three species of tyrannids that have overlapping breeding ranges across the southern Great Plains of North America. Our goals are to (1) describe interspecific variation in migratory biology of a group of closely related species that overlap greatly in body size, morphology, and ecology (Murphy 1989), (2) compare autumn and spring migratory behavior, and (3) integrate the data that we collected with information on annual molt to provide a comprehensive picture of the annual cycle of these species.

Methods

*Study sites*.―All flycatchers in this study bred in either Nebraska or Oklahoma. In Nebraska, Eastern Kingbirds were studied in riparian grasslands (40.48°N, 98.26°W) characterized by wet meadow habitats and associated accretion forest (e.g., Eastern Cottonwood [*Populus deltoides*] and Slippery Elm [*Ulmus rubra*]). In southwestern Oklahoma, we studied Western Kingbirds and Scissor-tailed Flycatchers on the campus of Cameron University, Elmer Thomas Park, and the Lawton Country Club, all within ~6 km of each other (34.38°N, 98.24°W). These sites were characterized by mowed grass and mainly scattered oak trees (*Quercus* spp.). Scissor-tailed Flycatchers were also studied at Fort Sill Military Reservation, Oklahoma (34.39°N, 98.29°W), an area composed of mixed forbs and grasses, with scattered mesquite (*Prosopis* spp.) and oak trees, and at the Wichita Mountains National Wildlife Refuge, Oklahoma (34.43°N, 98.37°W), which is characterized by mixed grass prairie and stands of oak.

*Field methods*.―During July of 2010 we captured 10 male Eastern Kingbirds in Nebraska, and in June and July of 2011 we captured two male Eastern Kingbirds, 38 Western Kingbirds, and 39 Scissor-tailed Flycatchers in Oklahoma. Both sexes were roughly equally represented in the captures of the latter two species. All were captured using 38 mm mesh mist nets placed near an active nest or within a territory. We often used conspecific vocalizations or a predator model to draw birds close to nets.

We banded all birds with an individually numbered federal band and a unique combination of three color bands. Birds were weighed, measured, sexed and aged using standard methods (Ralph et al. 1993, Pyle 1997). We then attached a model Mk10S (15 mm, 30° stalk; 1.2 g) or model Mk20ASLT (15 mm, 15° stalk, 0.9 g; British Antarctic Survey [BAS], Cambridge, United Kingdom) archival light-level geologger to birds with a Rappole-Tipton leg-loop harness (Rappole and Tipton 1991), using Filament Kevlar® (500 tex, Saunders Thread Co., Gastonia, North Carolina). The combined mass of geologger and harness was <4% of the body mass of the birds, all of which flew well upon release.

*Analytical methods*.―We analyzed data from geologgers using the single threshold method (Lisovski et al. 2012) with the program suite BASTrak (BAS). We adjusted for clock drift and visually inspected sunrise and sunset transitions, deleting those with very shallow slopes or with peaks in light intensity within 30 minutes of sunrise or sunset. Geologger sensitivity was calibrated using on-bird data for 10 days immediately after deployment, while birds were still at the breeding sites and usually raising nestlings or fledglings. Geologgers were calibrated individually, except for Western Kingbirds. Due to highly variable transition data for most Western Kingbirds, we used data from one Western Kingbird with good transition data to calibrate the geologgers of all Western Kingbirds. For this calibration period, we calculated a mean error between the location of the birds (hereafter, their “point locality”) and the location of the breeding site as 174 km (± 9.3 SE) for Eastern Kingbirds, 133 km (± 34.8 SE) for Western Kingbirds, and 104 km (± 8.5 SE) for Scissor-tailed Flycatchers. We used midnight position fixes because these species are primarily diurnal migrants (Peterjohn 1989, Stevenson and Anderson 1994).

Throughout the course of the nonbreeding season, there were extended periods (> 20 days) when the longitude of a given bird’s point localities did not vary widely (typically <8° longitude). Because light-level estimations of longitude are more accurate than those of latitude (Fudickar et al. 2012, Lisovski et al. 2012), we define these as stationary periods (i.e., wintering areas), similar to previous studies (e.g., Heckscher et al. 2011, Stanley et al. 2012). We defined the departure date from the breeding site or from wintering areas as the first date on which there was a large change in longitude (typically ≥2°) without subsequent returns, and defined arrival date on a wintering area as the first day the longitude was within the range of longitudes recorded for the stationary period (excluding outliers). Finally, we defined arrival at the breeding site in spring as the first day the longitude was within a degree of longitude of the previous year’s breeding site. For some birds, changes in longitude were ambiguous and we were unable to calculate arrival and departure dates (and therefore speed of migration; Tables 1 and 2).

We defined fall migration distance as the straight-line distance between the breeding site and the average location of all the point localities that made up the wintering area. For birds with more than one wintering area, we used the first wintering area. We define spring migration distance as the straight-line distance between the average location of the point localities that made up the wintering area (for birds with more than one wintering area, we used the last wintering area) and the location of the breeding site. The migration distances we report are therefore minimum distances traveled because birds likely did not migrate in a straight line between sites (Figs. 1-3). We define migration speed as the migration distance in fall or spring divided by the duration in days of the entire fall or spring migration period. Because of this, and because migration distances are minimum values, the speeds we report represent the minimum speed of the entire fall or spring migration journey.

To map wintering area(s) and migratory routes, we excluded point localities (1) from 15 days before and after the fall and spring equinoxes (Fox 2010) because of high latitude uncertainties, and those (2) outside of the known species’ range (based on InfoNatura [2007] and eBird [2012]), (3) that required movements of ≥1,500 km-d (which is highly unlikely given our knowledge of these species), and (4) over the ocean (except during migration). We did not create maps of wintering areas or migratory routes of some birds, or calculate their distance or speed of migration (Table 2) because we were unable to determine the location of at least one wintering area. This was usually because all point localities during that time of winter were primarily north or south of the known winter range (InfoNatura 2007). We suspect that the anomalous points were a result of artificially short photoperiods created by shading that resulted from extreme topography (i.e., shading due to nearby mountains results in shorter detected day lengths and therefore latitudinal error [Lisovsky et al. 2012]). Indeed, central Mexico and northern Central America, where Scissor-tailed Flycatchers and Western Kingbirds migrated through and overwintered, are largely hilly (e.g., Western Kingbirds occupy arid valleys in winter, Phillips 1994), and the Andes Mountains make up a large portion of the Eastern Kingbirds’ second wintering area in northwestern South America.

We mapped wintering areas using kernel density estimator analysis (Silverman 1986, Terrell and Scott 1992) in the Spatial Analysis tool of ArcMap, v 9.3 (ESRI, Redlands, California), using a search radius of 200 km and a grid cell size of 2 km (e.g., Bächler et al. 2010). We estimated the location of migratory routes using point localities that were consistent with the direction of migration and that did not require reversals in migration or successive days over the ocean. We then mapped routes as straight lines between these point localities using Hawth´s Analysis Tools for ArcGIS 9.3 (Beyer 2004). All statistics are reported as mean ± SE.

Results

*Return and recovery rates.—* Eight of 10, and 2 of 2 Eastern Kingbirds with geologgers returned to Nebraska in 2011, and Oklahoma in 2012, respectively; of those, we recovered 6 of 8, and 1 of 2. In 2012 we recovered the geologger from one of the previously uncaptured kingbirds in Nebraska. We recovered 20 of the geologgers from 25 Western Kingbirds that returned from the 38 individuals that were tagged in 2011. Only 17 of 39 Scissor-tailed Flycatchers with geologgers returned in 2012, and we recovered the geologgers of five. Because of geologger failure, usable data were available for 7, 14, and 5 Eastern and Western kingbirds, and Scissor-tailed Flycatchers, respectively, including two years for the Eastern Kingbird captured in Nebraska in 2012. Return rate for birds in the year following geologger deployment was 75.0% (9 of 12), 65.7% (25 of 38), and 43.6% (17 of 39) for Eastern and Western kingbirds, and Scissor-tailed Flycatchers, respectively. Return rate of Eastern and Western kingbirds did not differ (Fisher’s Exact Test, *P* = 0.73), but Scissor-tailed Flycatchers tended to have lower return rates than both Eastern (Fisher’s Exact Test, *P* = 0.057) and Western (Fisher’s Exact Test, *P* = 0.042) kingbirds.

*Eastern Kingbirds*.—The six Eastern Kingbirds from Nebraska (with 2 years of data for one bird) departed on fall migration in late August or early September. Due to proximity to the equinox, there were too few points to determine the fall migration routes for most birds, but at least one (A in Fig. 1) migrated to South America by crossing the Caribbean Sea. The five recaptured in 2011 arrived in the southern Amazon Basin (Bolivia and Brazil) from mid to late October, >6,400 km from the breeding site (Table 2, Fig. 1). Residence time in this first wintering area averaged 100 ± 13.8 d before all individuals moved to a second wintering area in northwestern South America (Colombia, Ecuador, and northern Peru; Fig. 1) where they stayed for an average of 75 ± 14.9 d.

Most Nebraska-nesting individuals left South America in April and migrated north through Central America before crossing the Gulf of Mexico, departing from or nearby the Yucatan Peninsula (Fig. 1). Most likely made landfall in Texas, though one bird (B in Fig. 1) entered the continent to the east, near the Alabama-Florida border. Arrival in Nebraska occurred over a 28-day period from late April to late May (Table 1).

The Eastern Kingbird from Oklahoma initiated fall migration earlier than the Nebraska birds (early August) and migrated over the Gulf of Mexico (Fig. 2). The location of the migration route between northern Central America and South America is uncertain because of a lack of point localities. It arrived in the southern Amazon Basin (Bolivia and Brazil) in October, ~6,500 km distant from the breeding site (Fig. 2 and G in Table 2). It remained there until January when, like all but one of the Nebraska Eastern Kingbirds, it moved to a second wintering area in northwestern South America (Colombia, Ecuador and Peru). It remained at this second location until early April, when it departed on spring migration, arriving in northern Central America by late April and soon after crossed the Gulf of Mexico (Fig. 2).

The individual with two years of data (F in Fig. 1) differed from all other Eastern Kingbirds by using only one wintering area in both years. It remained in Colombia, Ecuador, and Peru (~6° N-10° S), in the area that became the second wintering area for other Eastern Kingbirds (Fig. 1), for an average of 208 ± 4.0 d before departing on spring migration.

Spring migration for Eastern Kingbirds averaged 22 days, which is less than half as long and more than twice as fast as fall migration (Table 2; 277 km-d vs. 127 km-d; paired *t*-test = -2.88, df = 5, *P* = 0.035).

*Western Kingbirds*.—Upon departure from Oklahoma in July (Table 1), Western Kingbirds flew southwest to the Sonoran Desert region (Mexican states of Baja California, Baja California Sur, and Sonora), >1,400 km from the breeding site (Table 2). We detected no significant difference between sexes in migration distance (*t* = 0.87, df = 12, *P* = 0.400), speed (*t* = 0.85, df = 8, *P* = 0.421) or duration (*t* = 0.66, df = 8, *P* = 0.530) of this initial leg of migration. They remained in Sonora until October, a period varying between 62 and 85 days (Fig. 3). Of the five individuals with usable data, all except one moved to a wintering area in central Mexico, remaining there from October to December (Fig. 3). The individual that did not fit this pattern moved directly to Guatemala in November, remaining there until it departed in April for Oklahoma (H in Fig. 3). The other four then moved in November or December to another wintering area in northern Central America (Guatemala to Nicaragua; Fig. 3), although one bird (B in Fig. 3) traveled only as far south as southern Mexico. The four remained in their second wintering area until April, and arrived in Oklahoma from mid April to early May (Table 1 and Fig. 3). The initial leg of fall migration to the Sonoran Desert region was slower than spring migration from Central America, but small sample sizes precluded statistical comparisons. We mapped the spring migratory route for one bird (C in Fig. 3) overland through Mexico and Texas, back to Oklahoma.

*Scissor-tailed Flycatchers*.—None of the five Scissor-tailed Flycatchers departed the Oklahoma breeding site prior to 18 October (Table 1). The wintering areas of three individuals were located in northern Central America (El Salvador, Guatemala, Honduras and Nicaragua), on average 2,600 km from the breeding site (Table 2 and Fig. 3). Scissor-tailed Flycatchers migrated over the Gulf of Mexico during fall (Fig. 3), remained in the wintering area until late March to early April, and then returned to Oklahoma. Lack of data during spring migration precluded a definitive conclusion as to whether they are trans-Gulf or circum-Gulf spring migrants (Fig. 3).

Discussion

Return rates of Eastern and Western kingbirds were high, and for Eastern Kingbirds, exceeded apparent survival rates reported for Eastern Kingbirds from New York (Murphy 1996) and Oregon (Redmond and Murphy 2012). Return rates of Western Kingbirds were nearly as high, falling within the 95% confidence interval of apparent survival rates of Eastern Kingbirds (Redmond and Murphy 2012). Geologgers thus appeared to have no negative influence on the probability of return in either species. Male Eastern Kingbirds exhibit higher site fidelity than females (Murphy 1996), and if the same is true for Scissor-tailed Flycatchers, their lower return rates may be because 45% of the initial sample of Scissor-tailed Flycatchers was female compared to 100% male in Eastern Kingbirds. However, breeding dispersal of Scissor-tailed Flycatchers of both sexes appears to be relatively high (M. Husak and D. Landoll, pers. observ.), and thus we suspect that low return rates of Scissor-tailed Flycatchers reveals more about interspecific differences in site tenacity than true survival.

Our results also reveal large interspecific differences, along with moderate intraspecific variation, in the speed and timing of migration, existence of stopovers, and number of overwintering sites. For instance, Western Kingbirds left breeding grounds towards the end of July, but Eastern Kingbirds delayed their departure until August or early September, and Scissor-tailed Flycatchers postponed their departure for six more weeks until at least mid-October (Table 1). Eastern Kingbirds migrated on average slower than the other species in fall (Table 2). The slow speeds of Eastern Kingbirds are presumably tied to the much greater distance they must travel to the wintering grounds (>6,500 km on average) compared to either Scissor-tailed Flycatchers or Western Kingbirds (≤2,600 km; Table 2).

The early departure of Western Kingbirds from the breeding grounds is consistent with observations of large numbers of Western Kingbirds in the Sonoran desert region in late July, where they complete molt and remain until mid-October (Barry et al. 2009). Molt duration of Western Kingbirds (63 d [95% CI = 56 to 69 d; Rohwer and Broms 2012) closely matches the time spent in Sonora (Fig. 4). The later departure of Scissor-tailed Flycatchers has been previously documented (Sutton 1967, Withgott 1991), and likely allows adults to complete their annual molt prior to leaving the breeding grounds (Sutton 1986), consistent with the majority of most long-distance migrants from eastern North America (Leu and Thompson 2002). Scissor-tailed Flycatchers arrived at their sole wintering site from Guatemala to Nicaragua by late October (Fig. 4), a region where the species is common to fairly common along the Pacific slope in winter (Howell and Webb 1995). Our Eastern Kingbird arrival dates in the Amazon Basin coincide with observations of Eastern Kingbird roosts numbering in the hundreds to thousands in eastern Bolivia in October (A. Jahn, pers. observ.). Timing of Eastern Kingbird molt is not well known (Fig. 4), however A. Mamani and A. Jahn (unpubl. data) found that of 27 Eastern Kingbirds captured in eastern Bolivia in November 2008 (the same region occupied by some Eastern Kingbirds in the present study), >80% had a medium to high body molt, and >75% were molting flight feathers.

By mid-December Western Kingbirds began movement south to their second winter site, and by early March, Eastern Kingbirds moved north to their second winter site (Figs. 1 and 2). All three species then remained stationary until initiating spring migration (Fig. 4). Scissor-tailed Flycatchers and Western Kingbirds made their >2,300 km return to the breeding site in at least six days (Table 2, Fig. 4), arriving by mid-April and early May, respectively (Table 1), whereas Eastern Kingbirds took at least 11 days (Table 2, Fig. 4), most arriving before mid-May (Table 1).

Differences in the timing and location of molt among the study species are pronounced, revealing different molt strategies (Fig. 4). Eastern Kingbirds molt during winter, possibly exploiting high fruit availability in the Amazon Basin. Although partially frugivorous in summer (M. T. Murphy, pers. observ.), Eastern Kingbirds are highly frugivorous in winter (Morton 1971, 1980). Morton (1971) suggested Eastern Kingbirds remain nomadic for at least a portion of the northern winter as they track the abundant, but spatially variable, fruit upon which they feed heavily (see also Morton 1980). Abundant fruit, and fruiting phenology across the Amazon Basin, may support Eastern Kingbird molt, and in part explain their use of more than one wintering area.

In contrast, Western Kingbirds molt in late summer (as is typical of many western North American passerines [Rohwer et al. 2005]), in the Sonoran Desert region, presumably exploiting high food availability associated with the Mexican Monsoon (Barry et al. 2009). Movement of Western Kingbirds from Sonora to central Mexico (see also Howell and Webb 1995) is likely tied to rainfall. The predictably higher winter precipitation in eastern than in western Mexico (Magaña et al. 1999) may enhance primary productivity and food availability for overwintering migratory birds (e.g., Brown and Sherry 2006). Thus, temporal and spatial variation in rainfall and food availability may explain the winter movements of both Eastern and Western kingbirds, as suggested for Fork-tailed Flycatchers (Jahn et al. 2013), Veeries (Heckscher et al. 2011), Red-backed Shrikes (Tøttrup et al. 2012), and Bobolinks (*Dolichonyx oryzivorus*; Renfrew et al. in press).

Finally, Scissor-tailed Flycatchers have the latest departure of the three species from breeding grounds, delaying departure until after molting. The delayed departure may allow them take advantage of the high insect abundance in the southern Great Plains that reaches a peak in late summer (Robins 1970, Murphy 1986), to fuel their molt.

Although we have limited data on migration paths, at least one Eastern Kingbird (A in Fig. 1) and all Scissor-tailed Flycatchers crossed the Gulf of Mexico in fall and headed south to southeast. Scissor-tailed Flycatchers made landfall near the Isthmus of Tehuantepec in southern Mexico, a region where transient Scissor-tailed Flycatchers are fairly common on fall migration (Howell and Webb 1995, Regosin 1998). Eastern Kingbirds migrated further east, making landfall in the Yucatan, or possibly Colombia. All Eastern Kingbirds appeared to fly over the Gulf of Mexico on spring migration, departing from either the Yucatan or Isthmus of Tehuantepec (Figs. 1 and 2). Notably, data on eBird (2012) show a higher abundance of Eastern Kingbirds in the Yucatan in spring than fall, and Eastern Kingbirds are regular spring migrants in Central America from mid-March (Ridgely and Gwynne 1989) to mid-May (Morton 1971). Reports of large numbers of Eastern Kingbirds on the barrier islands off the Gulf Coast of Mississippi in spring (Moore et al. 1990) are likewise consistent with trans-Gulf migration.

More detailed data are needed to resolve migratory routes of Western Kingbirds, but Gamble et al. (2012) report that Western Kingbirds migrate in fall along the Pacific coast. Previous observations also suggest that Western Kingbirds are likely not trans-Gulf migrants in spring (Stevenson 1957, Oberholser 1974; but see [Monroe 1968](http://bna.birds.cornell.edu/bna/species/227/articles/biblio/bib072)), which is supported by the one bird for which we had spring migration data (C in Fig. 3).

*Future directions*

Emerging technologies such as light-level geologgers offer a new way to understand the lives of migratory animals and will likely play an important role in both descriptive and hypothesis-driven research on migration in the near future (Bridge et al. 2011). Given that basic patterns, such as seasonal population connectivity, remain unresolved for most migrant passerines, descriptions of migratory movements and wintering areas remain a priority. Such descriptions facilitate addressing such broad research questions as (1) What drives the location and use of multiple wintering areas and how do events in each area carry-over to the breeding season? (e.g., Fraser et al. 2012, MacDonald et al. 2012), (2) What time of year represents the greatest bottleneck to survival for different populations? (Jahn and Cueto 2012), (3) What is the relationship between molt, migration and climate? For example, northwestern Mexico -- the molt migration stopover site of Western Kingbirds -- experiences higher than normal rainfall during the El Niño phase of the global climate cycle than during the La Niña phase (Magaña et al. 2003). Therefore, given that Western Kingbirds go there to take advantage of the late summer monsoon to molt (Barry et al. 2009), it may represent a better place to molt in some years than in others; and (4) How does the relationship among migration timing and speed, and location of migratory routes and wintering areas vary between the sexes, with age, and among years?

Understanding the complex life histories of migratory passerines, some of which may be better classified as intra-tropical migrants during the non-breeding season (e.g., Veeries [Heckscher et al. 2011], Swainson’s Thrushes [Delmore et al. 2012], and Western and Eastern kingbirds in the present study), will require research at a finer grain and at broader spatial and temporal scales. And as our understanding of their movements, physiology and ecology during the non-breeding season accumulates, so too will our ability to develop appropriate conservation and management plans for these birds throughout their range.

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| Table 1. Individual fall departure from and spring arrival dates at breeding grounds of Eastern Kingbirds from Nebraska (except one from Oklahoma, denoted by “OK”), and Western Kingbirds and Scissor-tailed Flycatchers from Oklahoma, including those individuals for which insufficient data were available to construct maps of their migratory routes and wintering areas.   |  |  |  |  | | --- | --- | --- | --- | | Species | Sex | Fall departure date | Spring arrival date | | Eastern Kingbird (A) | M | 7-Sep-10 | 29-Apr-11 | | Eastern Kingbird (B) | M | 3-Sep-10 | 28-May-11 | | Eastern Kingbird (C) | M | 9-Sep-10 | 6-May-11 | | Eastern Kingbird (D) | M | 24-Aug-10 | 28-May-11 | | Eastern Kingbird (E) | M | 2-Sep-10 | 14-May-11 | | Eastern Kingbird (F) Year 1 | M | 14-Sep-10 | 10-May-11 | | Eastern Kingbird (F) Year 2 | M | 6-Sep-11 | 8-May-12 | | Eastern Kingbird (G) (OK) | M | 11-Aug-11 | 30-Apr-12 | | Western Kingbird (A) | F | 30-Jul-11 | -- | | Western Kingbird (B) | F | 29-Jul-11 | 2-May-12 | | Western Kingbird (C) | F | 17-Jul-11 | 5-May-12 | | Western Kingbird (D) | F | 26-Jul-11 | 5-May-12 | | Western Kingbird (E) | F | 17-Jul-11 | 26-Apr-12 | | Western Kingbird (F) | F | 26-Jul-11 | 9-May-12 | | Western Kingbird (G) | M | -- | 28-Apr-12 | | Western Kingbird (H) | M | 28-Jul-11 | -- | | Western Kingbird (I) | M | 13-Jul-11 | -- | | Western Kingbird (J) | M | 21-Jul-11 | -- | | Western Kingbird (K) | M | 17-Jul-11 | -- | | Western Kingbird (L) | M | 28-Jul-11 | -- | | Western Kingbird (M) | M | -- | -- | | Western Kingbird (N) | M | -- | 18-Apr-12 | | Scissor-tailed Flycatcher (A) | F | 21-Oct-11 | -- | | Scissor-tailed Flycatcher (B) | F | 22-Oct-11 | 17-Apr-12 | | Scissor-tailed Flycatcher (C) | F | 2-Nov-11 | 16-Apr-12 | | Scissor-tailed Flycatcher (D) | M | 18-Oct-11 | -- | | Scissor-tailed Flycatcher (E) | ? | 20-Oct-11 | -- |   Table 2. Individual migration histories of Eastern Kingbirds breeding in Nebraska (except one breeding in Oklahoma, denoted by “OK”), and Western Kingbirds and Scissor-tailed Flycatchers breeding in Oklahoma. Nebraska breeders were fitted with light-level geologgers in 2010 whereas Oklahoma birds had geologgers deployed in 2011. Data are provided for each individual’s sex, and duration, distance, and speed of migration in both fall and spring. “ID” is the alphabetic character used to identify individuals in Figures 1-3. Fall migration distance represents the straight-line distance between the breeding site and the first wintering site, spring migration distance is the straight-line distance between the last wintering site and the breeding site, while speed is the straight-line migration distance divided by duration of migration. | | |
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|  |  | Fall migration | | | Spring migration | | |
| Species (ID) | Sex | Duration (days) | Distance (km) | Speed (km/day) | Duration (days) | Distance (km) | Speed (km/day) |
| Eastern Kingbird (A) | M | 53 | 6,673 | 126 | 11 | 5,293 | 481 |
| Eastern Kingbird (B) | M | 55 | 7,052 | 128 | 25 | 5,616 | 225 |
| Eastern Kingbird (C) | M | 50 | 6,945 | 139 | 15 | 5,171 | 345 |
| Eastern Kingbird (D) | M | 53 | 6,442 | 122 | 42 | 5,177 | 123 |
| Eastern Kingbird (E) | M | 52 | 6,967 | 134 | 18 | 5,048 | 280 |
| Eastern Kingbird (F) Year 1 | M | -- | 5,319 | -- | 23 | 5,319 | 231 |
| Eastern Kingbird (F) Year 2 | M | -- | 5,588 | -- | 15 | 5,588 | 373 |
| Eastern Kingbird (G) (OK) | M | 56 | 6,510 | 116 | 26 | 4,779 | 184 |
| Mean (SE) |  | 53 (0.9) | 6,578 (207.4) | 127 (3.4) | 22 (3.8) | 5,220 (102.9) | 277 (44.2) |
|
| Western Kingbird (A) | F | 5 | 1,547 | 309 | -- | 2,337 | -- |
| Western Kingbird (B) | F | 9 | 1,306 | 145 | -- | 2,074 | -- |
| Western Kingbird (C) | F | 6 | 1,507 | 251 | 11 | 2,531 | 230 |
| Western Kingbird (D) | F | 4 | 1,555 | 389 | 11 | -- | -- |
| Western Kingbird (E) | F | 13 | 1,560 | 120 | 12 | -- | -- |
| Western Kingbird (F) | F | 6 | 1,320 | 220 | 16 | -- | -- |
| Western Kingbird (G) | M | -- | 1,371 | -- | 8 | 2,608 | 326 |
| Western Kingbird (H) | M | 7 | 1,433 | 205 | -- | 2,338 | -- |
| Western Kingbird (I) | M | 5 | 1,383 | 277 | -- | -- | -- |
| Western Kingbird (J) | M | 15 | 1,417 | 94 | -- | -- | -- |
| Western Kingbird (K) | M | 8 | 1,421 | 178 | -- | -- | -- |
| Western Kingbird (L) | M | -- | 1,230 | -- | -- | -- | -- |
| Western Kingbird (M) | M | -- | 1,640 | -- | -- | -- | -- |
| Western Kingbird (N) | M | -- | 1,396 | -- | 8 | -- | -- |
| Mean (SE) |  | 8 (1.1) | 1,435 (30.6) | 219 (28.7) | 11 (1.2) | 2,378 (92.7) | 278 (48.0) |
|
| Scissor-tailed Flycatcher (A) | F | 6 | 2,577 | 430 | -- | 2,577 | -- |
| Scissor-tailed Flycatcher (B) | F | 10 | 2,515 | 252 | 6 | 2,515 | 419 |
| Scissor-tailed Flycatcher (C) | F | 9 | -- | -- | 10 | -- | -- |
| Scissor-tailed Flycatcher (D) | M | 16 | 2,704 | 169 | -- | 2,704 | -- |
| Scissor-tailed Flycatcher (E) | ? | 7 | -- | -- | -- | -- | -- |
| Mean (SE) |  | 10 (1.7) | 2,599 (55.6) | 284 (77.0) | 8 (2.0) | 2,599 (55.6) | -- |
|

Figure legends

Fig. 1. Winter range (>50 %, 50–70 %, and 70–95 % kernel densities), and migration routes of Eastern Kingbirds captured in Nebraska (red star). Winter range distribution in 2010/Year 1 for individual “F” was similar as that for 2011/Year 2 (shown). Capitalized letters correspond to the individual ID for each bird in Tables 1 and 2. Dates in bold represent dates the bird was at a given wintering area (surrounded by a dashed rectangle), dates in bold italics represent dates the bird was at a given point along the fall migratory route, and underlined dates in bold italics represent dates the bird was at a given point along the spring migratory route. Black lines depicting the migration routes represent the shortest distances between locations for which we were able to calculate point localities during migration. Red lines represent those for which we have no data across large distances (~2000 km). Migratory routes in some seasons are missing because of a lack of data during those periods.

Fig. 2. Winter range (>50 %, 50–70 %, and 70–95 % kernel densities), and migration routes of an Eastern Kingbird captured in Oklahoma (red star). Capital letter corresponds to the individual’s ID in Tables 1 and 2. Dates in bold represent dates the bird was at a given wintering area, dates in bold italics represent dates the bird was at a given point along the fall migratory route, and underlined dates in bold italics represent dates the bird was at a given point along the spring migratory route. Black lines depicting the migration routes represent the shortest distances between locations for which we were able to calculate point localities during migration. Red lines represent those for which we have no data across large distances (~2000 km). Migratory routes in some seasons are missing due to lack of data during those periods.

Fig. 3. Winter range (>50 %, 50–70 %, and 70–95 % kernel densities), and migration routes of Western Kingbirds and Scissor-tailed Flycatchers captured in Oklahoma (red star). Capitalized letters correspond to the individual ID for each bird in Tables 1 and 2. Dates in bold represent dates birds were at a given wintering area (surrounded by a dashed rectangle), dates in bold italics represent dates birds were at a given point along the fall migratory route, and underlined dates in bold italics represent dates birds were at a given point along the spring migratory route. Lines depicting the migration routes represent the shortest distances between locations for which we were able to calculate point localities during migration. Migratory routes in some seasons are missing due to lack of data during those periods.

Fig. 4. Annual cycle of Eastern Kingbirds (top or left), Western Kingbirds (middle), and Scissor-tailed Flycatchers generated from estimated dates of migratory movements, and periods when birds remained stationary, based on light-level geologger data. Molting periods were established on the basis of literature sources or personal observations of molting birds. Duration of molt was assumed to be roughly for all species and equal to that of Western Kingbirds (~60 days); question marks represent ignorance of the actual dates when, on a population level, molt began and was completed.