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Duration Of Stopover In Relation To Date Of Arrival In Vagrant Western Kingbirds (Tyrannus verticalis)

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Abstract

Western Kingbirds (Tyrannus verticalis) are renowned for their repeated, long-distance dispersal to the East Coast of the United States. While they are known to migrate to the Mexican monsoon region after the breeding season, many individuals are found on the Atlantic coast each fall between Newfoundland and Florida, more than 2000 km east of their "normal" range. This seasonal pattern of occurrence of these vagrants raises many questions about the "intent" of birds engaged in dispersal and migration, and the selective pressures that lead to these behaviors. Using the web-based repository known as eBird, I collected available sighting records of Western Kingbirds along the Eastern Coast of the United States and parts of Canada during the months of August to February. For every bird, the date of arrival was recorded in relation to its duration of stay, and these patterns were analyzed in comparison to normal migratory behavior of the species. I concluded that the date of arrival of vagrants correlated to their duration of stay on the East Coast, with individuals staying significantly longer if they arrived later in the fall, than if they arrived earlier in the fall. These vagrants were also shown to engage in three distinct patterns of movement that correspond to migratory behaviors within their "normal" range. These results suggest that vagrant Western Kingbirds appear to be undertaking a more complex form of long-distance dispersal, perhaps exploring the East Coast as a possible place for new wintering grounds.

Keywords: Vagrancy, Long-distance dispersal, Kingbirds

1. Introduction

Western Kingbirds (Tyrannus verticalis), abundant neotropical migrants that breed in western North America, are renowned for their repeated, long-distance dispersal to the East Coast of the United States. While they are known to migrate to the Mexican monsoon region after the breeding season[1, 2], many individuals are found on the Atlantic coast each fall between Newfoundland and Florida, more than 2000 km east of a straight line track from their breeding to wintering ranges. This seasonal pattern of occurrence of these vagrants has yet to be understood, raising many questions about the "intent" of birds engaged in dispersal and migration, and the selective pressures that lead to these behaviors. Are these birds actively seeking out new territories and thus expanding their range, or are they just mis-oriented or displaced migrants?

In birds, vagrancy has variously been interpreted as mis-oriented migration[3, 4], displaced migration (i.e., by weather patterns)[5], "mirror-image" mis-orientation[3,4], or "reverse migration"[6, 7]. Each of these interpretations (except for displaced migration) leans on the old idea that vagrancy is the result of "navigational errors", arising from genetic abnormalities that affect aspects of innate migratory cues[8, 9]. Individuals engaging in these behaviors are considered defective, flying in the "wrong" direction[10] and thus showing up in areas that are not known to be part of the "normal" range of that species. However, while genetic mutations that lead to deviations from the "correct" orientation may be the cause of vagrancy in some birds[9], vagrancy occurs far too frequently in certain species to be attributed to these mutations alone.

According to Baker[11] and Veit[12], vagrants are not simply flying in the wrong direction, but are actively and intentionally engaging in the exploration of new environments. Vagrancy is "the regular thing [that is] to be expected", with those individuals expanding beyond the range of the population acting as "pioneers…testing out the adjoining areas for possibly new territory to occupy"[13]. In regards to vagrant Western Kingbirds, their regular occurrence on the coast annually seems to suggest that they are following this pattern of vagrancy as opposed to succumbing to navigational errors, engaging in a complex form of long-distance dispersal in an effort to explore the landscape, possibly in search of new wintering grounds.

I sought to test the hypothesis that Western Kingbirds are not mis-oriented, but are rather engaging in long-distance dispersal in search of new wintering grounds. I analyzed whether the duration of stay during dispersal is dependent upon the date of arrival of Western Kingbirds along the East Coast of the United States. I hypothesized that the duration of stay of kingbirds on the east coast is governed by an internal schedule that has its roots in this "normal" migration pattern of the Western Kingbird during their autumn movement down the west coast of North America[2]. After the breeding season has ended, Western Kingbirds migrate to the Mexican monsoon region of eastern Arizona, New Mexico, and northwestern Mexico in late July, where they undergo postbreeding molt before settling into their wintering grounds in mid-October[1, 2]. Kingbirds that arrive on the east coast during this time period are in the process of traveling to their molting grounds, and are thus disinclined to stay on the coast for extended periods of time, staying for only short durations. From mid-October to mid-December, Western Kingbirds migrate to, and utilize, a number of different wintering grounds in Central America, typically using two wintering sites in a single nonbreeding season. During this period of time, kingbirds that arrive on the east coast are preparing to stop at a wintering site, and are therefore more likely to settle, remaining on the coast for longer durations of time.

I used citizen-science data from the web-based repository eBird[14] to collect sighting records of Western Kingbirds along the Eastern Coast of the United States and parts of Canada during the months of August to February. Analysis of this data provided insights into the poorly understood migratory patterns of Western Kingbirds, reflecting upon the dispersal patterns of species, and possibly revealing the "intentions" of these birds as they progress through their autumn migration. Are Western Kingbirds searching for new wintering grounds, or is something else going on? While birds are probably the only group of organisms for which such an extensive dataset on vagrancy can be obtained, the basic process that we describe is likely to apply to other taxa as well.

2. Methods

2.1 Study area

The area comprised by this study was located on the Eastern Coast of North America, covering the two Canadian provinces of Nova Scotia and New Brunswick and the states of Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island, New York, Pennsylvania, New Jersey, Delaware, Maryland, Virginia, West Virginia, North Carolina, South Carolina and Georgia in the United States. Florida was not included in the study area because there is already a known established wintering population of Western Kingbirds in this state[15]. The large number of kingbirds staying for long durations in this area would have likely skewed the data in support of our hypothesis and thus were excluded from the dataset.

2.2 Data collection

As the geographical scope of this study was large, citizen-science data was utilized as opposed to traditional field studies to gather information on the Western Kingbird. While traditional field studies are useful, they cannot possibly cover the extensive spatial scale that is characteristic of migratory movements of birds[16]. The use of citizen-science data provides a broader spatial scale[17] that can be analyzed in an attempt to gather a better understanding of the migratory patterns and exploratory behaviors of this particular species.

The web-based repository known as eBird was used to collect available sighting records of the Western Kingbird in the established study area. Both fossil eBird data (pre-2002) and active eBird data (2002–present) were collected, with the earliest sighting recorded occurring in 1927 and the last sighting recorded occurring in February of 2014. Sightings from the months of August to February were collected. This particular time frame was chosen because it coincides with the migratory patterns of Western Kingbirds[2, 15]. The period from August to February reflects the time period in which most, if not all, Western Kingbirds should already be situated in their wintering grounds in Mexico and Central America[2]. Western Kingbirds typically leave their breeding grounds in late-July, arriving in the Mexican monsoon region by early August, where they undergo post-juvenile molt[1, 2]. They then migrate in mid-October, flying to central Mexico to their first wintering site, and then again in late-November, flying further south into Central America to their second wintering site, where they stay until mid-April[2]. For each bird sighted, the date of its first occurrence was recorded in relation to the duration of its stay at a particular site.

Collection of citizen-science data from eBird did require extensive interpretation of the sightings, and methods of interpretation remained consistent throughout the entire process of data collection. Since Western Kingbirds are a rarity on the Eastern Coast of the United States, the presence of one in this region triggers a massive reaction from birders and citizen-scientists alike, resulting in as many as ten sightings of a single kingbird in one day. It was up to our interpretation to understand that all of these sightings were likely to be the same bird. Also, if a kingbird was sighted in the same area on multiple days, it was recorded as one bird if a sighting was logged on most days until its disappearance, unless stated otherwise by those posting the sightings. Further analysis of notes and photographs posted with each sighting were particularly helpful in determining how many kingbirds were present in a particular area, and whether a kingbird was continuing or not. In the event we could not ascertain whether sightings pertained to one or more individuals, we directly contacted the individuals who logged the sighting. Our decision to allocate sightings to two or more individuals was conservative.

2.3 Statistical analyses of trends

I analyzed patterns between the Julian date of first occurrence and the duration of stay of each Western Kingbird and compared them to the migratory behavior Western Kingbirds west of the Rockies. Model selection was performed using the Akaike information criterion (AIC) as a criterion to determine which model best fit the data. This criterion was used because it allows a comparison of different models, estimating the quality of one model relative to others in order to select the best fit. Linear regression, Poisson, and Negative Binomial models were used[18].

From the data it was evident that the duration of stay of individual kingbirds changed depending on the date of arrival, and that the data could be separated into distinct biological groups[2]. I conducted a K-means cluster analysis with $k = 3$ to separate the data into three different clusters based on the Julian date of first occurrence and the duration of stay of the individual. Data from these three clusters were plotted separately for the duration of stay versus the Julian date of first occurrence, and slopes were determined via linear regression analysis to confirm the presence of three similar groups in the dataset. An analysis of variance (ANOVA) was performed to determine if there was any variability in the average duration of stay among the three clusters formed.

To further compare the data, two periods of time were defined – Early Fall and Late Fall. The period of Early Fall was meant to reflect the time period in which Western Kingbirds are migrating to the Mexican monsoon region, where kingbirds appearing on the East Coast stay for only very short periods of time (0 – 5 days). The period of Late Fall was meant to reflect the time period when kingbirds are already in their “established” wintering grounds, where kingbirds appearing on the East Coast stay for long periods of time (5 days or more). By running a K-means cluster analysis with $k = 2$, the periods of Early Fall and Late Fall were quantified. I used a Mann-Whitney U Test to determine if kingbirds stay for longer periods of time in the Late Fall as compared to kingbirds arriving in the Early Fall.

3. Results

3.1 Julian date of first occurrence versus the duration of stay of Western Kingbirds

Upon examination of the Julian date of first occurrence of each Western Kingbird in relation to the duration of their stay, it was evident that the duration of stay of any one kingbird increased as the arrival date extended later into the fall (Figure 1). There was a significant relationship was detected between the Julian date of first occurrence and the duration of stay of kingbirds ($y = 0.051x - 11.983$, $r^2 = 0.091$, $F_{1, 644} = 64.643$, $P < 0.001$; see Figure 1). The positive relationship indicates that kingbirds that arrive later in the fall stay for longer periods of time than those that arrive at earlier dates. The AIC for this model of the data was 4168. For the Poisson and Negative Binomial distributions, the AIC values were 4671 and 2840, respectively. The Negative Binomial distribution, due to its low AIC value, is the best model to fit the data. This model shows that the Julian date of first occurrence does affect the duration of stay of individual kingbirds (R^2 = 0.2217, P < 0.001; see Figure 2).

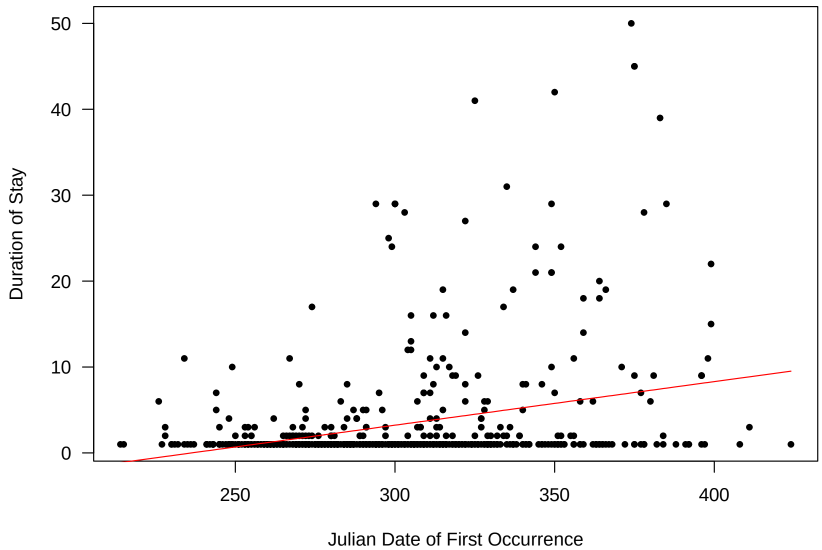

Figure 1. The Julian date of first occurrence for each Western Kingbird sighted in eastern North America and the two Canadian provinces of Nova Scotia and New Brunswick 1927—2014 versus the duration of its stay.

A positive significant relationship was found between these two variables for the 646 recorded sightings of kingbirds. The red line represents the regression line.

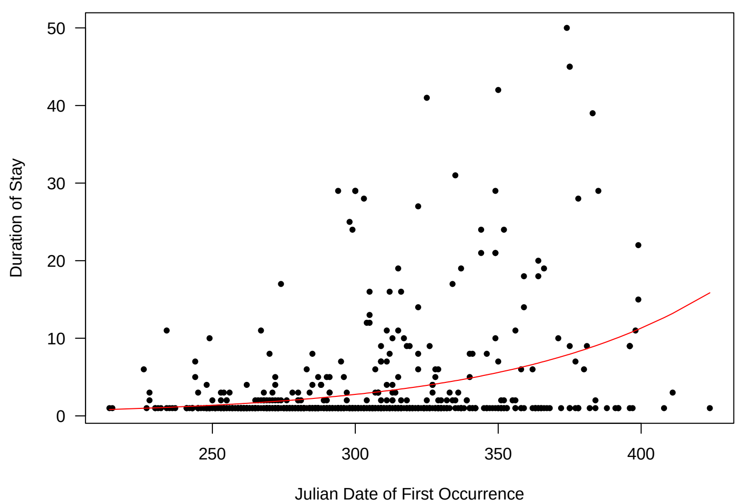

Figure 2. The best model to fit the data was a Negative Binomial distribution, which included the effect of their arrival on a certain Julian date versus the duration of stay of individual kingbirds.

The red line is a plot of the fitted values for the model.

Single day stays, a sighting where the duration of stay was equal to 1, are typical of vagrant Western Kingbirds, and were abundant throughout the months studied. However, while these single day durations persisted throughout the study period, longer durations of stay were rare in the early fall months, and became more frequent as the fall proceeded. This trend can be seen more clearly by plotting the average duration of stay of Western Kingbirds per month (Figure 3). Earlier in the fall, during the months of August and September, the average duration of stay of a typical Western Kingbird was 1.96 and 1.46 days, respectively. As the fall proceeded, the average duration of stay increased, with a typical Western Kingbird staying 2.42 days in October, 3.16 days in November, 5.97 days in December, and 10.36 days in January. The duration began to drop off in February, however, with the average duration of stay totaling 7.71 days. A clear trend was established, as the average duration of stay increases steadily from August to December, peaks in January, and decreases in February. An analysis of variance (ANOVA) confirmed that the average duration of stay between the months studied differ from each other significantly with a Tukey post-hoc test indicating that August is significantly different from January only ($F_{6, 639} = 13.792$, $P < 0.001$), September, October and November are each significantly different from both December and January only, December is significantly different from all months except August and February, and January is significantly different from all months except February.

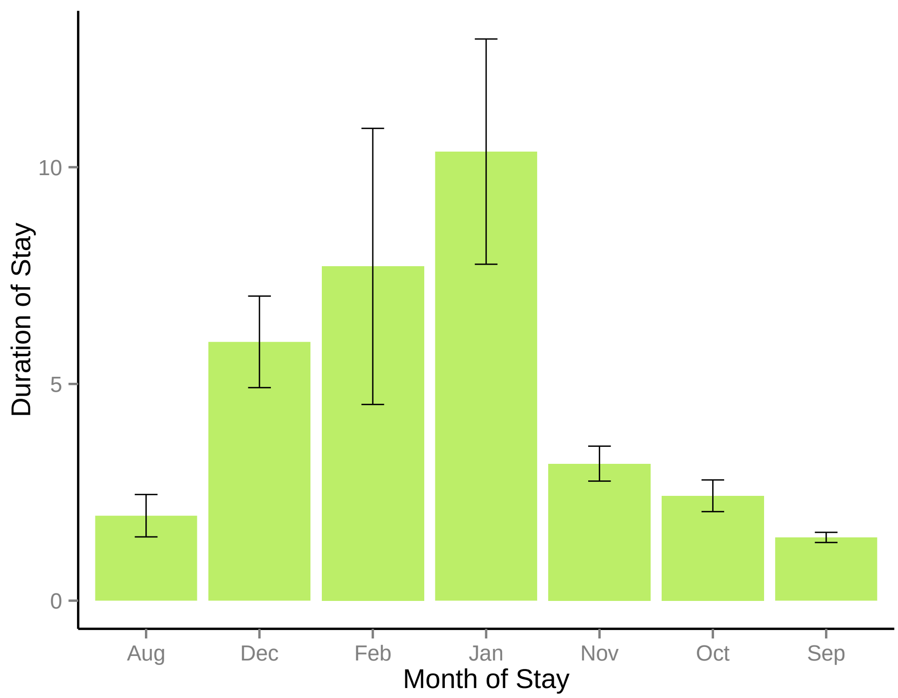

Figure. 3. The average duration of stay of kingbirds increases from August to December, peaks in January, and then declines again in February.

The average durations of stay per month are displayed above each bar of the graph. These durations of stay were found to be significantly different from each other. The black lines represent the standard error of the mean (SEM).

3.2 K-means Cluster Analysis

From the K-means cluster analysis, the raw data was separated into three different clusters (Figure 4). Cluster 1 included the dates from 214 to 285 (August 1 to October 12), cluster 2 included the dates from 286 to 334 (October 13 to November 30), and cluster 3 included the dates from 335 to 424 (December 1 to February 28). Linear regression analysis of the three separate clusters showed that there was little variability within the individual clusters themselves. No significant relationship was detected between the Julian date of first occurrence and the duration of stay within each of the clusters ($y = -0.005x + 2.924$, $r^2 = 0.002$, $F_{1, 252} = 0.517$, $P = 0.473$; $y = 0.015x – 1.559$, $r^2 = 0.001$, $F_{1, 277} = 0.377$, $P = 0.540$; $y = 0.044x – 8.425$, $r^2 = 0.006$, $F_{1, 111} = 0.715$, $P = 0.400$).

The average duration of stay of each cluster was 1.54 (*SD* = 1.753), 3.05 (*SD* = 5.627) and 7.46 (SD = 11.098) days, respectively. An ANOVA of the cluster data revealed that the average duration of stay of each differed among clusters ($F_{2, 643} = 37.965$, $P < 0.001$).

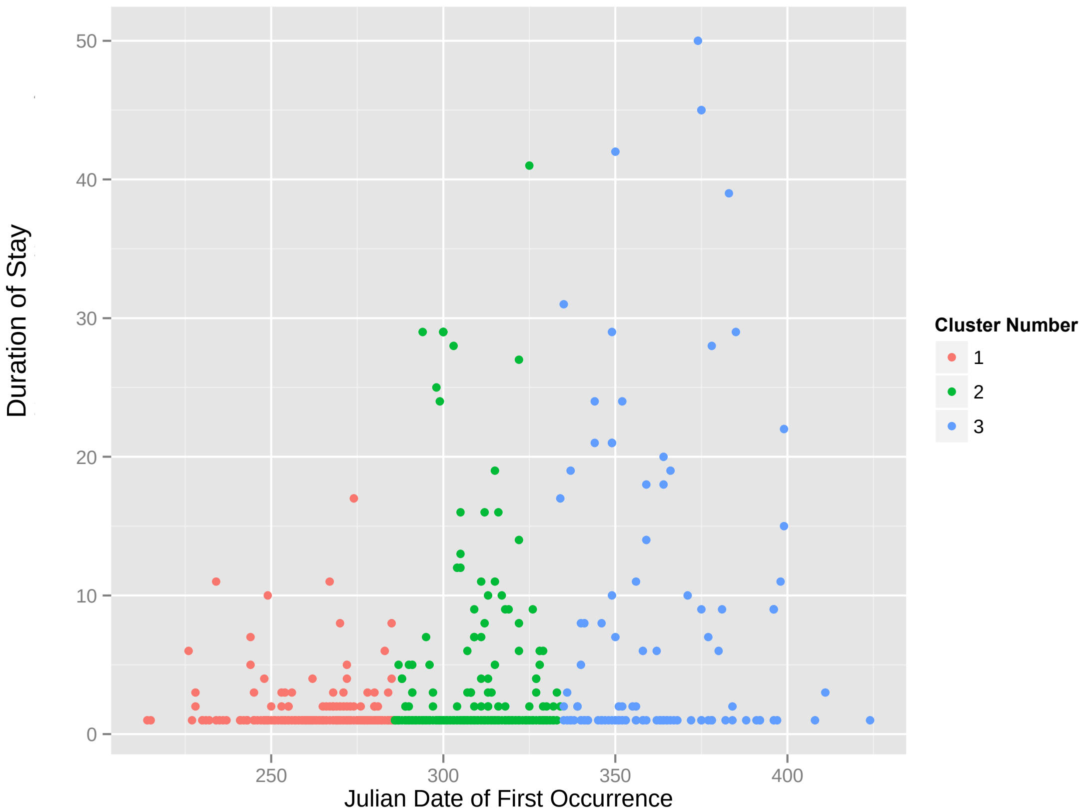

Figure 4. The three clusters determined by the K-means cluster analysis indicate that there are 3 distinct time periods in which Western Kingbirds appear on the East Coast.

3.3 Distinction Between Early Fall And Late Fall

In order to distinguish between Early Fall and Late Fall, a K-means cluster analysis was run on the raw data to separate it into two different clusters. The two different clusters identified by K-means included the dates from 214 to 306, and 307 to 424, respectively (Figure 5). Thus, the subset of data denoted Early Fall was from August 1 to November 2, and the subset of data denoted Late Fall was from November 3 to February 28.

The average duration of stay of a Western Kingbird in the Early Fall was 2.06 days, whereas the average duration of stay in the Late Fall was determined to be 4.98 days. A Mann-Whitney U Test was run as opposed to an independent samples t-test due to the nonparametric nature of the data. The results showed that U=39091.5, and $P < 0.001$. The mean rank of Early Fall was 295.25 and the mean rank of Late Fall was 365.98. These results show that the duration of stay later in the fall is significantly longer than that of the Early Fall.

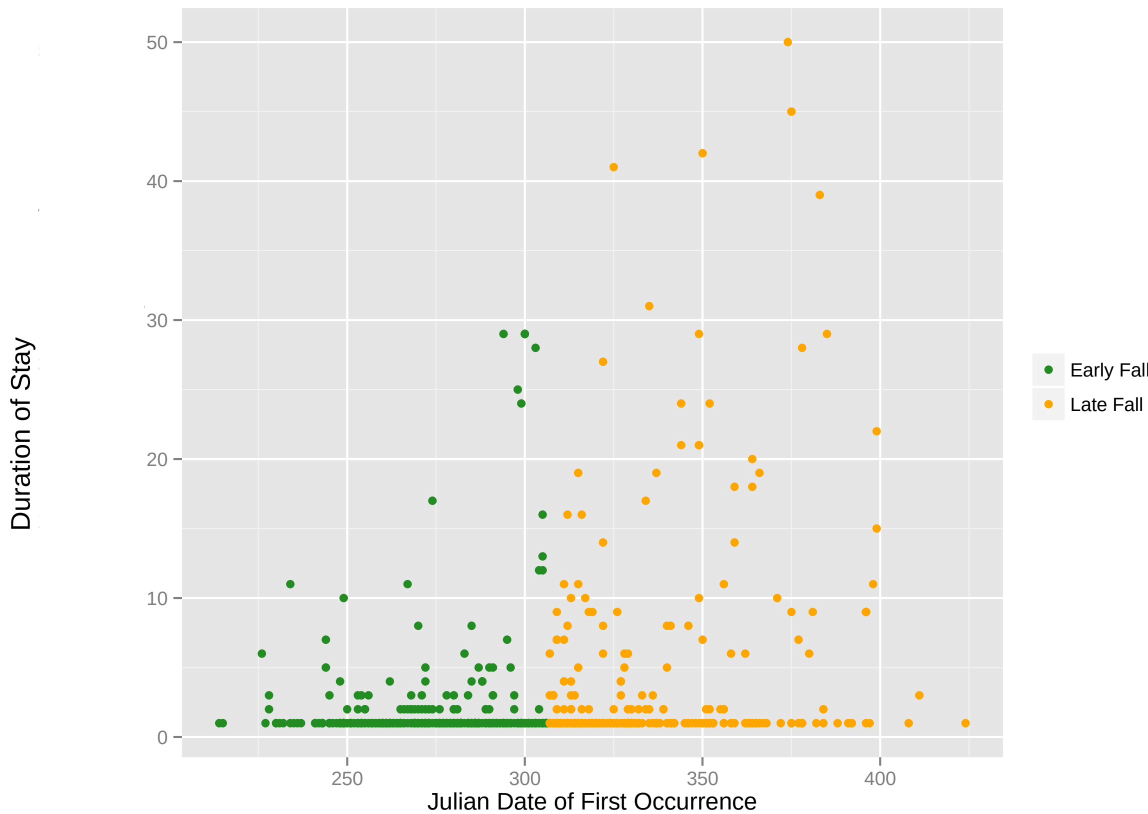

Figure 5. Early Fall and Late Fall were determined by K-means cluster analysis.

4. Discussion

This study has revealed that the arrival date of Western Kingbirds on the East Coast serves as a strong predictor of their duration of stay. Kingbirds that arrive later on the East Coast will stay for much longer periods of time. These patterns coincide with "normal" migratory patterns as outlined by Jahn et al.[2], with Western Kingbirds engaging in three different migration patterns from August to February that are similar to those of kingbirds within their "normal" range. It was detected that kingbirds first arrive on the East Coast on or around August 1. This corresponds with the timing of postbreeding molt described by both Barry et al.[1] and Jahn et al.[2], in which kingbirds leave their breeding grounds in late-July to molt in the Mexican monsoon region from August to mid-October. Western Kingbirds arriving during the time frame of August 1 to October 12 (cluster 1; see Figure 4) stay for short durations of time, with an average duration of stay of 1.54 days.

The second wave of kingbirds that arrived on the East Coast was detected from October 12 to November 30 (cluster 2; see Figure 4). The start of this time frame, October 12, reflects the period of time determined by Jahn et al.[2] in which kingbirds finish their postbreeding molt and undergo migratory movements to their first wintering ground site in Central Mexico, where they remain until early December. Kingbirds appearing on the coast, therefore, are most likely individuals who have completed their postbreeding molt and are searching for their first wintering ground site. Individuals from this set of kingbirds stay for a moderate duration of time, averaging 3.05 days, with a maximum duration of stay recorded during this time period of 41 days, from November 21 to December 31.

The third and final wave of kingbirds that was seen on the East Coast stayed within the time frame from December 1 to Feburary 28 (cluster 3; see Figure 4). Around late-November and early-December, Jahn et al.[2] discovered that Western Kingbirds travel to a second-wintering site located from southern Mexico to northern Central America where they remain until April. Kingbirds along the coast, therefore, may be those that are engaging in their second search for a wintering site. This is reflective in the duration of time spent along the coast – the average duration of stay for kingbirds from this set was 7.46 days, with maximum durations of stay recorded during this time period of 50 days, from January 9 to February 27. Behaviors exhibited by these kingbirds are similar to those that appear in mid-October. They are acting as though they are searching for new wintering grounds, staying in the area for extended periods of time, exploiting the resources available to them in this new or unfamiliar area.

These patterns suggest that Western Kingbirds are engaging in long-distance dispersal, flying to the East Coast in a possible attempt to expand their wintering range. While it has been previously hypothesized that vagrancy is due to navigational errors that arise from genetic abnormalities[3, 4, 6, 7] or displacement due to weather patterns[5], the spread of Western Kingbirds to the East Coast seems to suggest otherwise. Repeated patterns of long-distance dispersal by this species show that vagrancy is not accidental, but rather an intentional behavior performed by a small portion of the population. The fact that large numbers of Western Kingbirds show up on the East Coast each fall in correspondence with their "normal" migratory patterns is indicative of the idea that birds are inherently explorers[11, 12]. They do not mistakenly fly in the "wrong" direction, but are rather serving as pioneers to explore the landscape, and to possibly expand the range of the species into areas that can support them as well as those within their expected range.

The patterns exhibited by Western Kingbirds may also be a result of attempts to refuel before returning to migratory behaviors. During the early fall months, from August to late October, it is most likely much easier to find food before flying to a new area, and thus they will only stay for short periods of time in one location on the East Coast. Later in the fall, food resources are likely to be less abundant, forcing birds to stay for much longer periods of time to gain enough energy to move on. However, while this is likely, it does not detract from the fact that Western Kingbirds are dispersing to the East Coast throughout the fall months, and are doing so from year to year in large numbers. Therefore, while the time spent at any one location may be due to foraging behaviors, they are still dispersing to the East Coast for a reason. It is possible that they are migrating in a southerly direction along the East Coast to the established wintering ground in Florida, which would explain the varied departure dates from areas along the coast, and the hypothesis that they are stopping to refuel along the way.

The *P*-value for the relationship between the Julian date and the duration of stay for the Negative Binomial distribution is less than 0.001, and thus cannot be refuted, regardless of the large AIC value. Therefore, while the AIC value remains large, and the Julian date only explains approximately 22.2% of the variation in the duration of stay of individual kingbirds, it still significantly affects the duration of stay of Western Kingbirds, and shows that the date of arrival is a function of the vagrancy of these birds to the East Coast. There may be other factors involved in how long Western Kingbirds do stay on the East Coast, such as competition, climate, and availability of resources, but the Julian date is still significant in explaining how long they stay.

Vagrancy is intentional, and it is happening. But why are Western Kingbirds expanding their wintering range, searching for new places to stay during the nonbreeding season, instead of remaining within their "normal" range? A few hypotheses can be proposed for this novel behavior, including: competition, response to human actions in established wintering grounds, and climate change.

The exploration of new wintering grounds by Western Kingbirds may be inextricably linked to human exploitation of their current wintering grounds in Mexico and Central America. Western Kingbirds reside in dry tropical deciduous forests during the nonbreeding season[1], which is the most threatened type of tropical forest in the world[19]. In 2000, Trejo and Dirzo[20] estimated that only 27% of the original tropical deciduous forest remained intact in Mexico by 1990, with another 27% left considerably fragmented, 23% degraded, and the remaining 23% converted to open fields for agricultural use and cattle grazing. In the state of Morelos alone, 60% of the original vegetation was lost by 1990, with only 19% intact forest remaining[20]. Destruction of land in this way for human use reduces the amount of available habitat for Western Kingbirds to occupy, and depletes the available food supply, increasing competition amongst individuals for resources. This complete devastation of woodland habitat may be severely limiting the carrying capacity of kingbirds in this area[21], forcing them to move elsewhere in order to increase their chances of survival during the winter, and thus making it much more desirable to leave Mexico in search of more profitable, and spacious, wintering grounds. Studies conducted on the change in wintering distribution of the Rufous Hummingbird proposed a similar hypothesis, stating that the expansion to new wintering grounds in the southeastern United States was possibly due to a search for food, because competition in their deforested wintering areas in Mexico was intense[21]. Huge increases in food supply at feeders and ornamental plantings may have driven hummingbirds in this direction as well. Such as was hypothesized with the hummingbirds, Western Kingbirds that arrive in Mexico may be experiencing a decrease in availability of food due to environmental degradation, leading to increased competition. Some of them, in response to this, are migrating to the East Coast of the United States in search of places to use as their first and/or second wintering ground, rather than migrating further inland into Mexico and Central America where conditions for resources are much worse.

Another possible reason for the exploration of new wintering grounds could be related to climate change. Western Kingbirds, in occupying the East Coast during the winter, are wintering much further north than they have in the past. The fact that they are stopping over in northern areas, as opposed to elsewhere, may be a direct result of climate change that is driving many other species of migratory birds, and other taxa, poleward[22]. According to a study conducted by Valiela and Bowen[22], southern species of birds, such as the Western Kingbird, are becoming more prominent at more northerly latitudes as the local mean minimum winter temperatures are increasing[23]. While competition and human development may play an important role in the changing wintering distributions of Western Kingbirds, climate change seems to be a plausible main factor in causing this shift. Further studies recording mean winter temperatures along the coast in relation to the number of vagrant Western Kingbirds will need to be conducted in order to construct a clear picture on the correlation between climate change and their migratory patterns.

While it is still hypothesized that vagrants are flying in the wrong direction, data from this study largely refutes these claims. The numbers of Western Kingbird sightings have clearly increased over the years, and they continue to show up annually in large numbers along the coast. The migratory patterns that they engage in during dispersal to the East Coast coincide with the migratory patterns discovered by Jahn et al.[2], offering unique insights into the regular occurrence of these neotropical migrants on our coastline. Western Kingbirds are staying here for extended durations of time, and are thus actively exploring the landscape for new wintering grounds. As vagrancy in this species continues to increase, I predict that these behaviors will continue into the future, leading to established wintering populations along the entire East Coast. Western Kingbirds are expanding their range, and we should make an effort to understand why.

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