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Abstract

In migratory birds, among- and within-species heterogeneity in response to climate change may be attributed to differences in migration distance and environmental cues that affect timing of arrival at breeding grounds. We used eBird observations and a within-species comparative approach to examine whether migration distance (with latitude as a proxy) and weather predictors can explain spring arrival dates at the breeding site in a raptor species with a widespread distribution and diverse migration strategies, the American Kestrel *Falco sparverius*. We found an interactive effect between latitude and spring minimum temperatures on arrival dates, whereby at lower latitudes (short-distance migrants) American Kestrels arrived earlier in warmer springs and later in colder springs, but American Kestrels at higher latitudes (long-distance migrants) showed no association between arrival time and spring temperatures. Increased snow cover delayed arrival at all latitudes. Our results support the hypothesis that short-distance migrants are better able to respond to conditions on the breeding ground than long-distance migrants, suggesting that long-distance migrants may be more vulnerable to shifts in spring conditions that could lead to phenological mismatch between peak resources and nesting.

Keywords: citizen science, climate change, eBird, falcon, migratory bird, snow, spring arrival

Springtime events (i.e., vegetation green-up) are, on average shifting to an earlier onset in the Northern Hemisphere (Parmesan 2006, Schwartz *et al.* 2006, Jeong *et al.* 2011). Advances in growing seasons without shifts in arrival dates of migratory animals may result in phenological mismatch between peak resource availability and the timing of reproduction, which could lead to related fitness consequence such as reduced productivity (Miller-Rushing *et al.* 2010). Despite this fitness consequence, there is a high amount of within- and between-species heterogeneity in response to warmer spring temperatures (Miller-Rushing *et al.* 2008, Hurlbert & Liang 2012). In general, short-distance migrants are shifting their arrival dates earlier more than long-distance migrants (Butler 2003, Gunnarsson & Tómasson 2011, Kullberg *et al.* 2015). This pattern may emerge because short distant migrants are better able to respond to early spring environmental cues on their breeding grounds compared to long-distant migrants. Studies to test this migration distance hypothesis typically compare responses across species and results have been mixed, perhaps because species also differ in other life history characteristics such as diet, habitat, or lifespan (Murphy-Klassen *et al.* 2005, Jonzén *et al.* 2006, Rubolini 2007, Saino *et al.* 2011). Here, we examined correlates of spring arrival between short-distance and long-distance migrants of the same species, American Kestrels *Falco sparverius* a widespread falcon with diverse migration strategies.

Ultimately, birds benefit by timing their migration to coincide with resource availability (Thorup *et al*. 2017). Innate and environmental conditions cue departure from the wintering grounds and arrival to the breeding grounds (Meunier *et al*. 2008). Birds with different migration distances may use different types of environmental cues to time departure. Specifically, long-distance migrants may rely more on predictive cues, such as photoperiod, that are consistent year to year Coppack *et al.* 2003 Akesson *et al.* 2017). Alternatively, short-distance migrants may be more responsive to supplemental cues, such as temperature, that are indicative of conditions on breeding locations (Wingfield *et al.* 1992, Both & Visser 2001, Ramenofsky *et al.* 2012, Deppe *et al.* 2015, Winkler *et al.* 2014, Usui *et al.* 2017). In addition to migration onset, birds may adjust their migration strategy or migration pace in response to weather (Pulido & Berthold 2010, Resano-Mayor *et al.* 2020). In populations with both migrants and residents (i.e. partial migrant populations), the proportion of migrants can increase in colder winters and decrease with warmer winters (Resano-Mayor *et al.* 2020). Prolonged stopovers can slow migration if there is snow cover on the breeding grounds (Boelman *et al.* 2017, Oliver et al. 2020). For example, White-Crowned Sparrows (*Zonotrichia leucophrys orianthi*) delayed their arrival to high elevation breeding grounds by remaining at lower elevations until the snow melted (Morton 2002).

American Kestrels are a widespread falcon with resident, short- and long-distance migrant populations throughout North America. American Kestrels migrate in a north-south direction in a leapfrog pattern, with migration distances increasing along a latitudinal gradient (Heath *et al.* 2012), while there are no longitudinal patterns in migration distance (Goodrich et al. 2012). However, a recent genetic analysis shows genetically distinct groups along a longitudinal gradient, with a clear distinction between western and eastern flyways, and mixing within the central flyway (Ruegg *et al. in press*). Furthermore, in the western part of their range, American Kestrels show responses to climate change, such as shifts in nesting phenology and decreased migration distances with warmer winters (Heath *et al.* 2012, Anderson *et al*. 2016, Smith *et al.* 2017), but similar shifts have not been observed in American Kestrels in the eastern part of their range (de Corso 2016, Heath unpubl. data). This natural variation creates an excellent scenario for a comparative study of kestrel migration. In addition, American Kestrels are regularly reported in citizen science projects such as eBird. This type of citizen science program provides an opportunity to use data collected across a large-scale that would not otherwise be possible. Our objectives for this study were to estimate spring arrival dates for American Kestrels across North America, and assess the influence of climate (temperature and snow cover) and migration distance using latitude as a proxy. We predicted that spring temperatures would correlate with the arrival of short-distance migrants more so than long-distance migrants. In addition, we examined whether there were any temporal trends in arrival dates or whether location along west-east flyways influenced arrival.

Methods

Spatial Data, eBird Checklists, and Arrival Dates

We overlaid a grid of 200 km x 200 km grid cells over the North American breeding range of migratory American Kestrels using (Albers Equal Area Conic projection) based on the Geographic Coordinate System WGS84 and classified each grid cell to a flyway (western, central, and eastern) according to the grid cell centroid latitude and longitude (Figure 1) (La Sorte *et al.* 2014, Horton *et al.* 2019). We used eBird data (eBird (2017), accessed 11 October 2019) collected from 2002 to 2018 to estimate spring arrival in each grid cell for each year (data available, Powers *et al.* 2020). eBird (www.ebird.org; Sullivan *et al.* 2009, 2014), is a citizen science data repository that provides information about abundance and spatial distribution of different avian species. We used the R (R Development Core Team 2019) package *auk* (Strimas-Mackey *et al.* 2018) for extracting and processing eBird data. We created presence-absence data from the eBird checklists that report location, date, and count of species observed (presence). Absences were assumed when American Kestrels were not on a checklist.

We used an approach modified from Hurlbert and Liang (2012) and Mayor *et al.* (2017) to estimate spring arrival date for each grid cell by year combination. We fitted the proportion of daily checklists with American Kestrels present using generalized additive models (GAMs) with a binomial error distribution and day of year as a smooth term. Models were fit using restricted maximum likelihood (“REML”; Wood 2011). We identified the spring arrival date as the day of year in which the 50% of the amplitude of the fitted GAM was reached (Supporting Online Information, Figure S1).

There are some caveats to consider when using eBird observations to estimate spring arrival dates. Observations for eBird are not spatially or temporally even because some regions will have more observers than others during different times of the year (Zizka *et al.* 2020). In addition, there is a possibility of checklists overlapping spatially, meaning that some birds can be double counted. Fortunately, the GAM approach used to identify date of return looks at relative changes in the proportion of checklists per year, so changes in the number of observers or double counting are unlikely to bias data from year to year. Further, we took precautions to avoid systematic biases in the data.

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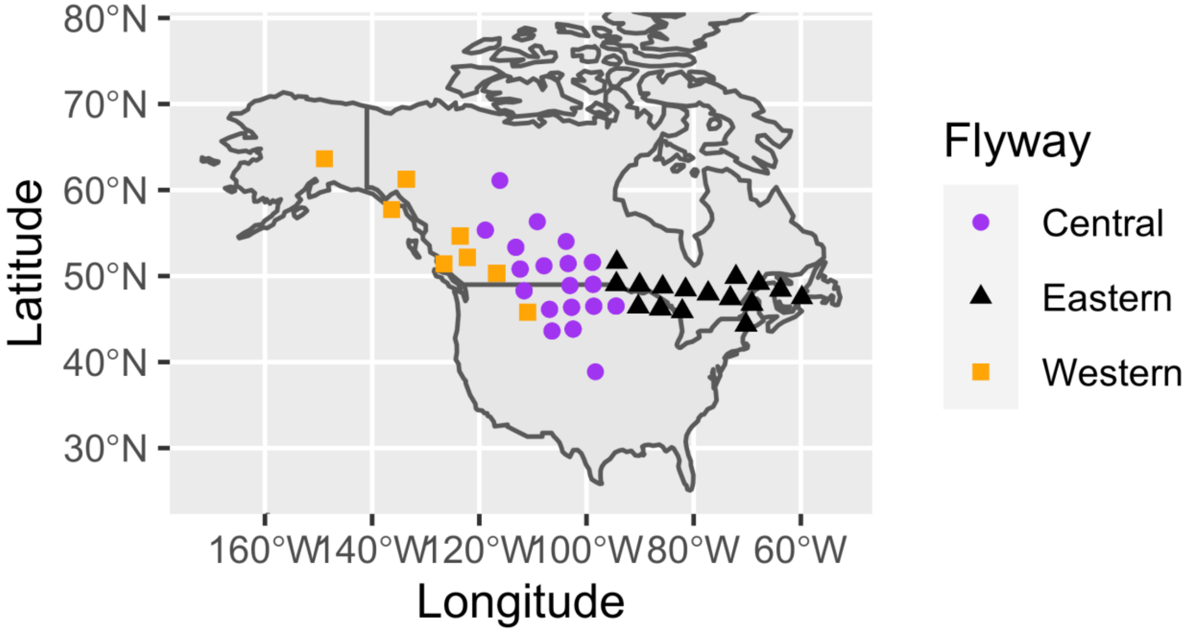

Figure 1. Grid cell locations used to bin eBird checklists for estimating the arrival of American Kestrels in 2002-2018. Each grid cell was assigned in to one of three flyways, Western (purple circles), Central (black triangles), and Eastern (orange squares) for North America.

We only included grid cells in our analyses that contained at least 30 checklists per year (43 cells out of 483), and further discarded cells that 1) showed no clear daily trend in the proportion of checklists with American Kestrels(because Kestrels in the cells were likely residents) 2) provided estimates that were likely to be outside of the arrival period (i.e., day of year less than 50 or greater than 160), and 3) had at less than 100 observations. We evaluated 483 cells across North America and only 43 met our criteria to ensure data quality.

We considered sightings of American Kestrels to be reliable because of their relatively large size and easily identifiable plumage. In addition, their use of open habitat aids in detection and identification. We used latitude as a proxy for American Kestrel migration distance because American Kestrels at higher latitudes migrate farther than American Kestrels at lower latitudes (Heath *et al.* 2012). We did not evaluate arrival of migrants to locations with partial migrant populations because the year-round presence of residents prevented a clear signature of kestrel arrival to a grid cell.

<u>Weather Data</u>

We accessed temperature and snow data from Daymet V3: Daily Surface Weather Data (Thornton *et al*. 2019) for each grid cell using Google Earth Engine (Gorelick *et al.* 2017). We collected the daily minimum temperature (*tmin*) from 1 February – 30 April for each year from 2002 to 2018. Then, we calculated four different indices of spring climate conditions that differed in temporal scale and representation of climate conditions. We calculated the average *tmin* across two months (1 March – 30 April, AvgTmin_2) and three months (1 February – 30 April, AvgTmin_3) prior to the start of the breeding season for American Kestrels in North America. Also, we calculated the lowest minimum temperature across two months (1 March – 30 April, MinTmin_2) and three months (1 February – 30 April, MinTmin_3). We selected these months because they preceded the typical arrival period of American Kestrels. We used two- and three-month period to test the effect interval. We used average minimum temperatures and minimum minimum temperatures (minimum of the temperature minimums) because both indices have been shown to be biologically relevant (McCarty 2002, Lobell *et al.* 2007). Averages can best represent relatively warmer or colder seasons and minimums often represent short cold snaps. For each temporal and statistical representation of climate, we calculated a 30-year baseline average from 1980 to 2009, and then calculated temperature anomalies for each year by subtracting the baseline from the annual minimum temperature. Temperature anomalies provide a relative index for temperature that is independent of location and are often used for large-scale assessments of weather on phenology (Foster *et al*. 2010, Heath *et al.* 2012). In addition to spring temperature anomalies, we used the average snow-water equivalent (SWE), a measurement for how much water is present in snowpack (kg/m²), for the month of March for each year from 2002 and 2018, which is available as a spatial output parameter in the Daymet V3 dataset (Thornton *et al.* 2019).

Statistical Analyses

We first evaluated how well each spring temperature index explained arrival dates using general additive mixed models (GAMMs) with random intercepts for grid cell identity. Arrival date was modeled using the Gamma distribution with a log-link function and models were fit using the restricted maximum likelihood method 'REML' (Wood 2011). We compared model support using Akaike information criterion (AIC) (Bozdogan 1987; Burnham & Anderson 2002) and selected the spring temperature index with the lowest AIC for further analysis. We expected that spring temperatures, grid cell centroid latitude (migration distance), SWE, flyway, and year (temporal trend) may explain kestrel arrival dates. If response to temperature depended on migration distance, then the best supported model would have an interaction term between latitude and temperature, so we included models with an interaction term for the smoother effect. We represented year, SWE, and flyway as fixed effects. All models included random intercepts by grid cell identity because cells were repeatedly sampled across multiple years. Before building models, we evaluated correlations between fixed effects to test for co-linearity and found no concerning correlations amongst predictor variables. We examined residual plots to assess model fit. We compared model support using Akaike information criterion (AIC) (Bozdogan 1987, Burnham & Anderson 2002). Delta AIC (ΔAIC) was calculated as the difference in AIC between each model and the lowest AIC value in the series. We considered the model with the lowest ΔAIC to be the most informative (Burnham & Anderson 2002), then used 85% confidence intervals to assess the biological reliability of each variable's effect (Arnold 2010). We performed all modeling in R (version 3.5.3; R Development Core Team 2019) and used the package *mgcv* to fit GAMMs (Wood 2019) and the function 'AIC' from the *stats* package for comparing models.

Results

We estimated arrival dates for 43 grid cells spanning North America from 38°87' N to 63°.63' N (Figure 1). Arrival dates ranged from 19 February to 8 June, with the earliest arrival dates for grid cells at lower latitudes (Supporting Online Information, Figure S2). Temperature anomalies ranged from -10.50°C to 15.95°C, with a mean for all of the grid cells of North America of 1.58 and SWE ranged from 0.73 to 386.88 (kg/m²).

The lowest minimum temperature from March and April (MinTmin_2) best explained the timing of American Kestrel arrival and was used in the subsequent models (Supporting Online Information, Table S1). The model that best predicted the arrival date of American Kestrels contained an interaction between temperature anomaly and latitude and additive effects of SWE and flyway (Table 1). Below 48° North, spring arrival was inversely associated with spring temperature anomaly, American Kestrels arrived earlier after warmer springs. Above 48° North, American Kestrels arrived at breeding grounds at the same time each year, regardless of spring temperature anomalies (Figure 2). As SWE increased, birds arrived later, regardless of latitude ($\beta = 0.0003$, CI = 0.0002 – 0.0005, Figure 2). Although flyway was in the top model, the 85% confidence intervals for flyway effects crossed zero so we considered these effects to be statistically unclear (Table 1). There was no evidence for a temporal trend in arrival dates.

Table 1. A summary of candidate models for the generalized additive models, number of parameters (K), Akaike's Information Criterion (AIC), and **Δ**AIC. Parameters include latitude, temperature anomaly, flyway, and snow water equivalent (SWE). We used AIC to assess which models best fit explained American Kestrel spring arrival dates on North American breeding grounds 2002-2018.

Model	**K**	**AIC**	**ΔAIC**	**AIC Wt.**
arrival ~ te(latitude, anomaly) + SWE + flyway + s(cell)	44.8	2565.8	0.0	0.18
arrival ~ te(latitude, anomaly) + SWE + s(cell)	44.1	2565.9	0.1	0.17
arrival ~ te(latitude, anomaly) + flyway + s(cell)	44.3	2566.2	0.4	0.15
arrival ~ te(latitude, anomaly) + s(cell)	44.4	2566.5	0.7	0.13
arrival ~ te(latitude, anomaly) + SWE + year + flyway + s(cell)	45.8	2567.2	1.4	0.09
arrival ~ te(latitude, anomaly) + SWE + year + s(cell)	45	2567.2	1.4	0.09
arrival ~ te(latitude, anomaly) + flyway + year + s(cell)	45.2	2567.4	1.6	0.08
arrival ~ te(latitude, anomaly) + year + s(cell)	45.2	2567.7	1.9	0.07
arrival ~ s(anomaly) + s(cell)	40.8	2570.1	4.3	0.02
arrival ~s(latitude) + s(cell)	37	2570.6	4.8	0.02
arrival ~ s(cell)	37.4	2573	7.2	0.00

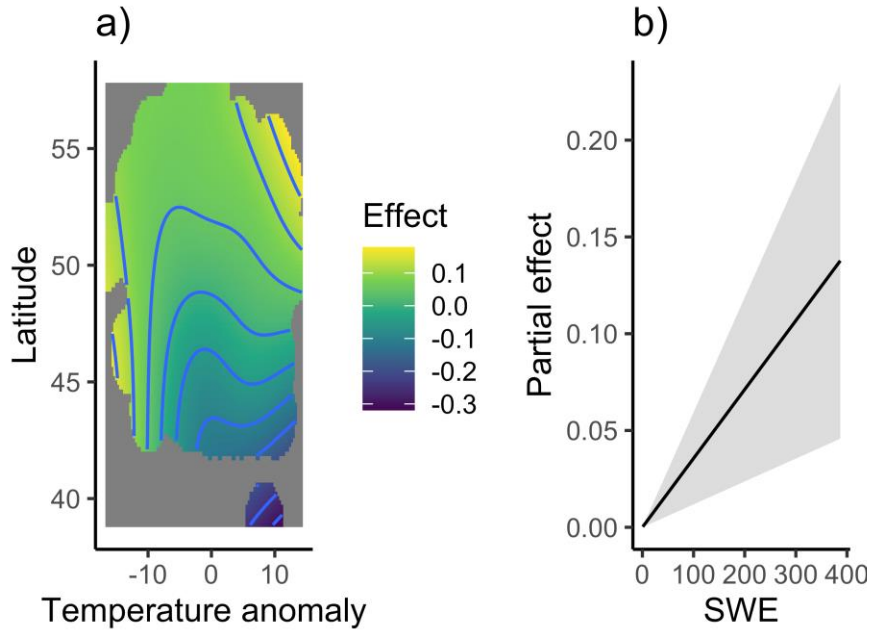

Figure 2. The interaction between minimum temperature anomaly in March and April and latitude on spring arrival dates of American Kestrels in North America, 2002-2018 (a). At lower latitudes, American Kestrels arrived earlier after a warmer spring and later after a colder spring (a) . At higher latitudes, American Kestrels arrived at the same time regardless of spring minimum temperature anomaly conditions (a). Partial effect of snow-water equivalent (SWE) on spring arrival dates of American Kestrels in North America, 2002-2018 (b). American Kestrels arrived later if there was more SWE in March (b).

Discussion

The phenology of migratory birds is known to be affected by climate change (Gordo 2007) as temperature is related to the timing of migration events and reproduction (Cotton 2003, Both *et al*. 2005, Both & Marvelde 2007, Møller *et al*. 2008, Visser *et al*. 2009, Smallegange *et al*. 2010, Zaifman *et al*. 2017). Studies have shown the link between spring mean temperature and arrival dates for different migratory species (Murphy-Klassen *et al.* 2005, Tøttrup *et al.* 2006; Courter 2017, Lehikoinen *et al.* 2019). However, there are few studies that have compared differences in arrival between short-and long-distance migrants within the same species (but see MacMynowski & Root 2007, Hedlund *et al.* 2015). We found that American Kestrels at lower latitudes (short-distance migrants) were affected by spring temperatures at their breeding location and arrived earlier in warmer springs, but there was no relationship between temperatures and arrival dates at higher latitudes (long-distance migrants). Snow delayed arrival for all American Kestrels, regardless of migration distance. These results support the hypothesis that short distance migrants are more responsive to conditions on the breeding ground compared to long distance migrants. Thus, migration distance is an important component of understanding species vulnerability to phenological mismatches with trends in warming spring temperatures and earlier growing seasons.

The temperature anomaly that best predicted American Kestrel arrival was the minimum of the minimum temperature in March and April on their breeding grounds. This suggests that shorter, near-term temperature windows may be a more important cue than longer term (3 month) averages. Cold snaps in March and April may delay migration onset or slow migration pace. Global climate models forecast for minimum temperatures in April and May to increase (IPCC 2014) suggesting that American Kestrels may be able to respond and perhaps cope with advancing springs at latitudes lower than 48 degrees North, where they likely overwintered within a few hundred kilometers of their breeding site Heath *et al.* 2012). In addition to warming spring temperatures, warming winter temperatures may influence migration distance through short-stopping and northward shifts in wintering distributions (Paprocki *et al.* 2014). For example, Blue Tits' *Cyanistes caeruleus*, in central Europe, migration distances between breeding grounds and wintering grounds decreased with warming winters (Smallegange *et al.* 2010).American Kestrels in western United States were found to have shorter migration distances in warmer winters (Heath *et al.* 2012). It may be that as winters continue to warm, American Kestrels above 48 degrees North will have shorter migration distances and their winter distributions shift north. If this is the case, then northern American Kestrels may become responsive to warmer springs on their breeding grounds. Alternatively, if sensitivity to environmental cues is hard-wired, then long-distance migrant dependence on predictive cues for migration timing may not allow for the required flexibility to adapt to a changing climate (Pulido & Widmer 2005, Coppack *et al*. 2008). We did not consider whether conditions on American Kestrel wintering grounds influenced timing of departure. Other studies have found that wintering ground temperatures influence arrival dates for long-distant migrants more than spring temperatures for several Afro-Palearctic migrant birds such as Spotted Flycatcher *Muscicapa striata* and the Common Redstart *Phoenicurus phoenicurus* (Haest *et al*. 2020). It is possible that long-distance American Kestrels are sensitive to weather conditions on their wintering grounds more so than conditions on their breeding grounds.

We found that a positive association between March snow-water equivalent and arrival dates of American Kestrels. In years with higher SWE American Kestrels arrived later to their breeding grounds. This result is consistent with results from previous research. Specifically, snow cover at the breeding grounds of two migratory passerine species resulted int later arrival dates and clutch initiation (Boelman *et al*. 2017) and Lesser Scaups *Aythya affinis* have later arrival dates with increasing SWE (Finger *et al*. 2016). Snowscapes are important to consider in terms of influencing wildlife species' behavior, movement, migration, phenology, survival, predator-prey dynamics, and food availability, especially for migratory species that are affected by seasonality (Boelman *et al*. 2017, Le Corre *et al*. 2017, La Sorte *et al*. 2018, Boelman *et al*. 2019). If migratory birds arrive too early to breeding grounds, snow or colder temperatures can delay spring green up (Green 2006) and access to food (Carey 2009). For American Kestrels, a higher SWE might delay arrival dates as hunting for food is more difficult with higher snow cover. Interestingly, the effect of SWE did not depend on latitude suggesting that regardless of migration distance, American Kestrels might delay arrival at breeding grounds with higher snow cover. These sorts of delays may be achieved through prolonged stop-over on the migration route (Briedis *et al*. 2017, Oliver *et al*. 2020).

We did not find a statistically clear effect of flyway on spring arrival timing, suggesting that short distance migrants in all three flyways respond similarly to warming springs. Therefore, it is unlikely that differences in cues that affect spring arrival explain why some western American Kestrels are advancing their breeding season while eastern American Kestrels are not. Genetic differences between populations could possibly explain or factor into the differences in arrival timing (Hess *et al*. 2016, Thompson *et al*. 2020), although this difference is not documented in American Kestrels. However, we had fewer grid cells in the West compared to the other flyways because there are several partial migrant populations in the West. Therefore we may not have had the power to detect flyway effects. Furthermore, we did not find support for temporal trends in arrival dates for American Kestrels. The relatively short period used in this paper (2002-2018) might not have been long enough to reveal a statistically clear trend in arrival dates. Indeed, we did not detect a temporal trend in our temperature or SWE variables.

The methodological approach (eBird) used here was useful to determine spatio-temporal changes in migratory bird arrival dates and the environmental variables that are influencing the arrival timing. Others have taken a similar methodological approach (eBird) to understand how temperature or other climate variables can predict timing of spring arrival among different species and generally found that spring arrival dates are advancing (Hurlbert &Liang 2012, Zaifman *et al*. 2017). We took a modified approach to assess arrival dates of a widespread species with ecoregional differences as it creates a strong comparative approach. Analyzing a single species with varied migration strategies and widespread distribution revealed within-species heterogeneity in response to climate change. Arrival of long-distance migrants were not associated with spring temperatures whereas the short-distance migrants' arrival timing was associated with spring temperatures, supporting the hypothesis that short-distance migrants are better able to respond to environmental conditions at the breeding grounds than long-distance migrants. In American Kestrels, long-distance migrants might change their migration strategy or adjust their arrival timing otherwise, they will be suspectable to phenological mismatches. Continued monitoring and data collection at a large scale is critical to understand migratory bird behavioral responses to changing climate.

Data Availability

The data that support the findings of this study are available in [Scholar Works Boise State University] with the identifier DOI: 10.18122/bio_data/5/boisestate.

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Supplementary

Table S1. A table of candidate models, and the results from the AIC model, delta AIC (ΔAIC), and degrees of freedom (DF) selection based upon different temperature anomalies. The model MinTmin_2 had the lowest AIC score and no other models had a delta score of less than two. The models are named for the anomaly calculated, either average temperature minimum (AvgTmin) or the lowest minimum temperature (MinTmin) and the number of months are indicated by the underscore, where February through April are indicated by underscore 3 and the months of the March to April are indicated by the underscore 2.

Model	**df**	**AIC**	**ΔAIC**	**AIC Wt.**
MinTmin_2	40.8	2570.1	0.0	0.82
AvgTmin_3	38.5	2573.7	3.6	0.14
AvgTmin_2	41.5	2576.8	6.7	0.03
MinTmin_3	40.8	2578.0	7.9	0.02

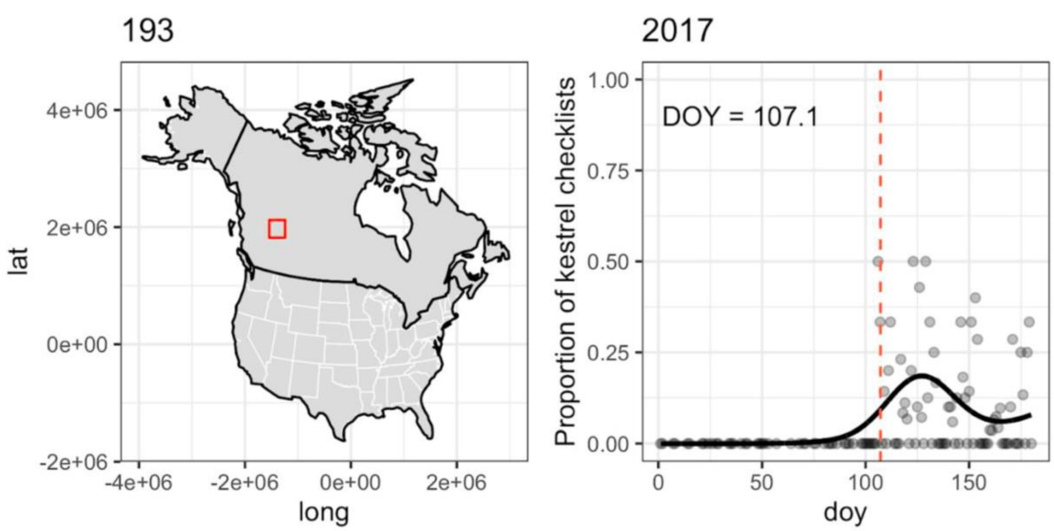

Figure S1. Using eBird data we estimated date of arrival for American Kestrels modified from the methodology in Hurlbert and Liang (2012). This figure is an example of the fitted generalized additive model using the proportion of kestrel checklists with the point in curve (dashed red line) corresponding to the day of year (doy) for the year 2017 (figure on the right). The figure on the left shows the grid cell (identification = 193) location for the estimated arrival.

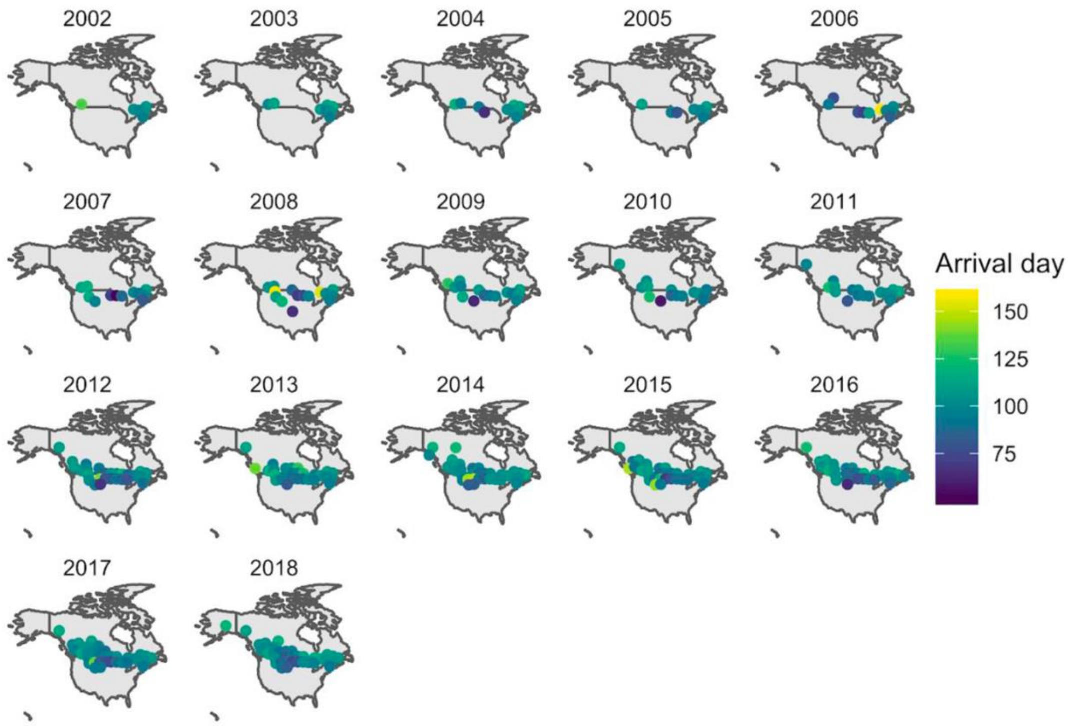

Figure S2. The spatial distribution of spring arrival dates in North America for American Kestrels (scaled dark to warm colors, where purple is the earliest and yellow is the latest) for the years 2002-2018. Note that most of the arrival dates are in Canada and the northern United States due to the availability of enough checkpoints of American Kestrels in the eBird dataset for fitting the generalized additive model.