J. Raptor Res. 57(2):146–153 DOI: 10.3356/JRR-22-17 © 2023 The Raptor Research Foundation, Inc.

THIRTY YEARS OF MIGRATION AND WINTER COUNT DATA INDICATE REGIONAL DIFFERENCES IN POPULATION TRAJECTORIES FOR AMERICAN KESTRELS IN NORTH AMERICA

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ABSTRACT.—Using fall migration trend data from the Raptor Population Index analyses (n=59 count sites) paired with winter Christmas Bird Count trend data at the USA state and Canadian province level, we evaluated continental and regional patterns in trends of American Kestrels (*Falco sparverius*) over the last 30 yr. Long-term trends at the continental and regional level showed widespread declines in the number of kestrels counted during both fall migration and winter. The lone exception was in western North America where declining migration counts were evident, but could at least partly be explained by increasing winter counts. These results suggest that western kestrels are shifting migratory tendencies, migrating shorter distances (short-stopping), or are not migrating at all. This contrasts with patterns in central and eastern North America where kestrel counts declined in both fall and winter over the last 20- and 30-yr periods. Recent trends (2009–2019) showed less widespread declines in both fall and winter across North America and for most regions, suggesting kestrel declines might have moderated in the past decade. However, the species remains at significantly reduced abundance levels compared to the recent past and has not rebounded.

KEY WORDS: American Kestrel; Falco sparverius; Christmas Bird Count; migration trends; population trends; Raptor Population Index; trend summary index; winter trends.

TREINTA AÑOS DE DATOS DE MIGRACIÓN Y CONTEOS INVERNALES INDICAN DIFERENCIAS REGIONALES EN LAS TRAYECTORIAS POBLACIONALES DE *FALCO SPARVERIUS* EN AMÉRICA DEL NORTE

RESUMEN.—Evaluamos los patrones continentales y regionales de las tendencias poblacionales de *Falco* sparverius durante los últimos 30 años. Para esto, utilizamos los datos de tendencias migratorias otoñales a partir del análisis del Índice Poblacional de Rapaces (n = 59 sitios de conteo) combinado con datos de tendencias invernales aportadas por el Conteo de Aves de Navidad existentes para los estados de EEUU y las

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provincias de Canadá, Las tendencias a largo plazo a nivel continental y regional mostraron disminuciones generalizadas en el número de individuos de *F. sparverius* contados durante la migración otoñal e invernal. La única excepción fue en el oeste de América del Norte, donde la disminución en el número de *F. sparverius* durante los conteos migratorios fue evidente, lo que podría ser explicado, al menos en parte, por el aumento de los conteos de invierno. Estos resultados sugieren que *F. sparverius* está cambiando sus tendencias migratorias, migrando distancias más cortas (paradas cortas), o no está migrando en absoluto. Esto contrasta con los patrones en el centro y este de América del Norte, donde los conteos de *F. sparverius* disminuyeron tanto en otoño como en invierno durante los últimos 20 y 30 años. Las tendencias recientes (2009–2019) mostraron disminuciones menos generalizadas tanto en otoño como en invierno en América del Norte y en la mayoría de las regiones, lo que sugiere que las disminuciones de *F. sparverius* podrían haberse moderado en la última década. Sin embargo, la especie permanece en niveles de abundancia significativamente reducidos en comparación con el pasado reciente y no se ha recuperado.

[Traducción del equipo editorial]

INTRODUCTION

Assessing large-scale patterns of wildlife population trends can be challenging, especially for species that are dispersed over broad geographical areas and are secretive or inconspicuous during portions of the year. Many raptor species fall into this category during the breeding season, which makes surveys during other parts of the year logistically more appealing and effective for achieving some monitoring goals (Fuller and Mosher 1981). Counting raptors during fall migration is a long-running and widespread effort across much of North America. Some such efforts span decades, making these types of data invaluable to assessing population trajectories for a number of diurnal raptor species (Bildstein et al. 2007).

The Raptor Population Index (RPI) program is a partnership established in 2003 that analyzes migration count data from count sites across the continent in a standardized manner (Farmer and Hussell 2008, Crewe et al. 2016a). Minimum requirements for inclusion in the RPI program are adoption of a standardized count protocol and a minimum of 10 yr of data with similar seasonal and daily effort across those years. Since Farmer and Smith's (2009) analyses of American Kestrel (Falco sparverius) trends based on migration counts at 20 sites through 2004, the network of sites meeting the threshold of 10 yr of data has increased to 76 sites across North America, increasing the geographical coverage of count sites. Species-specific analyses occur for each site and the results are then collectively assessed across sites for regional or continental patterns.

The Audubon Christmas Bird Count (CBC) is a well-established and long-running effort-corrected assessment of bird abundance trends across the continent during winter (Meehan et al. 2020). Trends in winter can add layers of nuance when interpreting fall migration trends and vice versa (Paprocki et al. 2017). For instance, a species with declining migration-count trends and increasing winter-count trends in a region may not warrant the same level of conservation attention as a species with declining trends in fall and winter. The former case may indicate populations undergoing changes in migratory tendencies or patterns, whereas the latter case would suggest populations in true decline.

We used results from the most recent RPI (Oleyar et al. 2021) and CBC (Meehan et al. 2020) trend analyses for fall migration and winter, respectively, to examine continental and regional trends for the American Kestrel. The American Kestrel is one of the most wide-spread raptors in the Americas. Although it is considered a partial migrant, with portions of some populations year-round residents, large portions of populations in Canada and the USA migrate south in autumn. Kestrel population declines are well documented, with numerous efforts underway to understand the drivers behind them (e.g., Smallwood et al. 2009, McClure et al. 2017). Examining regional differences can also be useful in assessing the status of a species, especially because taking a continent-wide approach may not be the best use of limited conservation resources or offer effective solutions (Bled et al. 2013). Moreover, population trends and the drivers behind those trends can vary geographically (e.g., Ethier et al. 2017). We therefore evaluate fall migration and winter trend data to address the following questions: (1) What do trends for American Kestrels in fall and winter indicate over the past three decades?; (2) Is regional variation in count trends evident during fall and/or winter?; (3) What is the current outlook for American Kestrel populations in North America?

METHODS

Raptor Population Index. The RPI analyses examine data from raptor migration count sites that submit data to hawkcount.org, an online database for raptor migration data operated by the Hawk Migration Association of North America (Hussell and Ruelas 2008, Oleyar et al. 2021). For our assessment of American Kestrel count trends, we included sites that had at least 10 yr of data extending through 2019. Most count sites occur along leading lines (mountain ridges) and diversion lines (coastlines), which are landscape features that tend to concentrate migrating raptors (Bildstein 2006). Included sites also had consistent seasonal and daily effort across the migration season and span of sampled years. Fall migration sites typically count migrating raptors daily, as weather allows, from late August through mid-November. Prior to analysis and to standardize the sampling window for each site, we filtered data to exclude days of the year and hours of the day that were not typically sampled at a count site, by including only those days of the year and hours of the day that included the inner 95% of observations at a count site. We excluded sites from the analyses if kestrels were not detected during at least 50% of all years surveyed at the given monitoring site, or if the mean count was <10 individuals/yr. We aggregated hourly data to daily totals following the recommendations in Crewe et al. (2016b).

We used hierarchical linear regression in a Bayesian framework, implemented using the R-INLA software package (R Core Team 2022; and see Rue et al. 2009) to estimate the linear change (%/yr) in the number of individuals migrating past each count site each day over the past 10-, 20- and 30-yr periods. The regressions for each period assumed either a negative binomial or Poisson distribution of counts, and estimated first- and second-order effects for day of year in addition to the continuous year (trend) effect. We also assumed a random effect for year to account for temporal auto-correlation of counts among years, and a random effect for day of year, for which we assumed independent and identically distributed errors. We estimated annual indices of population size (mean number of falcons per hour \pm SD) from the posterior distribution of each trend model.

We summarize the results of well-supported trends (i.e., where the credible interval for a slope estimate excluded zero and the posterior probability was ≥ 0.95) and consider sites lacking supported increases or decreases in counts of migrating kestrels (credible interval for estimated slope included zero and the posterior probability was <0.95) as showing no trends. Additional analytical details and site-specific results are available at: https://www.rpi-project.org/2019-analysis/.

Christmas Bird Count. The Audubon CBC is a continent-wide, citizen-science effort that monitors birds in winter across North America. The CBC dates back to 1900, with an increasing number of count circles and participants since its inception (Arbib 1981, Link and Sauer 1999). The counts take place between 14 December and 5 January, and occur on a single day in that period within each of hundreds of individual 24.1-km diameter count circles. We downloaded CBC state- and province-based trend estimates calculated by Meehan et al. (2020) following the approach of Soykan et al. (2016). Specifically, we used state and province trend results for 1993-2019 and 2009-2019, which are similar to the periods reflected in the RPI output. We summarize the results of well-supported trends (i.e., 95% credible interval excluded zero) for states and provinces at continental and regional scales, and we consider sites lacking well-supported trends as showing no winter population trends.

Trend Summary Indices. We synthesize separate fall migration and winter trends from multiple count sites or multiple states/provinces, respectively, by calculating spatial- and period-specific trend summary indices (TSI) as follows: TSI = (number of increasing trends - number of declining trends)/total number of trends. Negative TSI values indicate declining trends, values close to zero indicate no trends, and positive values indicate increasing trends. Values closer to -1 or 1 suggest more widespread declines or increases, respectively, for a given geography and timespan.

We calculated fall migration TSIs (TSI_{Migration}) for three decadal periods (1989–2019, 1999–2019, and 2009–2019) at the continental scale and for four geographic regions intended to capture the geography that different count sites likely sample (Fig. 1). We calculated winter TSI scores (TSI_{Winter}) for two periods (1993–2019 and 2009–2019) at the same geographic scales. We assigned each fall migration count site and CBC circle to one state/ province, and one state/province to one region (Fig. 1). We also plotted TSI_{Migration} and TSI_{Winter} together to visualize population trajectories using data from both seasons. We used TSI_{Winter} for 1993–2019 for evaluating both 1989–2019 and

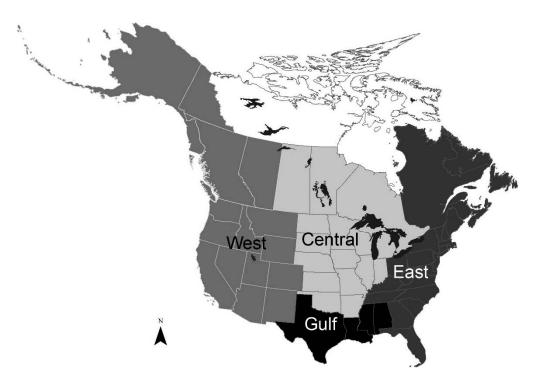


Figure 1. USA states and Canadian provinces included in four geographic regions of North America assessed by the Raptor Population Index (RPI) as a basis for estimating regional population trends for American Kestrels based on fall migration counts and Audubon Christmas Bird Counts.

1999-2019 TSI_{Migration} values. We interpreted positive TSI values for both migration and winter within a region as indicative of a growing population, and negative values for both as indicative of a declining population. We considered paired negative TSI_{Migration} and positive TSI_{Winter} regional indices as indicative of shifting migration tendencies, reflecting more individuals choosing not to migrate at all or migrating shorter distances, or some combination of the two. We considered paired positive TSI_{Migration} and negative TSI_{Winter} indices as potentially indicative of shifting distributions (in this case a contracting winter range), inaccurate migration and/or winter indices, or mismatched migration and wintering areas (Paprocki et al. 2017).

RESULTS

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Long-Term Trends (1989–2019). Across the continent, fall counts of migrating American Kestrels declined by 75% across 12 count sites between 1989 and 2019 (Fig. 2A, Table 1), and declined by 62% across 29 count sites between 1999 and 2019 (Fig. 2B, Table 1). All other analyzed sites showed no significant trends over the two periods (Table 1, Supplemental Material Table S1).

From 1993 to 2019, CBC winter counts of kestrels decreased in 70%, increased in 15%, and showed no trend in 15% of the 54 USA states and Canadian provinces with relevant data (Table 1). Migration TSIs were -0.750 and -0.621 over these 30-yr and 20-yr periods, respectively, and the Winter TSI was -0.556 (Table 1, Fig. 2D, E).

Migration counts of American Kestrels declined at most sites in all regions over the 20- and 30-yr periods. Eight of 12 30-yr fall migration sites and 15 of 29 20-yr fall migration sites with RPI trends for American Kestrels were in eastern North America. In this region, 75% of the counts declined over the 30yr period and 67% of the counts declined over the 20-yr period (Table 1). Migration counts also declined at both western sites with data for 1989– 2019, and at five of seven (71%) western sites with data for 1999–2019. In the central region, one of two sites with a 30-yr dataset showed a declining trend and two of three sites with 20-yr datasets showed

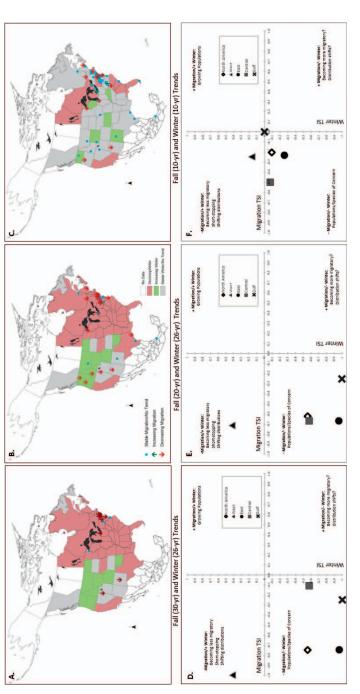


Figure 2. (A–C) Trends for American Kestrels (*Falco sharverius*) counted over 30-, 20-, and 10-yr time series for fall migration based on Raptor Population Index analyses, and 26- and 10-yr time series for winter based on Christmas Bird Count analyses. (D–F) Trend Summary Indices (TSIs; see Table 1) for fall and winter over the same time periods.

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Table 1. Summary of 30-yr, 20-yr, and 10-yr fall migration count trends based on data contributed to the Raptor
Population Index (RPI) project, and 26-yr and 10-yr winter trends in Audubon Christmas Bird Counts (CBC) for American
Kestrels across North America and by region.

SEASON AND YEARS	Metric	North America	REGION ^a			
			WEST	CENTRAL	Gulf	East
Fall migration 1989–2019	# Sites	12	2	2	0	8
	% Declining	75	100	50		75
	% Stable	25	0	50		25
	% Increasing	0	0	0		0
	TSI _{Migration}	-0.75	$^{-1}$	-0.5		-0.75
Fall migration 1999–2019	# Sites	29	7	3	4	15
	% Declining	62	71	67	25	67
	% Stable	38	29	33	75	33
	% Increasing	0	0	0	0	0
	TSI _{Migration}	-0.621	-0.714	-0.667	-0.25	-0.667
Fall migration 2009–2019	# Sites	59	8	9	4	38
	% Declining	24	25	22	0	26
	% Stable	73	75	67	100	71
	% Increasing	3	0	11	0	3
	TSI _{Migration}	-0.203	-0.25	-0.111	0	-0.237
Winter 1993–2019	# States/Provinces	54	12	14	4	24
	% Declining	70	8	71	100	96
	% Stable	15	42	14	0	4
	% Increasing	15	50	14	0	0
	TSI _{Winter} c	-0.556	0.417	-0.571	-1	-0.958
Winter 2009–2019	# States/Provinces	54	12	14	4	24
	% Declining	20	8	21	0	29
	% Stable	69	67	64	100	67
	% Increasing	11	25	14	0	4
	TSI _{Winter} ^c	-0.093	0.167	-0.071	0	-0.25

^a See Fig. 1 for descriptions of the USA states and Canadian provinces in each region.

^b $TSI_{Migration}$ index = (number of sites with increasing RPI trends minus number of sites with declining RPI trends) / Total number sites with estimated RPI trends.

 c TSI_{Winter} index = (number of states and provinces with increasing CBC trends minus number of states and provinces with declining CBC trends)/total number of USA states and Canadian provinces with estimated CBC trends.

declining trends. No gulf region sites had 30-yr count data and only one of four gulf sites with 20-yr data showed a declining trend; all other sites showed no trend (Table 1).

While long-term winter CBC counts of kestrels also declined as a whole across North America (in 70% of 54 states and provinces), some regional variation was evident (Table 1). The extent of states and provinces with declines of wintering kestrels from 1993–2019 was widespread except in the western region. The declines amounted to 71% in the central region, 100% in the gulf region, and 96% in the eastern region. Conversely, only one of 12 (8%) western states and provinces experienced kestrel declines over the 26-year period, whereas 50% of those sites showed increasing trends and 42% showed no trends for wintering American Kestrels (Table 1, Fig. 2D, E). **Recent Trends (2009–2019).** At 59 migration count sites across North America with 10-yr datasets spanning 2009–2019, fall counts of kestrels declined at 24%, showed no trend at 73%, and increased at 3% of the sites (Table 1, Fig. 2C). During this same period, CBC counts of wintering kestrels declined in 20%, showed no trend in 69%, and increased in 11% of the relevant states and provinces. Over the more recent 10-yr period (2009–2019), kestrel population trends across the continent generally appeared more stable than over the longer 26–30-yr periods.

Winter trends differed regionally, with proportionally more states and provinces showing growing kestrel numbers in the west (25%), whereas proportionally more eastern sites showed declines (29%; Table 1). Two-thirds of North American states and Canadian provinces showed no trends in counts of

DISCUSSION

Widespread, long-term declines of American Kestrels persist across North America, but regional differences in population trajectories emerged when we considered fall and winter trends together. RPI data indicated widespread declines in counts of migrating kestrels across North America between 1989 and 2019. CBC data for roughly the same period (1993-2019) also showed widespread declines in wintering kestrels in the eastern and central regions, but increasing trends for 50% of western states and provinces. Taken together, these two longterm monitoring datasets paint a picture of two separate stories for American Kestrels in North America over the last 30 yr, with eastern populations in decline while western populations appear to be shifting their migratory tendencies and remaining farther north during winter. Our results are consistent with previous research documenting shifting migratory tendencies in western kestrels (Heath et al. 2012, Paprocki et al. 2015), and are consistent with other work documenting declines during the breeding season based on results from Breeding Bird Surveys (McClure et al. 2017) and nest-box occupancy studies (Smallwood et al. 2009).

Declines in migration counts alone can indicate either actual population declines, shifting migration routes, or shifting migratory tendencies of different populations. By examining migration and winter trends together we were able to clarify the scenario for American Kestrels. If migration-route changes alone explained declines, then we would have expected to see increased counts at migration sites along new routes, provided activity along those alternative routes was monitored. Our results did not show such increases. If kestrel distributions were shifting northward across North America as a whole, then we would have expected some combination of increasing winter counts and a latitudinal pattern in migration count trends. Our results showed only increasing winter counts in the western region. Gaps in the distribution of migration sampling sites certainly could be masking patterns in some portions of North America, particularly in the central region and far north, but new RPI sites are included with each new analysis and hopefully those gaps will continue to shrink.

Recent patterns offer some hope for this diminutive falcon. Fall migration data from recent years showed fewer declines overall, with a noticeable shift to more stable trends in all regions (Fig. 2C, F). Paired with winter data, these recent trends suggested kestrel populations are stabilizing and no longer declining at the rates seen over the long-term. This appeared to be true continent wide, suggesting that declines may be slowing in the east and shifts in migratory tendency may be slowing in the west based on stabilizing fall and winter counts in those regions.

Here we describe only the geography and extent of trends in migration and winter kestrel counts to highlight broad spatial and temporal patterns. The TSI metrics do not consider the magnitude of trends summarized at each fall migration site or for each state/province in winter, nor the absolute numbers of kestrels documented by each survey method. Future work to do so could be informative, but also comes with analytical challenges and caveats. We note that trends at high-volume count sites within each region are consistent with the general regional patterns described by the TSI metrics (Table S1).

Our results indicating long-term declines of migrating kestrels agree with previous work looking at migration trends (Farmer and Smith 2009) and trends during winter or the breeding season (Smallwood 2009, McClure et al. 2017). We took one further step by deriving and plotting simple trend summary indices for winter and migration; an approach that adds context to trends and highlights that there are at least two distinct stories unfolding for North American kestrel populations. Despite our findings, which offer hope that declines of kestrels may be slowing, the data do not indicate recovery or rebounds in this once common raptor. Ongoing and future work to identify the drivers of kestrel declines, especially in the central and eastern regions, is essential to conservation efforts and any future return to previous population levels for the American Kestrel.

SUPPLEMENTAL MATERIAL (available online). Table S1: Compilation of American Kestrel trend results for raptor population index fall monitoring sites.

Acknowledgments

We acknowledge the hundreds of individuals who contribute their time and talents to community science efforts such as the Christmas Bird Count and raptor migration counts each year. Without them and the organizations that coordinate, fund, and otherwise support these efforts, our understanding and appreciation of kestrels, other birds, and the natural would be far less. We also thank previous contributors to RPI for setting the groundwork for a strong partnership to monitor raptor populations. This manuscript benefited from independent reviews by Chris Farmer and Ernesto Ruelas Inzunza. This paper is Hawk Mountain conservation science contribution 375.

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Received 1 February 2022; accepted 18 September 2022 Associate Editor: Jeff P. Smith