Ornithology, 2026, **00**, 1–16
https://doi.org/10.1093/ornithology/ukaf071
Advance access publication 19 December 2025
Research Article

AMERICAN ORNITHOLOGICAL SOCIETY
Ornithology
OXFORD

How much can local weather conditions explain intra- and inter-annual variation in raptor migration counts at a Neotropical hotspot? A new analytical approach

Yolotli Morales-Góngora,[1] Simoneta Negrete-Yankelevich,[1,*] Gordon A. Fox,[2,3] Amanda S. Gallinat,[4] Sonia Gallina-Tessaro,[5] Laurie J. Goodrich,[6] Stephen W. Hoffman,[7] and Ernesto Ruelas Inzunza[8,*]

[1]Instituto de Ecología A.C., Red de Ecología Funcional, Xalapa, Veracruz, Mexico
[2]Department of Biology, University of New Mexico, Albuquerque, New Mexico, USA
[3]Department of Integrative Biology, University of South Florida, Tampa, Florida, USA
[4]Department of Environmental Studies, Colby College, Waterville, Maine, USA
[5]Instituto de Ecología A.C., Red de Biología y Conservación de Vertebrados, Xalapa, Veracruz, Mexico
[6]Hawk Mountain Sanctuary, Acopian Center for Conservation Learning, Orwigsburg, Pennsylvania, USA
[7]HawkWatch International, Salt Lake City, Utah, USA
[8]Universidad Veracruzana, Instituto de Biotecnología y Ecología Aplicada, Xalapa, Veracruz, Mexico

*Corresponding authors: Ernesto Ruelas Inzunza, ruelas.uv@gmail.com; Simoneta Negrete-Yankelevich, simoneta.negrete@inecol.mx

ABSTRACT

Every year, millions of raptors migrate between their breeding areas in North America and their nonbreeding areas in Central and South America. Many investigations have demonstrated that weather plays a significant, yet complex role in the timing of bird migration at northern localities that, in turn, shapes their seasonal migration phenology. However, very little information is available for the Neotropical region. Here, we analyzed the relationship between local weather variables (wind-related components, humidity, and atmospheric pressure) and the intra- and inter-annual migration patterns of 8 raptor species with different migration ecologies. Our dataset spans between 23–26 years and was obtained at a raptor migration monitoring site at Mexico's Gulf coastal plain, a well-known, globally important migration hotspot. Perhaps due to the often erratic and pulsed daily variation in migration phenology each year, classical analytical approaches do not consider quantifications of intra-annual variation. To address this, we devised a new method based on a finite approximation to the second derivative of the counts (roughness) to analyze the role of weather drivers in the patterns of daily counts. Additionally, we analyzed the inter-annual variation in migration timing, subtracting the mean number of individuals across all years for each day (deviations from the mean). Although we found significant differences in roughness across days, we observed a subtle association between weather and roughness in migration counts, regardless of the species' flight strategy (such as thermal soaring and flapping). Only tailwind affected the intra-annual migration, although the models had a low explanatory power (marginal $R^2 \leq 0.17$). Similarly, we found inter-annual effects of tailwind and sidewind, depending on the type of migrant (long- and short-distance), but the models exhibited high variation and low explanatory power (marginal $R^2 \leq 0.18$). Moreover, the lagged effect of weather variables does not improve the variance explained by weather variables at any of the two timescales evaluated. The low association between migrant counts and weather calls for future research at larger spatial and temporal scales, as well as on assessing the cumulative effect of weather along raptor migration routes.

Keywords: autumn migration, environmental variables, Gulf coast, Gulf of Mexico, landbird migration, Neotropics, raptors

How to Cite
Morales-Góngora, Y., S. Negrete-Yankelevich, G. A. Fox, A. S. Gallinat, S. Gallina-Tessaro, L. J. Goodrich, S. W. Hoffman, and and E. Ruelas Inzunza (2025). How much can local weather conditions explain intra- and inter-annual variation in raptor migration counts at a Neotropical hotspot? A new analytical approach. *Ornithology* 143:ukaf071.

LAY SUMMARY

- The key role of local weather variables on the passage of raptors tracked at migration monitoring sites has been documented in many northern localities, but their effect on migration timing within and across seasons in the Neotropics is unknown.
- We devised a novel method that captures the day-to-day variation (i.e., roughness) in migration counts within years to assess how the passage of 8 species of raptors varies in response to local weather at a well-known migration hotspot along Mexico's Gulf coast.
- Additionally, we explored the effect of weather variables on year-to-year variation in migration counts.
- We found a subtle association between weather factors and migration counts at the two timescales evaluated, regardless of raptor flight strategy and migration distance.
- Our research suggests that the impact of weather on raptor migration counts in the Neotropics may need to be assessed at larger spatial or temporal scales, and accounting for cumulative effects along migration routes.

Submission Date: August 19, 2025. Editorial Acceptance Date: October 29, 2025

¿Qué tanto explican las condiciones locales del estado del tiempo la variación intra- e inter-anual en los conteos de rapaces migratorias en un sitio de importancia global en el Neotrópico? Un nuevo enfoque analítico

RESUMEN

Cada año, millones de rapaces migran entre sus áreas reproductivas en Norteamérica y sus áreas no reproductivas en Centro y Sudamérica. Muchas investigaciones han demostrado que el estado del tiempo juega un papel importante, aunque complejo, en la temporalidad de la migración en localidades norteñas y a su vez moldea la fenología estacional de su migración. Aquí, analizamos la relación entre variables locales del tiempo (componentes del viento, humedad y presión atmosférica) y los patrones migratorios intra- e inter-anuales de ocho especies de rapaces con diferente ecología de la migración. Los datos abarcan entre 23–26 años y fueron obtenidos en dos sitios de monitoreo de rapaces localizados en un conocido hotspot migratorio de importancia global en la planicie costera del Golfo de México. A pesar de que la variación de la migración intra-anual a menudo es errática y pulsada, los enfoques analíticos clásicos no toman en cuenta la cuantificación de esta variación. Para abordar esto, desarrollamos un nuevo método basado en una aproximación finita de las segundas derivadas de los conteos (denominado en inglés "roughness") para analizar el rol de las variables del estado del tiempo en el patrón de los conteos diarios. Adicionalmente, analizamos la variación interanual en la temporalidad de la migración, sustrayendo el número promedio de individuos contabilizados a través de todos los años para cada día (desviaciones de la media). A pesar de encontrar diferencias en el roughness entre los días, observamos una escasa asociación entre esta variable y aquellas del estado del tiempo, independientemente de la estrategia de vuelo de las especies (p. ej. aves planeadoras y de vuelo activo). De manera general, solo los vientos de cola afectaron la migración a escala intra-anual, sin embargo, su poder explicativo fue bajo (R^2 parciales ≤ 0.17). De manera similar, encontramos un efecto inter-anual de los vientos de cola y vientos laterales de acuerdo al tipo de migrante (corta y larga distancia), aunque el poder explicativo de éstas fue bajo (R^2 parciales ≤ 0.18). Además, los modelos con el efecto retrasado de las variables del estado del tiempo no mejoraron el poder explicativo en ninguna de las dos escalas evaluadas. La escasa asociación entre los conteos migratorios y las variables del estado del tiempo indican que se necesitan futuras investigaciones a mayores escalas de temporales y espaciales, así como analizar los efectos acumulativos de estos factores a lo largo de toda la ruta migratoria.

Palabras clave: costa del Golfo, Golfo de México, migración de aves terrestres, migración otoñal, Neotrópico, rapaces, variables ambientales

INTRODUCTION

Birds rely on a combination of endogenous factors and environmental cues to make decisions en route during spring and autumn migration. These decisions, such as staying at or departing from a migratory stopover location, impact birds' migration speed and timing, energy costs, migratory route, and physiological condition, ultimately affecting their reproductive success and survivorship (Mueller and Berger 1967, Kerlinger et al. 1985, Kerlinger and Gauthreaux 1985, Alerstam and Lindström 1990, Horton et al. 2019). Compared to spring migration, where departure seems to be primarily driven by endogenous schedules as birds experience pressure to arrive at their breeding grounds and establish territories (Berthold 1996, Tan et al. 2018), autumn migrants respond more to deteriorating weather conditions and food availability in their northern, breeding range (Jenni and Schaub 2003, Bildstein 2006, Xu and Si 2019). Autumn migration is also characterized by a higher proportion of inexperienced hatch-year birds, making it a particularly high-mortality journey, and therefore critical to bird population trajectories (Murray 1964, Oppel et al. 2015). Despite its importance and relative complexity, autumn migration has been less studied than spring migration from a phenological point of view (Gallinat et al. 2015), and the factors that influence migration timing vary among species (Ellwood et al. 2015).

Many raptor species are experiencing shifts in breeding and nonbreeding season distributions, abundance, migration timing, and survival rates due to climate change (Paprocki et al. 2014, Therrien et al. 2017). This underscores the urgent need to understand their migration patterns and the potential effects of climate change. Selecting the migration timing and route that maximizes exposure to favorable weather conditions is crucial for raptors, as they rely on supporting tailwinds and strong thermal updrafts to fly (Pennycuick 1969, Rayner 1985, Acácio et al. 2022). The timing and route are also strongly affected by weather conditions (Alerstam 1979, Able 1980, Tan et al. 2018), and raptors minimize the energetic costs of migration using atmospheric updrafts from thermal convection or orographic lift (Pennycuick 1969, Verhelst et al. 2011). Therefore, their migratory routes are most often pathways situated along geographical and topographical features that provide favorable atmospheric conditions for these phenomena to occur (Verhelst et al. 2011, Nourani et al. 2016) or that allow them to avoid barriers, such as large water bodies (Kerlinger 1989). The importance of such immediate environmental conditions in the migration of raptors suggests that day-to-day variation in their migration can be modeled by local weather conditions, including wind speed, wind direction, vertical air movement, and humidity, among others.

In addition to environmental factors, individual-specific traits like body size and migration distance also affect raptors' migration timing and routes (Kerlinger et al. 1985, La Sorte et al. 2015). Consequently, the specific conditions that are considered favorable vary among species, according to their ecology, body condition, and morphology (Panuccio et al. 2016). In general, flapping and soaring birds benefit from tailwinds, which help them travel faster. However, flapping birds are less affected by crosswinds due to their active flight, which minimizes the risk of drifting off course (Vansteelant et al. 2014). Soaring migrants often decrease their airspeed in tailwind conditions as a mechanism to minimize flight height loss during their gliding phase. This adjustment allows birds to cover greater distances more quickly by reducing the time spent in the thermal circling phase of flight (Becciu et al. 2018). However, birds can exhibit different behaviors between regions with different wind conditions, depending on their fuel reserves, whether they are migrating over land or water, and the need to avoid further delay (Newton 2024).

To understand population status, as well as the timing and drivers of migration for different raptor species, scientists and volunteers make daily observations during autumn and spring, recording millions of birds yearly at migration monitoring sites worldwide (Bildstein et al. 2008, Nourani and Yamaguchi 2017). At monitoring sites, the interplay of environmental and species' endogenous factors results in large variations in the number of birds recorded daily (Hussell and Ruelas Inzunza 2008). Single-species counts of migrants are highly variable from day to day, with high-count days followed by days of low to no counts at all, which makes it challenging to parameterize migratory phenology using classical metrics (e.g., "peak date" that rely on an assumed Gaussian distribution), especially when trying to predict temporal and spatial variation (Bildstein 2006, Moussus et al. 2010).

A common approach to analyzing variation in migration intensity is to use generalized linear models or linear mixed models with counts as the dependent variable (e.g., Farmer et al. 2007, Panuccio et al. 2016, Becciu et al. 2018). However, this approach does not consider how abrupt these changes are between one day and the next, and only describes certain phenology features. Most prior studies have ignored day-to-day variation altogether and instead focused on modeling the factors driving variation in summaries of migration phenology, such as annual mean passage dates (Allen et al. 1996, Miles et al. 2017, Thurber et al. 2020). But ultimately, it is the variation in, and drivers of, day-to-day migration phenology that determine the timing of arrival to nonbreeding grounds.

Most studies that analyze bird intra- and inter-annual variation and their association with weather conditions have been geographically and taxonomically limited (Denny et al. 2014), with the majority of autumn studies conducted in Europe and North America (Bednarz et al. 1990, Bildstein et al. 2008, Ellwood et al. 2015). By contrast, studies in the Neotropics are still scarce (Bussjaeger et al. 1967, Smith 1980, Thiollay 1980, Porras-Peñaranda et al. 2004, Olivo 2005, Ruelas Inzunza et al. 2005, 2009, Phillips et al. 2023, Juhant 2025), so it is crucial to ask if the mechanisms and factors that affect raptor migrations in temperate regions are the same in the tropics, in order to understand the entire annual cycle and migration drivers of these species.

To date, there have not been clear links of environmental factors to migration phenology in the tropics, and some results at northern latitudes are contrasting. Some studies have established a clear link between migration timing and environmental factors (Allen et al. 1996, Vansteelant et al. 2014, Panuccio et al. 2016, Dumandan et al. 2022), while others have found the relationship to be weak (Bohrer et al. 2012) or nonexistent (Thorup et al. 2006, Chevallier et al. 2010, Filippi-Codaccioni et al. 2011). This highlights the importance of analyzing migration patterns using different methods and datasets from different regions to elucidate the drivers that govern intra- and inter-annual autumn migration.

In this study, we aim to analyze the influence of local weather variables (humidity, a suite of wind-related variables, and ground-level air pressure) on the intra- and inter-annual patterns of autumn migration of 8 raptor species at a migration monitoring site in Veracruz, Mexico. To understand the effects of weather on intra-annual variation, we devised a new methodological approach to account for abrupt oscillations in daily migration counts and overcome the limitations of previous methods. Our main questions are: (1) How do weather variables affect within- and among-season migration patterns? and (2) Do species have different responses (in terms of daily and annual variability) according to their flight strategies? At an inter-annual level, we expect more variable responses in facultative, short-distance migrants due to their plastic responses to migration timing (e.g., Barton and Sandercock 2018) in contrast with obligate, long-distance migrants who exhibit a seemingly more consistent migration timing (Maynard et al. 2022). At the intra-annual level, we expect larger, soaring migrants to be more sensitive to weather conditions due to their dependence on thermal updrafts (Pennycuick 1969, Acácio et al. 2022), compared to smaller, flapping birds that can alternate between soaring and flapping and can compensate for wind drift (Kerlinger 1989, Nourani and Yamaguchi 2017, Sergio 2022).

METHODS

Study Sites

Central Veracruz, Mexico, lies at the intersection of two major mountainous systems, the Sierra Madre Oriental and the Central Volcanic Belt, which constrain the width of the Gulf Coastal Plain at about 19°N. This reduction in the course of the Gulf lowland coastal plain forms a geographic bottleneck that funnels spring and autumn raptor migrations (Ruelas Inzunza et al. 2010). Here, raptor migration counts are systematically made every year by Pronatura Veracruz (a non-profit conservation organization) from 2 fixed locations placed 11 km apart and perpendicular to the migration front: Cardel (19.3666°N, 96.3666°W), closer to the coast, and Chichicaxtle (19.35°N, 96.4666°W, Figure 1), a more inland site. Because raptor migration over the coastal plain is relatively unconstrained by geographic features and occurs over a broad front, we consider these 2 sites independent samples of the same migration flow.

Migration Data

Veracruz is a well-known raptor migration bottleneck of global importance, with around 5 million raptors of over 20 species monitored annually during the autumn (Ruelas Inzunza et al. 2000, 2010). To have sufficient data for robust analyses, we limited the migration count data to the 8 most frequent migrant raptor species passing our 2 sites, including birds with different ecologies (listed in phylogenetic order): *Cathartes aura* (Turkey Vulture), *Pandion haliaetus* (Osprey), *Buteo platypterus* (Broad-winged Hawk), *B. swainsoni* (Swainson's Hawk), *Astur cooperii* (Cooper's Hawk), *Accipiter striatus* (Sharp-shinned Hawk), *Ictinia mississippiensis* (Mississippi Kite), and *Falco sparverius* (American Kestrel; Table 1). We analyzed daily count data from the autumn migration seasons 1995–2022 for Chichicaxtle and 1995–2019 for Cardel (counts at this second site were suspended in 2020 and 2021 and restarted thereafter, and data from 1997 are missing for both sites). Daily autumn counts have been collected annually from August 20–November 20 following the protocol of the Hawk Migration Association of North America (HMANA 2009). Further details of our study system and data collection protocols can be found in Ruelas Inzunza et al. (2009, 2010).

Weather Data

The weather data were obtained from the National Centers for Environmental Prediction (NCEP) and National Center for Atmospheric Research (NCAR) Reanalysis data set using the RNCEP package in R (Kemp et al. 2012). These data have a spatial resolution of 2.5 × 2.5° and a temporal resolution of

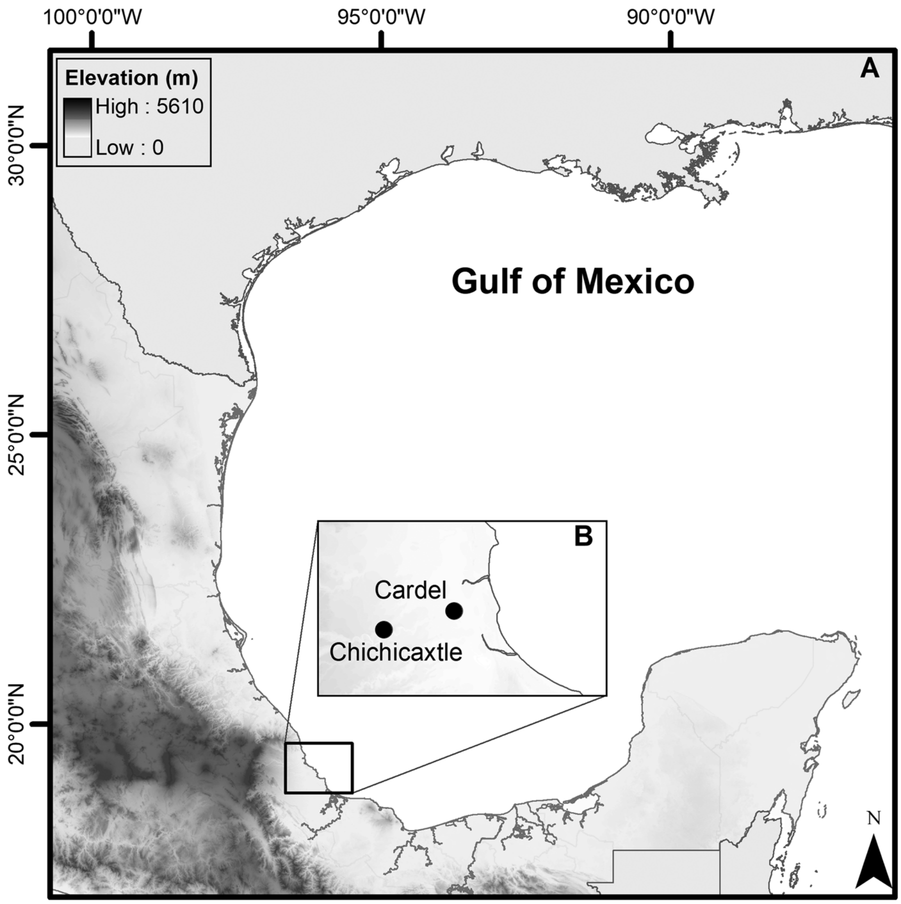

FIGURE 1. (A) Geographic location of the study area in the coastal plain of the Gulf of Mexico. (B) Location of the 2 monitoring sites (black dots) where yearly autumn migration counts were conducted between 1995–2024. Gray scale refers to elevation.

TABLE 1. Migration ecology of the 8 raptor species analyzed in the present study. Migration type refers to partial or facultative migrant (for species whose breeding and nonbreeding ranges overlap) and complete or obligate migrant (for species whose breeding and nonbreeding ranges do not overlap, and the entire population vacates the breeding range during the nonbreeding season). Migrant refers to the distance from the centroid of their breeding range to the centroid of their nonbreeding range, and are classified as short-distance migrants (SD; <2,500 km) and long-distance migrants (LD; >4,000 km). The last two columns are the mean number of individuals per species recorded throughout the autumn season (±SD). Ospreys are listed as flapping-and-soaring, as they locally use either flight strategy.

Scientific name	Species	Flight strategy	Migration type	Migrant	Cardel $\bar{x}$ (± SD)	Chichicaxtle $\bar{x}$ (± SD)
Cathartes aura	Turkey Vulture	Soaring	Partial	LD	**991,064** (230,119)	**804,355** (202,037)
Pandion haliaetus	Osprey	Soaring-and-flapping	Partial	SD	**1,748** (637)	**844** (196)
Buteo platypterus	Broad-winged Hawk	Soaring	Complete	LD	**931,385** (212,334)	**813,707** (173,600)
Buteo swainsoni	Swainson's Hawk	Soaring	Complete	LD	**303,912** (139,350)	**393,762** (164,348)
Astur cooperii	Cooper's Hawk	Flapping	Partial	SD	**1,089** (475)	**1,067** (271)
Accipiter striatus	Sharp-shinned Hawk	Flapping	Partial	SD	**1,559** (1,030)	**1,562** (718)
Ictinia mississippiensis	Mississippi Kite	Flapping	Complete	LD	**89,786** (58,269)	**177,469** (80,502)
Falco sparverius	American Kestrel	Flapping	Partial	SD	**3,652** (2,651)	**1,547** (1,386)

6 hr. We extracted the following variables: air pressure (Pa), south-north wind component (Vwind; m s^{-1}), east-west wind component (Uwind; m s^{-1}), vertical wind component (Omega; Pa s^{-1}), temperature (°C), and relative humidity (%). All variables, except for pressure, were extracted at the surface and at a 925 hPa level (pressure level nearest to our perceived mean flight height of migrants). Data were interpolated linearly to our study sites (latitude and longitude) and at midday, coinciding with the local peak activity. Using the east-west and north-south wind components, we calculated the component of the flow parallel to the preferred direction of movement (tailwind) and the component of the flow perpendicular to the preferred direction of movement (sidewind) using the RNCEP package (Kemp et al. 2012). Before our analyses, all variables were checked for collinearity using Pearson correlation coefficients (Supplementary Material Figure S1—see Online Supplementary Material for a color version of this figure). For variables with $|r > 0.5|$, we selected the variable that we considered to provide the greatest ecological insight (Table 2).

TABLE 2. Description of the weather variables used in our analysis of intra- and inter-annual variation in raptor migration counts. The 925 hPa is the atmospheric pressure level nearest to the perceived mean flight height for raptor migration at our sites.

Variable	Description	Measurement units	Atmospheric level
Tailwind	Component of the flow parallel to the preferred direction of movement	m s^{-1}	925 hPa
Sidewind	Component of the flow perpendicular to the preferred direction of movement	m s^{-1}	925 hPa
Omega	Vertical wind	Pa s^{-1}	925 hPa
Pressure	Pressure at the surface level	Pa	Surface
Humidity	Relative humidity	%	Surface

Analytical Approach

Bird migration phenology tends to be long-tailed (e.g., Both et al. 2009, Dunn and Møller 2019), and the first and last days of occurrence are sensitive to sampling effort and changes in population size (Moussus et al. 2010, Dorian et al. 2020). To minimize noise from these factors, the analysis focused solely on the data window from the 5th to the 95th percentiles for each year. We analyzed migration patterns and their relationship with weather conditions at 2 timescales: (1) daily scale variation (intra-annual variation) and (2) yearly scale variation (inter-annual variation).

Intra-annual variability estimates

Variation in migration intensity can be associated with weather conditions, as birds may exhibit abrupt behavioral responses to gradual atmospheric changes. This may occur if individuals delay departure until suitable conditions are met (conditions that evolve progressively but elicit sudden movement once a critical threshold is crossed). To analyze fluctuations in daily migrant counts, we used a finite approximation to the second derivative of the counts, hereafter called "roughness." Because we have discrete data, we used second differences, which are the discrete analogues of derivatives, to identify abrupt changes in the number of migrants.

To our knowledge, this method has not been used in previous studies of migration; we describe it in detail below (see also Supplementary Material). First, we calculated the first differences between each pair of successive migrant counts (Δx_i):

$$\Delta_{x(i)} = x_{i+1} - x_i$$

Then we normalized the entire sequence of first differences by subtracting the mean of the first differences and dividing by the standard deviation:

$$\left|\Delta\left(x_i\right)\right| = \frac{\Delta\left(x_i\right) - \overline{\Delta\left(x\right)}}{\sigma\left(\Delta\left(x\right)\right)}$$

Finally, the first differences for each of these Studentized first differences is an approximation to the second derivative:

$$\Delta^2(x_i) = \Delta\left(\left|\Delta\left[x_i\right]\right|\right)$$

We squared these differences (treating troughs and peaks in migrant numbers the same), and divided it by 4 (because of the squared quantity), giving:

$$R(x_i) = \frac{\left[\Delta_2\left(x_i\right)\right]^2}{\left(2h\right)^2}$$

The resulting metric allows us to estimate how abrupt the change in migrant numbers is at each point in the season. First differences removed linear trends, and second differences removed quadratic trends. Studentizing makes the measure scale-free, so we can now compare roughness among seasons, sites, or species. Finally, we can multiply the roughness $R(x_i)$ by the sign of their second difference, hereafter called "signed roughness," which allows us to quantify the abruptness of downturns or upswings in daily counts (Figure 2). Unlike models based on a discrete probability distribution function such as the Poisson, whose estimated parameter is the mean observed count of birds each day (μ_i), the roughness metric provides useful information beyond the counts themselves or the first differences since it allows us to identify large deviations from the "usual" jagged behavior of migration numbers through time contrary to simply analyzing counts that incorporates a large amount of "usual" variability to be explained into the analysis that may limit the statistical power to detect the more unusual pulses and downturns (Supplementary Material Figure S1 and Table S1).

Inter-annual variability estimates

To detect unusual variation in daily migration counts from long-term expectations, we analyzed the inter-annual variation by the deviations from the mean daily counts. For each day, we estimated the mean count of individuals across all years and subtracted this value from the registered count for that day in each year. The resulting deviations allowed us to estimate how much each daily count differed from the long-term mean for that date. This metric was used as the dependent variable in subsequent analysis.

Statistical analyses

We fit generalized linear mixed models (GLMMs) assuming a Tweedie distribution to evaluate the influence of weather variables on roughness (intra-annual) and deviation from the mean counts (inter-annual). We expected overdispersion because many different variables are likely to affect migrant numbers in different ways, including species (measured), population within species (unmeasured), and weather conditions at other stopover sites several days prior to passage by our sites (unmeasured). Using the R package *glmmTMB* (Brooks et al. 2017), we fit Tweedie models, which are especially useful for overdispersed data. Tweedie distributions are also appropriate here because both roughness and deviation from mean counts are non-negative. Indeed, a range of Tweedie dispersion coefficients estimated by *glmmTMB* yield distributions that reduce to the compound Poisson-gamma distribution (also called negative binomial). In a rough sense, this model for daily count data (or

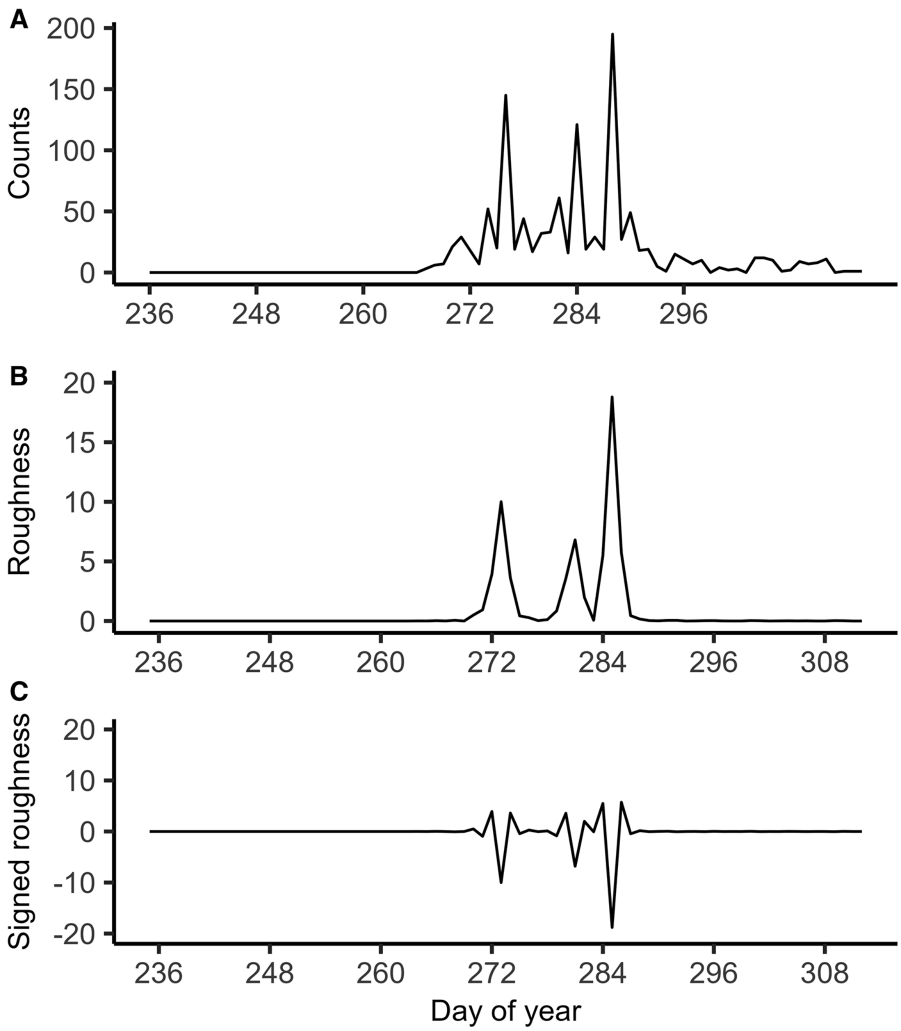

FIGURE 2. Example of a roughness estimate. (**A**) Daily count of *Accipiter striatus* (Sharp-shinned Hawk) recorded in the autumn of 1995 at Cardel. (**B**) Estimate of roughness. (**C**) Sign of second difference. The variation in counts (**A**) is primarily influenced by fluctuations over 3 days (**B**), which mainly consist of declines in the counts (**C**).

roughness) can be thought of as a Poisson distribution, in which the Poisson parameter λ varies over time. Tweedie models are used with growing frequency in ecology (e.g., Law et al. 2000, Hollister et al. 2015, Thorson et al. 2022).

On the intra-annual scale, in addition to weather variables, we included site, flight strategy (flapping or soaring), and the sign of the second difference (upswing or downturn) as categorical fixed effects. Including the sign of the second difference as a predictor allowed us to address questions about the relative importance and magnitude of upswings and downturns. Finally, as continuous fixed terms, we included the interactions of tailwind and sidewind with flight strategy, and we accounted for an estimate of the temporal trend within the season by including a third-order orthogonal polynomial for the Julian day (Day). For the inter-annual scale, we included site, type of migrant (long-distance or short-distance migrant), and sign (positive or negative deviations from the mean) as categorical fixed effects, and (as above), a third-order orthogonal polynomial for Day, as well as the interactions of tailwind and sidewind with the type of migrant as continuous fixed terms. We examined the raptor response to weather variables within the same-day, 1, 2, and 3-day lagged effects.

For both time scales, we included species and day of year (DOY) nested within year, as random effects. DOY: Year is a categorical variable that estimates the variance among days within a year. Another way to understand the use of both Day and DOY is to begin by realizing that days are the basic sample unit in this study; thus, including DOY:Year as a random term ensures the models' correspondence with the study design. Unless one expected no temporal trend within the season, it is also necessary to model it; we do so with the continuous fixed effect of the polynomial for Day.

Before the analysis, the explanatory variables were standardized by centering the values on the mean and dividing them by 2 standard deviations (SD). Finally, we used the Schwarz Information Criterion (SIC) to select the best models for the intra- and inter-annual analysis. There are a number of arguments as to why the SIC (also called Bayesian Information Criterion) can be preferable to the more widely used Akaike Information Criterion (AIC). The AIC is designed to be used to identify the best predictive model (given the data) from a group of models. As such, it tends to include more terms because they improve predictions. This can lead to overfitting. By contrast, the SIC is designed to identify the model that is closest to the underlying process—the "truth"—and is less prone to overfit models. Dennis et al. (2019) show that the SIC is "consistent" (its error goes to zero as sample sizes increase), and this is true even when the model is mis-specified; neither of these is true for the AIC. The goodness of fit of the models was evaluated through marginal and conditional R^2 using the *MuMIn* R package (Bartón 2022), and compliance with model assumptions was checked from diagnostic residual plots. All analyses were performed in R (V4.4.1; R Core Team 2024).

RESULTS

Migration Timing

For the 8 focal study species, we recorded an annual mean of 2,105,181 individuals at Cardel and 1,959,766 individuals at Chichicaxtle, with the expected variation in abundances among species. *Cathartes aura* was the most abundant species at Cardel, while the *Astur cooperii* was the least abundant. At Chichicaxtle, the *B. platypterus* was the most abundant, and *P. haliaetus* was the least abundant (Table 1). The passage window for most of the species was recorded from the middle to the second half of the field season, except for the *I. mississippiensis*, which was recorded from the start to the middle of the field season. *Buteo swainsoni* had the narrowest 90% migration window, while *P. haliaetus* had the broadest migration window and was recorded throughout the entire season (Figure 3).

Weather Variables

In our study area, the mean humidity value per season was 94% (±3.02 SD) for both sites. The prevailing sidewinds were

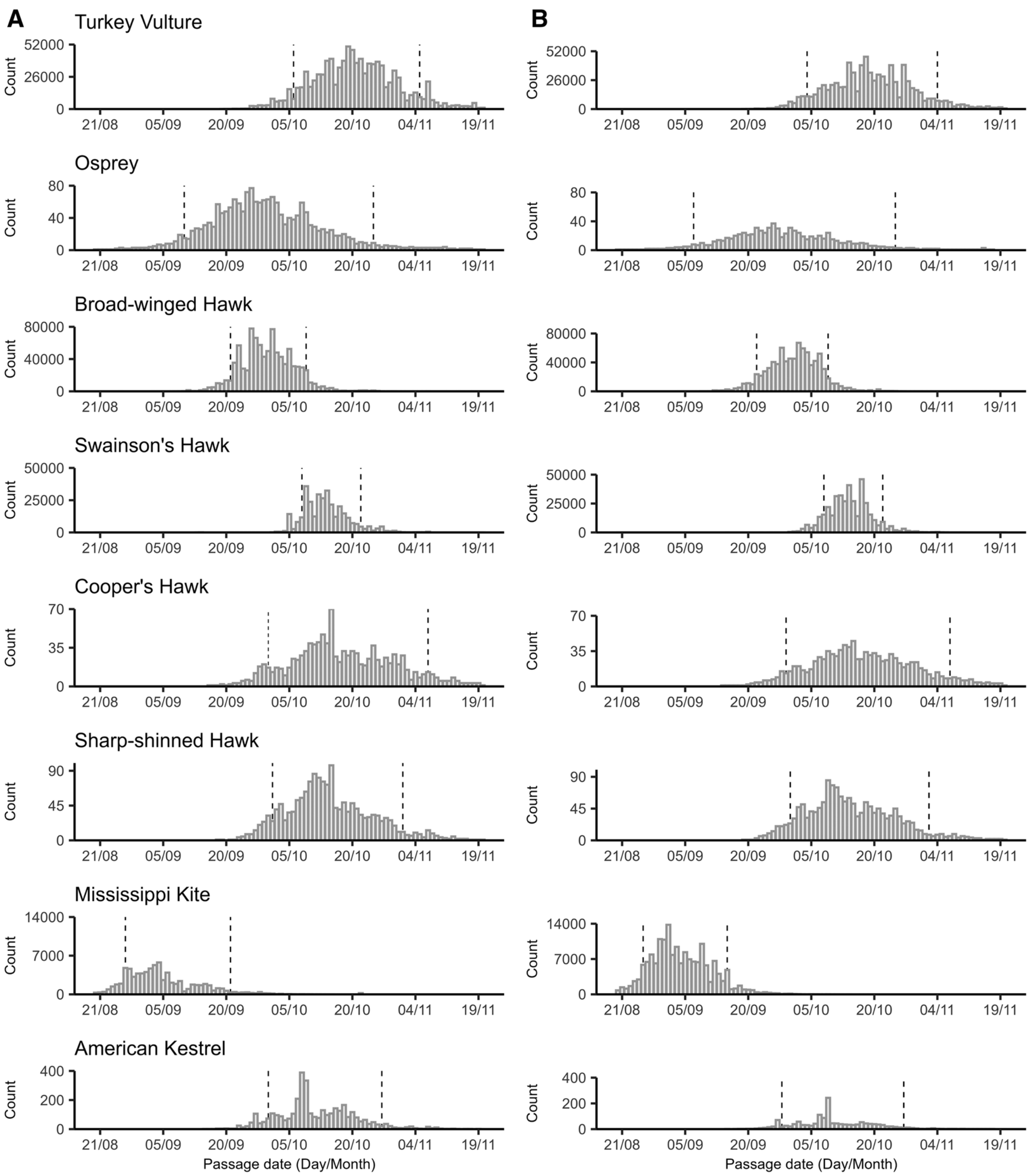

FIGURE 3. Mean daily counts of migrating raptors of 8 species recorded at (**A**) Cardel (1995–2024; no data in 1997, 2020, and 2021) and (**B**) Chichicaxtle (1995–2024, no data in 1997), Veracruz, Mexico. Vertical dashed lines show the central 90% passage window.

mainly positive (wind blowing from west to east), with a mean value of 1.75 m s^{-1} (±3.16 SD) for Cardel and 1.33 m s^{-1} (±1.33 SD) for Chichicaxtle. The tailwind had a mean value per season of –0.63 (±3.01 SD) for Cardel and 0.37 m s^{-1} (±3.39 SD) for Chichicaxtle, indicating tailwinds for Cardel while Chichicaxtle experienced a trend towards weak headwinds. These components translate to a mean wind speed of 4.19 m s^{-1} (±2.23 SD) for Cardel and 3.86 m s^{-1} (±2.34 SD) for Chichicaxtle, corresponding to a gentle breeze and light breeze, respectively, in the Beaufort wind scale. The Omega variable was predominantly negative in Cardel with a mean value per season of –0.065 Pa s^{-1} (±0.06 SD), indicating uplift movements (Brønnvik et al. 2022), while in Chichicaxtle the mean value per season was 0.001 Pa s^{-1} (±0.05 SD; Supplementary Material Figure S3—see Online Supplementary Material for a color version of this figure).

Intra-annual Patterns in the Roughness of Bird Migration Counts

The best-fit models for the intra-annual variability in the roughness of raptors' autumn migration include random effects for DOY nested within year, year, and species. Among these factors, the term DOY nested within year accounted for the greatest amount of variation (Table 3). Overall, the global models exhibited strong explanatory power, with a conditional R^2 of 0.57. However, the variance that corresponds to the fixed variables was relatively modest, with a marginal R^2 of 0.17 or lower. The fixed variables included in the best model were: Day, site, the sign of second difference, tailwind, and flight strategy (Table 3). In general, we observed higher roughness of bird abundance values at the beginning of the season, and these values decreased as the migration season progressed (Figure 4A). In the presence of headwinds (positive tailwind values), raptor species abundance exhibited an increase in roughness (Figure 4B). Our results indicated that raptor migration experienced more abrupt downturns than upsurges, as shown by the sign of the second difference variable, which exhibited greater negative values compared to positive ones (Figure 4C). In the case of the site variable, Cardel showed higher roughness values than Chichicaxtle (Figure 4D) and, in terms of flight strategy, soaring species showed higher and more variable roughness values than flapping birds (Figure 4E). Although the models incorporating the lagged effects of weather variables showed lower SIC values, they did not explain more variation (Table 3). Notably, none of the best-fit models included two-way interactions between explanatory variables.

Inter-annual Patterns in the Deviation from the Mean of Bird Migration Counts

The best-fit models for the inter-annual variability in deviation from the mean autumn migration counts include random effects for DOY nested within year, year, and species. Among these factors, the term species accounted for the greatest amount of variation (Table 4). The models exhibited a strong overall explanatory power, with a conditional R^2 of 0.96. However, the variance that corresponds to the fixed variables was relatively modest, with a marginal R^2 of 60.18 or lower. Moreover, when we compared daily deviations from the mean in migration counts across different years, we observed substantial variability, reflected in a large confidence interval (CI) in estimated model parameters. Yet, fixed effects suggested larger deviations from the mean at the start of the autumn season, and as the season progressed (Day), the deviation from the mean tended to decrease (Figure 5A). The only weather variables that influenced inter-annual changes were tailwind and sidewind in interaction with the type of migrant. In general, long-distance migrants showed greater deviations from the mean when headwinds were present (indicated by positive tailwind values) and when sidewinds came from the west. In contrast, short-distance migrants did not exhibit a differential response to varying tailwind and sidewind conditions (Figures 5B–C). Additionally, we found that positive deviations from the mean were generally more extreme than negative deviations (Figure 5D). This suggests that in certain years, bird counts were higher than the mean on specific days. Finally, the highest deviations from the mean were recorded at the Cardel station compared to Chichicaxtle (Figure 5E). The models incorporating lagged terms had lower SIC values. However, these models did not improve the explanatory power of fixed variables (marginal R^2) over variation in the number of migrants observed across the years (Table 4).

DISCUSSION

We found no strong effect of local weather variables on either intra- or inter-annual patterns of migration counts. While we identified some statistically significant relationships between local wind conditions and day-to-day variation in raptor counts, particularly for intra-annual patterns, the explanatory power of the weather variables was subtle in both of the timescales we evaluated, indicating that raptor species show little selectivity for local weather conditions to migrate over the coastal plain of the Gulf of Mexico. However, the inclusion of random effects greatly increased the models' explanatory power. At the intra-annual scale, most of the explained variance was attributed to the random factor DOY (day of year) nested within year, this could be related to the characteristics of our study sites, since this area serves as a convergence zone for populations from various geographic origins (Ruelas Inzunza et al. 2009) that likely experience different prior conditions that could influence their migration decisions. At the inter-annual scale, most of the variance explained by the random effects was associated with species identity, indicating that intrinsic species traits, such as ecology, migration strategy, route selection, and population size, may play a major role in shaping these year-to-year variations.

Weather Effects on Intra- and Inter-annual Variation

The seasonal patterns of migration are known to influence, and be influenced by, various aspects of birds' behavior, including migration speed, timing, energy expenditure, migratory route, reproductive success, and mortality (Horton et al. 2019). Moreover, these factors can also impact population dynamics beyond individual fitness (Becciu et al. 2018). Identifying the environmental drivers of intra- and inter-annual migration patterns is central to forecasting future migration dynamics under a changing climate.

In contrast to our study, research in other regions of the world has shown that variables such as wind and temperature

TABLE 3. Summary statistics of the best general linear mixed models relating the intra-annual roughness values with weather variables without lag (LAG0) and lagged by 1, 2, and 3 days (LAG1, LAG2, and LAG3, respectively) for 8 raptor species at 2 monitoring sites in Mexico's Gulf coast. Day² and Day³ refer to second and third-order terms in the orthogonal polynomials for Day (day of year). SIC refers to the Schwarz Information Criterion. SD refers to standard deviation.

Model	Fixed effect	Coefficients ± SE	Random effect	SD	SIC
LAG0	Intercept	−0.17 ± 0.08	DOY:Year	1.04	12,491.9
	Day	−53.59 ± 4.33	Year	0.17	
	Day²	−22.44 ± 3.45	Species	0.15	
	Day³	−18.68 ± 2.90			
	Site	−0.10 ± 0.03			
	Sign of the second difference	−0.46 ± 0.03			
	Tailwind	0.31 ± 0.02			
	Flight strategy	0.72 ± 0.12			
Conditional R^2	0.57				
Marginal R^2	0.17				
LAG1	Intercept	−0.22 ± 0.08	DOY:Year	1.05	12,442.9
	Day	−53.40 ± 4.32	Year	0.16	
	Day²	−21.42 ± 3.45	Species	0.16	
	Day³	−20.07 ± 2.90			
	Sign of the second difference	−0.46 ± 0.03			
	Tailwind	0.24 ± 0.02			
	Flight strategy	0.72 ± 0.12			
Conditional R^2	0.57				
Marginal R^2	0.16				
LAG2	Intercept	−0.23 ± 0.08	DOY:Year	1.05	12,303.5
	Day	−52.72 ± 4.38	Year	0.15	
	Day²	−21.37 ± 3.45	Species	0.16	
	Day³	−20.13 ± 2.90			
	Sign of the second difference	−0.46 ± 0.03			
	Tailwind	0.23 ± 0.02			
	Flight strategy	0.73 ± 0.12			
Conditional R^2	0.57				
Marginal R^2	0.16				
LAG3	Intercept	−0.19 ± 0.08	DOY:Year	1.06	12,152.1
	Day	−51.17 ± 4.23	Year	0.14	
	Day²	−22.35 ± 3.46	Species	0.16	
	Day³	−18.92 ± 2.94			
	Site	−0.07 ± 0.03			
	Sign of the second difference	−0.46 ± 0.03			
	Tailwind	0.22 ± 0.02			
	Flight strategy	0.72 ± 0.12			
Conditional R^2	0.57				
Marginal R^2	0.15				

had a strong association with daily counts in raptors (e.g., Spaar 1997, Panuccio et al. 2016, Becciu et al. 2018, Dumandan et al. 2022). Similar to our study, research on *P. haliaetus* migrating between northern Europe and Africa showed a minor effect of winds and precipitation on their travel or stopover decisions (Thorup et al. 2006). However, the statistical methods used in the aforementioned studies do not provide a measure of the percentage of variation explained by environmental factors for comparison. Using our approach, we were able to quantify effect sizes directly (proportion of variance explained by fixed variables) and show that weather explained a relatively small proportion of the variation in migration counts. The mixed results of studies, regardless of the time scale or the metric used to analyze this phenomenon, seem to indicate that the influence of weather variables on avian migration is context-dependent and that species can exhibit a flexible response across their migratory route.

Interannually, both long and short-distance migrant species exhibited effects from wind-related variables, but we observed substantial variability. The weak effect of weather on the inter-annual migration patterns may be explained by geography, moderate variation in wind conditions, and cumulative effects. Geographically, North America's wind patterns seem to generally favor flight directions, resulting in birds being less exposed to adverse wind conditions than migrants in Europe (Erni et al. 2005). In addition, small-scale winds are more variable in time and space at northern latitudes, and wind speeds are weaker above land and at low altitudes (Liechti 2006). At our study sites, mean seasonal wind speeds were moderate (4.19 m s^{-1} for Cardel and 3.86 m s^{-1} for Chichicaxtle). It may not be surprising, therefore, that raptor migration intensity was little affected by weather, since the conditions experienced in the study sites appear fairly stable and less extreme when compared to other regions (e.g., Erni et al. 2005, Panuccio

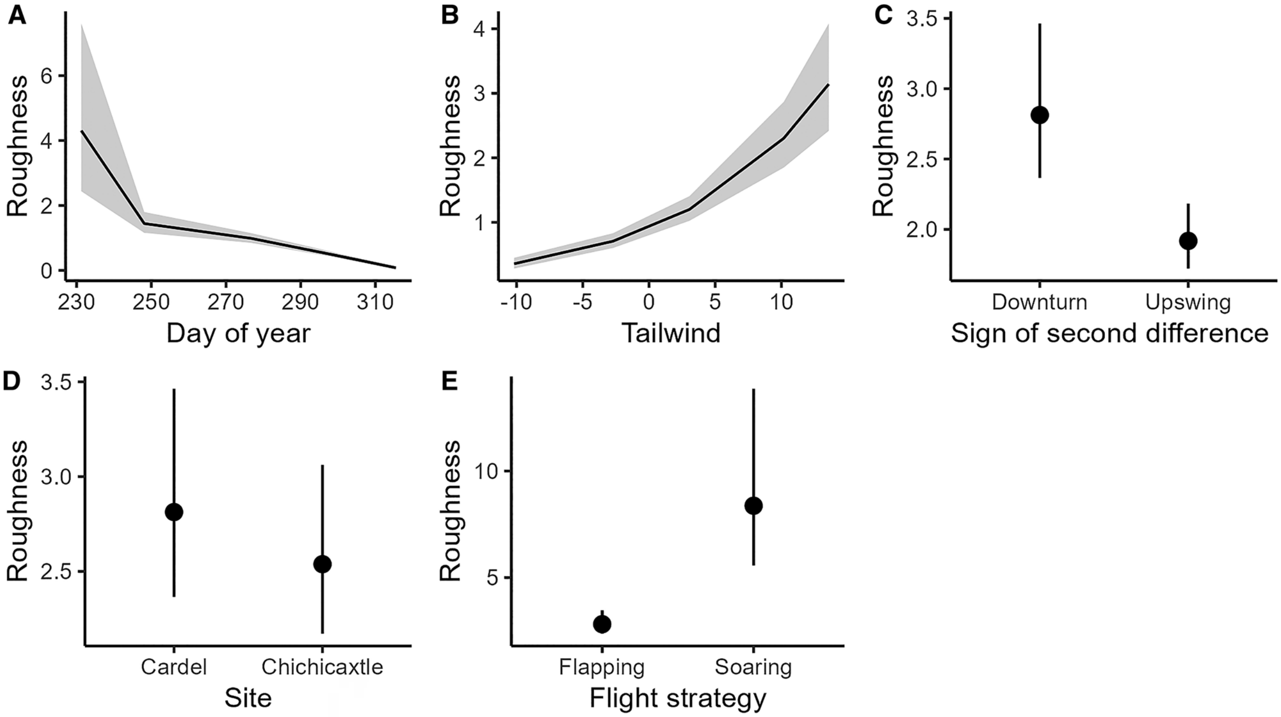

FIGURE 4. Effect of (**A**) day of year, (**B**) tailwind, (**C**) sign of second difference, (**D**) site, and (**E**) flight strategy on the roughness of 8 raptor species. In plots (**A**) and (**B**), solid line indicates the response curve, and the 95% confidence interval (CI) is shaded grey. Here we plot the best model without the lagged effect of weather variables (LAG0 model).

et al. 2016, Concepcion et al. 2017). Collectively, these geographic and meteorological features likely dampen weather-driven variability in our counts.

Lastly, as our study sites are situated near the halfway point to the southern end of our focal species' migration pathways, it is reasonable to suspect that a cumulative effect of weather at locations north of our study sites (e.g., the weather conditions encountered by birds several days before they reach our study sites) affects the pace and flow of migration at our sites. Thus, if a lagged effect exists, it could be better modeled by linking weather variables measured at sites elsewhere on the migration route, or in advance of peak flights. Future work coupling movement data (e.g., from telemetry and radar tracking) with spatially explicit weather surfaces could test for such lagged carryover effects.

Interspecific Differences in Responses to Weather Factors and Issues of Scale

In agreement with our prediction at the intra-annual scale, we observed a differential response between soaring and flapping raptors. Soaring species exhibited the highest roughness values, indicating a strong response to wind conditions, particularly in the presence of headwinds. This pattern is consistent with the greater costs of sustained flapping under unfavorable winds and the reliance of soaring migrants on atmospheric support. On the other hand, at the inter-annual scale, we expected a more variable response in short-distance migrants. Instead, we found the opposite pattern: long-distance migrants exhibited greater variation in daily migration counts from year to year. It is commonly suggested that short-distance migrants exhibit a more flexible migratory behavior related to year-to-year variations in weather conditions (Brisson-Curadeau et al. 2020); however, the opposite response observed in this study may be explained by the geographic location of our study sites, as it serves as a convergence zone for various raptor populations. Additionally, different sex and age groups usually do not migrate together (Moussus et al. 2010), suggesting that variation in migration timing could be influenced by sex- and age-specific factors.

However, neither of the time scales evaluated showed a high proportion of variance explained by weather conditions; moreover, only the wind-related variables showed an effect on migration counts. The lack of influence of the other weather variables analyzed may be a matter of the temporal scale of our study (e.g., daily weather and count data), as other works have detected an influence of weather on an hourly scale (Seeland et al. 2012), suggesting that the response to environmental conditions may occur on a finer temporal scale than daily counts allow. Higher-resolution temporal sampling and vertical profiles of wind structure may reveal relationships that are obscured by daily aggregation.

An important aspect to consider is that meteorological phenomena occur at different scales in space and time (Shamoun-Baranes et al. 2017). Therefore, we can expect birds to modulate their responses according to the atmospheric conditions encountered on their en route journey (Becciu et al. 2018), and consequently, we cannot assume that the same behavior can be extrapolated to the entire migration route (Schmaljohann et al. 2017). Moreover, the decision to migrate is determined by a combination of intrinsic factors including body condition, sex, and age, as well as extrinsic factors such as weather conditions, food abundance, date, and distance from migratory goal or the starting point of migration (Kerlinger et al. 1985, Dossman et al. 2016,

TABLE 4. Summary statistics of the best general linear mixed models relating the inter-annual variation (deviations from the mean) in the number of migrants and weather variables without lag (LAG0) and lagged by 1, 2, and 3 days (LAG1, LAG2, and LAG3, respectively) for 8 raptor species at 2 monitoring sites in Mexico's Gulf coast. Day^2 and Day^3 refer to second and third-order terms in the orthogonal polynomials for Day (day of year). SIC refers to the Schwarz Information Criterion. SD refers to standard deviation.

Model	Fixed effect	Coefficients ± SE	Random effect	SD	SIC
LAG0	Intercept	7.4 ± 1.4	DOY:Year	0.33	178,324.3
	Day	–39.09 ± 2.28	Year	0.10	
	Day^2	–13.76 ± 1.63	Species	2.95	
	Day^3	–18.5 ± 1.2			
	Site	–0.20 ± 0.01			
	Sign of deviation	0.56 ± 0.02			
	Tailwind	0.12 ± 0.01			
	Sidewind	0.01 ± 0.01			
	Type of migrant	–2.35 ± 2.08			
	Tailwind*type	–0.13 ± 0.02			
	Sidewind*type	0.07 ± 0.02			
Conditional R^2	0.96				
Marginal R^2	0.18				
LAG1	Intercept	7.4 ± 1.4	DOY:Year	0.33	177,249.3
	Day	–39.68 ± 2.25	Year	0.10	
	Day^2	–12.34 ± 1.63	Species	2.95	
	Day^3	19.84 ± 1.26			
	Site	–0.21 ± 0.01			
	Sign of deviation	0.56 ± 0.02			
	Tailwind	0.12 ± 0.01			
	Sidewind	0.002 ± 0.01			
	Type of migrant	–2.34 ± 2.08			
	Tailwind*type	–0.13 ± 0.02			
	Crosswind*type	0.06 ± 0.02			
Conditional R^2	0.96				
Marginal R^2	0.18				
LAG2	Intercept	7.39 ± 1.4	DOY:Year	0.33	175,048.4
	Day	–39.78 ± 1.20	Year	0.10	
	Day^2	–11.35 ± 1.63	Species	2.95	
	Day^3	–21.07 ± 1.26			
	Site	–0.21 ± 0.01			
	Sign of deviation	0.56 ± 0.02			
	Tailwind	0.12 ± 0.01			
	Sidewind	0.006 ± 0.01			
	Type of migrant	–2.33 ± 2.08			
	Tailwind*type	–0.13 ± 0.02			
	Crosswind*type	0.06 ± 0.02			
Conditional R^2	0.96				
Marginal R^2	0.17				
LAG3	Intercept	7.38 ± 1.4	DOY:Year	0.34	171,806.4
	Day	–38.14 ± 2.12	Year	0.11	
	Day^2	–11.48 ± 1.64	Species	2.95	
	Day^3	–21.7 ± 1.28			
	Site	–0.23 ± 0.01			
	Sign of deviation	0.56 ± 0.02			
	Tailwind	0.10 ± 0.01			
	Type of migrant	–2.31 ± 2.08			
	Tailwind*type	–0.08 ± 0.01			
Conditional R^2	0.96				
Marginal R^2	0.17				

McCabe et al. 2018, Linscott et al. 2022), this means that a bird's migratory strategy depends on the ecological and geographical context in which it is situated. Accounting for these interacting drivers will likely improve predictive models of migration timing and intensity, particularly under scenarios of rapid environmental change.

Methodological Considerations

In the past, we have been limited in our capacity to predict day-to-day variation in migration phenology due to local weather conditions because we lacked an appropriate measure of change at this scale. Here, we present a novel approach to measure and describe within-season variation in bird migration

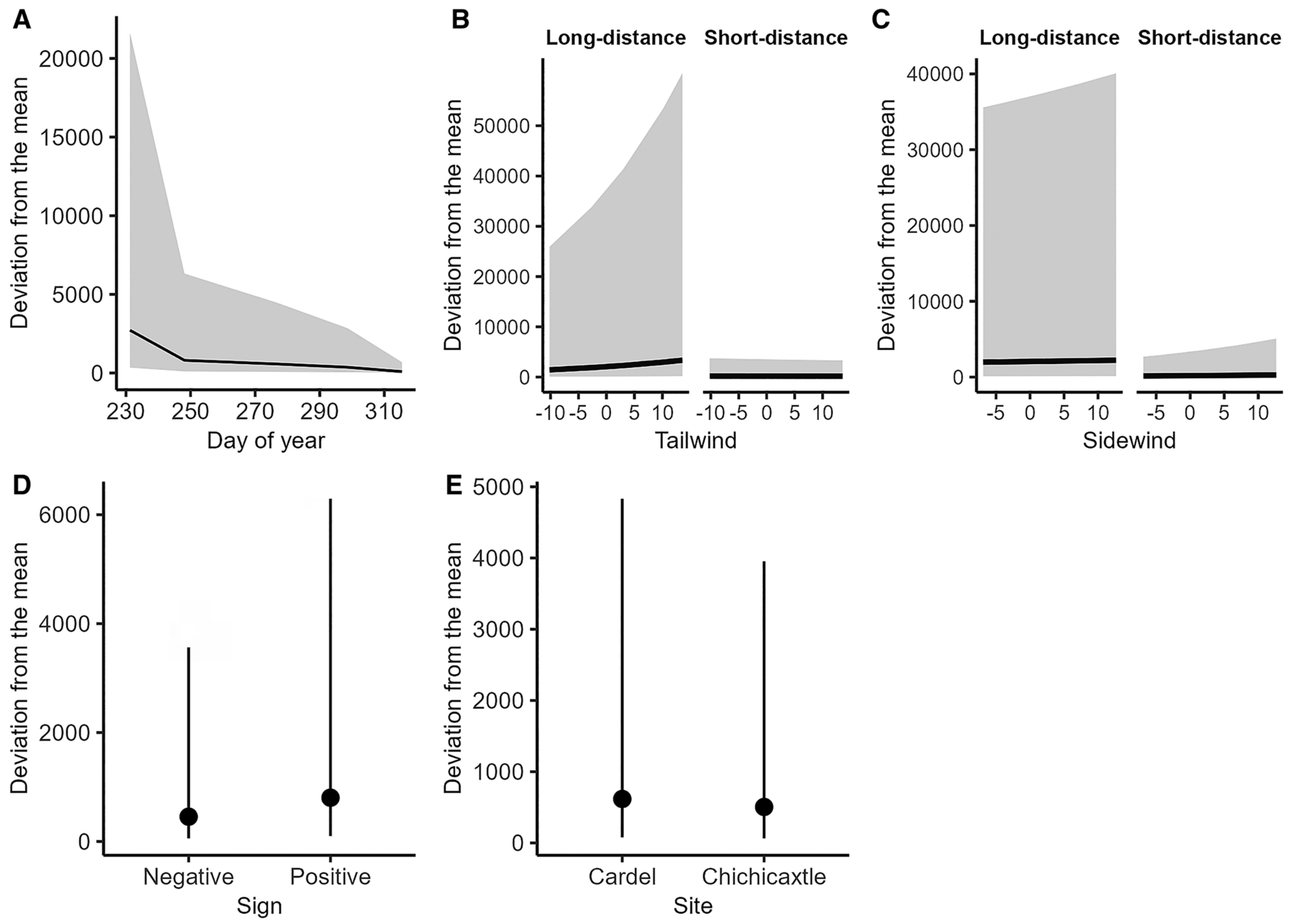

FIGURE 5. Effect of (**A**) day of year, (**B**) tailwind in interaction with type of migrant, (**C**) sidewind in interaction with type of migrant, (**D**) sign of the deviation of the mean, and (**E**) site on the inter-annual variation in autumn migration counts of 8 raptor species. In plots (**A**), (**B**), and (**C**), the solid line indicates the response curve, and the 95% confidence interval (CI) is shaded grey. Here we plot the best model without the lagged effect of weather variables (LAG0 model).

intensity. The roughness metric we describe can be used not only on a daily scale but also on different timescales (e.g., hours, weeks, etc.) and can be related to environmental and ecological variables beyond those tested here. One advantage of this metric is that the estimate of roughness values takes into account the previous number of individuals, so it can be useful to analyze abrupt changes in migration intensity that occur over short periods or between successive times. Because roughness explicitly incorporates the magnitude of change between successive counts, it provides a sensitive index of variation that is well-suited to detecting sharp pulses in migration and relating them to rapidly varying drivers. We encourage its application to other taxa, methods (e.g., radar and acoustic monitoring), and spatial scales.

Conclusion

Our study shows that, at the stopover scale, local weather conditions account for less than 20% of the variation in raptor migration intensity along the coastal plain of the Gulf of Mexico, a region renowned as a global hotspot for migratory raptors (Ruelas Inzunza et al. 2009). This finding suggests that raptors may exhibit variable responses to weather, depending on their geographic location, highlighting the importance of considering how weather dynamics vary across larger spatial and temporal scales, as well as their cumulative effects. However, further research in the Neotropics is needed to fully understand how raptors adapt to local weather conditions along their migratory routes. By investigating the intrinsic and extrinsic factors that influence migration at different points along their migratory routes, we can gain deeper insights into the complex dynamics of migration, as well as its drivers. Finally, roughness analysis, as presented here, can be used as a tool to more adequately model sharp changes in temporal variation in bird counts. Broader adoption of this approach will facilitate cross-site comparisons and improve our ability to forecast migration responses to future atmospheric change.

Supplementary material

Supplementary material is available at *Ornithology* online.

Acknowledgments

We deeply thank Pronatura Veracruz A.C. for giving us the opportunity to use its valuable monitoring data, obtained at their raptor migration monitoring sites in Cardel and Chichicaxtle. We extend our recognition to all the Pronatura Veracruz A.C. field crews, whose dedication has been fundamental for the collection of these data. We appreciate the insights of Gil Bohrer (Ohio State University) and Adalberto Tejeda (Universidad Veracruzana) regarding weather data analyses. This is Hawk Mountain's contribution to conservation science number 417.

Funding statement

Mexico's Secretaría de Ciencia, Humanidades, Tecnología e Innovación provided a PhD scholarship to Yolotli Morales-Góngora (No. 848543). Data acquisition was supported by Veracruz River of Raptors Project (VRR), a cooperative effort between Pronatura Veracruz, Hawk Mountain Sanctuary, and HawkWatch International. We thank Pronatura Veracruz's individual donors, members of "Amigos del Río de Rapaces," hundreds of Veracruz River of Raptors (VRR) birding tour attendants, and donors of equipment (Birder's Exchange, Optics for the Tropics, Eagle Optics/Vortex, and Aveoptica). Over the years, VRR received grant funding from National Fish and Wildlife Foundation, Lannan Foundation, John D. and Catherine T. MacArthur Foundation, U.S. Fish and Wildlife Service (Neotropical Migratory Bird Conservation Act), Center for the Study of Tropical Birds, Hawk Mountain Sanctuary Association, HawkWatch International, Hawk Migration Association of North America, Raptor Research Foundation, Fondo Mexicano para la Conservación de la Naturaleza, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, The United States Agency for International Development's Mexico Program, Secretaría de Educación y Cultura de Veracruz, and American Bird Conservancy. This project has received sustained and incredibly generous contributions from Jennifer P. and Randolph C. Speers, George Perkins, Nancy Claflin, John and Janice Faaborg, Patrick and Andy Lannan, Bill Johnston, and Mary Pat Day.

Ethics statement

No animals were handled as part of this research. Our investigation follows recommendations of authorship and inclusion, equity, and citation ethics.

Conflict of interest statement

The authors have no conflict of interest.

Author contributions

E.R.I., S.N.-Y., G.A.F., and Y.M.-G. conceived the original research idea. Y.M.-G., G.A.F., and S.N.-Y. analyzed the data. The statistical methodology used was developed by G.A.F. Y.M.-G. wrote the manuscript. E.R.I., S.N.-Y., and A.S.G. substantially edited the manuscript. All authors contributed to the interpretation of data, review and revision of the manuscript, and gave final approval for publication.

Data availability

Analyses reported in this article can be reproduced using the data provided by Morales-Góngora et al. (2025).

LITERATURE CITED

Able, K. P. (1980). Mechanisms of orientation, navigation, and homing. In *Animal Migration, Orientation, and Navigation* (S. A., Gauthreaux, Editor). Academic Press, New York, NY, USA. pp. 283–373.

Acácio, M., I. Catry, A. Soriano-Redondo, J. P. Silva, P. W. Atkinson, and A. M. Franco (2022). Timing is critical: Consequences of asynchronous migration for the performance and destination of a long-distance migrant. *Movement Ecology* 10:28.

Alerstam, T. (1979). Optimal use of wind by migrating birds: Combined drift and overcompensation. *Journal of Theoretical Biology* 79:341–353.

Alerstam, T, and Å. Lindström (1990). Optimal bird migration: The relative importance of time, energy, and safety. In *Bird Migration* (E. Gwinner, Editor). Springer, Heidelberg, Germany. pp. 331–351.

Allen, P. E., L. J. Goodrich, and K. L. Bildstein (1996). Within- and among-year effects of cold fronts on migrating raptors at Hawk Mountain, Pennsylvania, 1934–1991. *The Auk* 113:329–338.

Barton, G. G., and B. K. Sandercock (2018). Long-term changes in the seasonal timing of landbird migration on the Pacific Flyway. *The Condor: Ornithological Applications* 120:30–46.

Bartón, K. (2022). MuMIn: Multi-model Inference. R package version 1.47.1. https://CRAN.R-project.org/package=MuMIn

Becciu, P., M. Panuccio, C. Catoni, G. Dell'Omo, and N. Sapir (2018). Contrasting aspects of tailwinds and asymmetrical response to crosswinds in soaring migrants. *Behavioral Ecology and Sociobiology* 72:1–13.

Bednarz, J. C., D. , Klem, L. J. Goodrich, and S. E. Senner (1990). Migration counts of raptors at Hawk Mountain, Pennsylvania, as indicators of population trends 1934–1986. *The Auk* 107:96–109.

Berthold, P. (1996). *Control of Bird Migration*. Springer, Dordrecht, The Netherlands.

Bildstein, K. L. (2006). *Migrating Raptors of the World, Their Ecology and Conservation*. Comstock, Cornell University Press, Ithaca, NY, United States.

Bildstein, K. L., J. P. Smith, E. R. Inzunza, and R. R. Veit (Editors) (2008). *State of North America's Birds of Prey*. *Series in Ornithology* No. 3. American Ornithologists' Union and Nuttall Ornithological Club, Cambridge, MA, USA.

Bohrer, G., D. Brandes, J. T. Mandel, K. L. Bildstein, T. A. Miller, M. Lanzone, T. Katzner, C. Maisonneuve, and J. A. Tremblay (2012). Estimating updraft velocity components over large spatial scales: Contrasting migration strategies of Golden Eagles and Turkey Vultures. *Ecology Letters* 15:96–103.

Both, C., M. Van Asch, R. G. Bijlsma, A. B. Van Den Burg, and M. E. Visser (2009). Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? *The Journal of Animal Ecology* 78:73–83.

Brisson-Curadeau, É., K. H. Elliott, and P. Côté (2020). Factors influencing fall departure phenology in migratory birds that bred in northeastern North America. *Ornithology* 137:ukz064.

Brønnvik, H., K. Safi, W. M. Vansteelant, P. Byholm, and E. Nourani (2022). Experience does not change the importance of wind support for migratory route selection by a soaring bird. *Royal Society Open Science* 9:220746.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9:378–400.

Bussjaeger, L. J., C. C. Carpenter, H. L. Cleveland, and D. L. Marcellini (1967). Turkey Vulture migration in Veracruz, México. *The Condor* 69:425–426.

Chevallier, D., Y. Handrich, J. Y. Georges, F. Baillon, P. Brossault, A. Aurouet, Y. Le Maho, and S. Massemin (2010). Influence of weather conditions on the flight of migrating Black Storks. *Proceedings of the Royal Society B:. Biological Sciences* 277:2755–2764.

Concepcion, C. B., P. T. Dumandan, M. R. Silvosa, K. L. Bildstein, and T. E. Katzner (2017). Species composition, timing, and weather correlates of autumn open-water crossings by raptors migrating along the east-Asian oceanic flyway. *Journal of Raptor Research* 51:25–37.

Dennis, B., J. M. Ponciano, M. L. Taper, and S. R. Lele (2019). Errors in statistical inference under model misspecification: Evidence, hypothesis testing, and AIC. *Frontiers in Ecology and Evolution* 7:372.

Denny, E. G., K. L. Gerst, A. J. Miller-Rushing, G. L. Tierney, T. M. Crimmins, C. A. Enquist, P. Guertin, A. H. Rosemartin, M. D. Schwartz, K. A. Thomas, and J. F. Weltzin (2014). Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. *International Journal of Biometeorology* 58:591–601.

Dorian, N. N., T. L. Lloyd-Evans, and J. M. Reed (2020). Non-parallel changes in songbird migration timing are not explained by changes in stopover duration. *PeerJ* 8:e8975.

Dossman, B. C., G. W. Mitchell, D. R. Norris, P. D. Taylor, C. G. Guglielmo, S. N. Matthews, and P. G. Rodewald (2016). The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. *Behavioral Ecology* 27:567–574.

Dumandan, P. K. T., T. M. B. Prado, W. Limparungpatthanakij, C. Hansasuta, C. B. Concepcion, and P. D. Round (2022). Among-species differences in seasonal timing and weather correlates of autumn raptor migration at Khao Dinsor, Thailand, 2015. *Journal of Raptor Research* 56:323–332.

P. O, Dunn, and A. P. Møller (Editors) (2019). *Effects of Climate Change on Birds*, second edition. Oxford University Press, Oxford, UK.

Ellwood, E. R., A. Gallinat, R. B. Primack, and T. L. Lloyd-Evans (2015). Autumn migration of North American landbirds. In *Phenological Synchrony and Bird Migration: Changing Climate and Seasonal Resources in North America* (E. M. Wood and J. L. Kellermann, Editors). Studies in Avian Biology 47. CRC Press, Boca Raton, FL, USA. pp. 193–205.

Erni, B., F. Liechti, and B. Bruderer (2005). The role of wind in passerine autumn migration between Europe and Africa. *Behavioral Ecology* 16:732–740.

Farmer, C. J., D. J. T. Hussell, and D. Mizrahi (2007). Detecting population trends in migratory birds of prey. *The Auk* 124:1047–1062.

Filippi-Codaccioni, O., J. P. Moussus, J. P. Urcun, and F. Jiguet (2011). Advanced autumn migration of the Common Crane *Grus grus* over Western Pyrenean passes. *Acta Ornithologica* 46:37–45.

Gallinat, A. S., R. B. Primack, and D. L. Wagner (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution* 30:169–176.

HMANA (2009). A standard data-collection protocol for raptor migration monitoring. Hawk Migration Association of North America. http://www.hmana.org/

Hollister, R. D., J. L. May, K. S. Kremers, C. E. Tweedie, S. F. Oberbauer, J. A. Liebig, T. F. Botting, R. T. Barret, and J. L. Gregory (2015). Warming experiments elucidate the drivers of observed directional changes in tundra vegetation. *Ecology and Evolution* 5:1881–1895.

Horton, K. G., B. M. Van Doren, F. A. La Sorte, E. B. Cohen, H. L. Clipp, J. J. Buler, D. Fink, J. F. Kelly, and A. Farnsworth (2019). Holding steady: Little change in intensity or timing of bird migration over the Gulf of Mexico. *Global Change Biology* 25:1106–1118.

Hussell, D. J. T., and E. Ruelas Inzunza (2008). Long-term Monitoring: The Raptor Population Index in Principle. In *State of North America's Birds of Prey* (K. L. Bildstein, J. P. Smith, E. Ruelas Inzunza, and R. R. Veit, Editors). Series in Ornithology No. 3. American Ornithologists' Union and Nuttall Ornithological Club, Cambridge, MA, USA. pp. 151–164.

Jenni, L., and M. Schaub (2003). Behavioural and physiological reactions to environmental variation in bird migration: A review. In *Avian Migration* (P. Berthold, E. Gwinner, and E. Sonnenschein, Editors). Springer, Berlin Heidelberg, Germany. pp. 155–171.

Juhant, M. A. (2025). Seasonal migration patterns of the Rufous-thighed Kite (*Harpagus diodon*). *The Wilson Journal of Ornithology* 138:1. https://doi.org/10.1080/15594491.2025.2535115.

Kemp, M. U., E. Emiel van Loon, J. Shamoun-Baranes, and W. Bouten (2012). RNCEP: Global weather and climate data at your fingertips. *Methods in Ecology and Evolution* 3:65–70.

Kerlinger, P. (1989). *Flight Strategies of Migrating Hawks*. University of Chicago Press, Chicago, IL, USA.

Kerlinger, P., V. P. Bingman, and K. P. Able (1985). Comparative flight behaviour of migrating hawks studied with tracking radar during autumn in Central New York. *Canadian Journal of Zoology* 63:755–761.

Kerlinger, P, and S. A. Gauthreaux., (1985). Flight behavior of raptors during spring migration in South Texas studied with radar and visual observations. *Journal of Field Ornithology* 56:7–12.

La Sorte, F. A., W. M. Hochachka, A. Farnsworth, D. Sheldon, D. Fink, J. Geevarghese, K. Winner, B. M. Van Doren, and S. Kelling (2015). Migration timing and its determinants for nocturnal migratory birds during autumn migration. *The Journal of Animal Ecology* 84:1202–1212.

Law, B., C. Mackowski, L. Schoer, and T. Tweedie (2000). Flowering phenology of myrtaceous trees and their relation to climatic, environmental and disturbance variables in Northern New South Wales. *Austral Ecology* 25:160–178.

Liechti, F. (2006). Birds: Blowin' by the wind? *Journal of Ornithology* 147:202–211.

Linscott, J. A., J. G. Navedo, S. J. Clements, J. P. Loghry, J. Ruiz, B. M. Ballard, M. D. Weegman, and N. R. Senner (2022). Compensation for wind drift prevails for a shorebird on a long-distance, transoceanic flight. *Movement Ecology* 10:11.

Maynard, L. D., J. F. Therrien, J. Lemaître, T. Booms, T. A. Miller, T. Katzner, S. Somershoe, J. Cooper, R. Sargent, and N. Lecomte (2022). Interannual consistency of migration phenology is season-and breeding region-specific in North American Golden Eagles. *Ornithology* 139:ukac029.

McCabe, J. D., B. J. Olsen, B. Osti, and P. O. Koons (2018). The influence of wind selectivity on migratory behavioral strategies. *Behavioral Ecology* 29:160–168.

Miles, W. T., M. Bolton, P. Davis, R. Dennis, R. Broad, I. Robertson, N. J. Riddiford, P. V. Harvey, R. Riddington, D. N. Shaw, D. Parnaby, and J. M. Reid (2017). Quantifying full phenological event distributions reveals simultaneous advances, temporal stability and delays in spring and autumn migration timing in long-distance migratory birds. *Global Change Biology* 23:1400–1414.

Morales-Góngora, Y., S. Negrete-Yankelevich, G. A. Fox, A. S. Gallinat, S. Gallina-Tessaro, L. J. Goodrich, S. W. Hoffman, and E. Ruelas Inzunza (2025). Data from: How much can local weather conditions explain intra- and inter-annual variation in raptor migration counts at a Neotropical hotspot? A new analytical approach. *Ornithology* 143: ukaf071. https://doi.org/10.5061/dryad.3xsj3txvs [Dataset].

Moussus, J. P., R. Julliard, and F. Jiguet (2010). Featuring 10 phenological estimators using simulated data. *Methods in Ecology and Evolution* 1:140–150.

Mueller, H. C., and D. D. Berger (1967). Wind drift, leading lines, and diurnal migrations. *The Wilson Bulletin* 79:50–63.

Murray, B. G.Jr. , (1964). A review of Sharp-shinned Hawk migration along the northeastern coast of the United States. *The Wilson Bulletin* 81:119–120.

Newton, I. (2024). *The Migration Ecology of Birds*, second edition. Academic Press, Cambridge, MA, USA.

Nourani, E, and N. M. Yamaguchi (2017). The effects of atmospheric currents on the migratory behavior of soaring birds: A review. *Ornithological Science* 16:5–15.

Nourani, E., N. M. Yamaguchi, A. Manda, and H. Higuchi (2016). Wind conditions facilitate the seasonal water-crossing behaviour of Oriental honey-buzzards *pernis ptilorhynchus* over the East China Sea. *Ibis* 158:506–518.

Olivo, C. (2005). Cold fronts and raptor migration in Bolivia. *Ornitología Neotropical* 16:109–115.

Oppel, S., V. Dobrev, V. Arkumarev, V. Saravia, A. Bounas, E. Kret, M. Velevski, S. Stoychev, and S. C. Nikolov (2015). High juvenile mortality during migration in a declining population of a long-distance migratory raptor. *Ibis* 157:545–557.

Panuccio, M., C. Barboutis, G. Chiatante, A. Evangelidis, and N. Agostini (2016). Pushed by increasing air temperature and tailwind speed: Weather selectivity of raptors migrating across the Aegean Sea. *Ornis Fennica* 93:159–171.

Paprocki, N., J. A. Heath, and S. J. Novak (2014). Regional distribution shifts help explain local changes in wintering raptor abundance: Implications for interpreting population trends. *PLOS One* 9:e86814.

Pennycuick, C. J. (1969). The mechanics of migration. *Ibis* 111:525–556.

Phillips, R., K. Wolf, R. Bourbour, J. Urbina, J. Eduardo Ruano, V. Bonilla, V. Gamez, I. Mai, I. Morataya, R. Martinez *et al.* (2023). Intratropical migration of the Hook-billed Kite (*Chondrohierax uncinatus*) in Middle America. *Journal of Field Ornithology* 94:5.

Porras-Peñaranda, P., L. Robichaud, and F. Branch (2004). New full season count sites for raptor migration in Talamanca, Costa Rica. *Ornitología Neotropical* 15: S267–S278.

R Core Team (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org.

Rayner, J. M. V. (1985). *Vertebrate Flight: A Bibliography to 1985*. University of Bristol, Bristol, UK.

Ruelas Inzunza, E., L. J. Goodrich, and S. W. Hoffman (2010). North American population. estimates of waterbirds, vultures, and hawks from migration counts in Veracruz, Mexico. *Bird Conservation International* 20:124–133.

Ruelas Inzunza, E. L. J. Goodrich, S. W. Hoffman, E. Martínez Leyva, J. P. Smith, E. Peresbarbosa, R. Rodríguez, K. L. Scheuermann, S. L. Mesa, Y. Cabrera, N. Ferriz, R. Straub, M. M. Peñaloza, and J. G. Barrios (2009). Long-term conservation of migratory birds in México: The Veracruz River of Raptors Project. In *Tundra to Tropics: Connecting Birds, Habitats, and People* (T. D. Rich, C. Arizmendi, D. Demarest, and C. Thompson, Editors). *Proceedings of the 4th International Partners in Flight Conference, Partners in Flight*, Washington, D.C., USA. pp. 577–589.

Ruelas Inzunza, E. S. W. Hoffman, and L. J. Goodrich (2005). Stopover ecology of Neotropical migrants in Veracruz, Mexico. In *Proceedings of the III International Partners in Flight Conference* (C. J. Ralph, T. D. Rich, and L. L. Long, Editors). USDA Forest Service General Technical Report PSW-GTR-191, Pacific Southwest Research Station, Asilomar, CA, USA. pp. 657–673.

Ruelas Inzunza, E., L. J. Goodrich, S. W. Hoffman, and R. Tingay (2000). Conservation strategies for the World's largest raptor migration flyway: Veracruz, the river of raptors. In *Raptors at Risk* (R. D. Chancellor and B.-U. Meyburg, Editors). World Working Group on Birds of Prey. Durban, South Africa. pp. 591–596

Schmaljohann, H., S. Lisovski, and F. Bairlein (2017). Flexible reaction norms to environmental variables along the migration route and the significance of stopover duration for total speed of migration in a songbird migrant. *Frontiers in Zoology* 14:17–16.

Seeland, H. M., G. J. Niemi, R. R. Regal, A. Peterson, and C. Lapin (2012). Determination of raptor migratory patterns over a large landscape. *Journal of Raptor Research* 46:283–295.

Sergio, F., J. M. Barbosa, A. Tanferna, R. Silva, J. Blas, and F. Hiraldo (2022). Compensation for wind drift during raptor migration improves with age through mortality selection. *Nature Ecology & Evolution* 6:989–997.

Shamoun-Baranes, J., F. Liechti, and W. M. Vansteelant (2017). Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *Journal of Comparative Physiology A* 203:509–529.

Smith, N. G. (1980). Hawk and vulture migration in the Neotropics. In *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, Editors). Smithsonian Institution Press, Washington, D.C., USA. pp. 51–65.

Spaar, B. (1997). Flight strategies of migrating raptors: A comparative study of interspecific variation flight characteristics. *Ibis* 139:523–535.

Tan, K., C. Y. Choi, H. Peng, D. S. Melville, and Z. Ma (2018). Migration departure strategies of shorebirds at a final pre-breeding stopover site. *Avian Research* 9:10.

Therrien, J. F., N. Lecomte, T. Zgirski, M. Jaffré, A. Beardsell, L. J. Goodrich, J. Bêty, A. Franke, E. Zlonis, and K. L. Bildstein (2017). Long-term phenological shifts in migration and breeding-area residency in Eastern North American raptors. *The Auk: Ornithological Advances* 134:871–881.

Thiollay, J.-M. (1980). Spring hawk migration in Eastern Mexico. *Raptor Research* 14:13–19.

Thorson, J. T., M. L. Arimitsu, T. Levi, and G. H. Roffler (2022). Diet analysis using generalized linear models derived from foraging processes using R package mvtweedie. *Ecology* 103:e3637.

Thorup, K., T. Alerstam, M. Hake, and N. Kjellén (2006). Traveling or stopping of migrating birds in relation to wind: an illustration for the osprey. *Behavioral Ecology* 17:497–502.

Thurber, B. G., C. Roy, and J. R. Zimmerling (2020). Long-term changes in the autumn migration phenology of dabbling ducks in Southern Ontario and implications for waterfowl management. *Wildlife Biology* 2020:1–11.

Vansteelant, W. M., B. Verhelst, J. Shamoun-Baranes, W. Bouten, E. E. van Loon, and K. L. Bildstein (2014). Effect of wind, thermal convection, and variation in flight strategies on the daily rhythm and flight paths of migrating raptors at Georgia's Black Sea Coast. *Journal of Field Ornithology* 85:40–55.

Verhelst, B., J. Jansen, and W. Vansteelant (2011). South West Georgia: An important bottleneck for raptor migration during autumn. *Ardea* 99:137–146.

Xu, F, and Y. Si (2019). The frost wave hypothesis: How the environment drives autumn departure of migratory waterfowl. *Ecological Indicators* 101:1018–1025.