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RESEARCH ARTICLE

Combining migration and wintering counts to enhance understanding of population change in a generalist raptor species, the North American Red-tailed Hawk

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ABSTRACT

An increasing body of scientific evidence supports the idea that many avian species are changing their migratory behavior as a result of climate change, land-use change, or both. We assessed Red-tailed Hawk (*Buteo jamaicensis*) population trends in 2 parts of the annual cycle (fall migration and winter) to better understand regional population trends and their relationship to changes in migration. We conducted 10 yr, 20 yr, and 30 yr trend analyses using pan–North American standardized fall migration counts and Christmas Bird Counts. We quantitatively compared trends in seasonal counts by latitude within the eastern and western migratory flyways. Our combined analysis of migration and wintering count data revealed flyway-specific patterns in count trends suggesting that Red-tailed Hawks are undergoing substantial changes in both migratory behavior and population size. Decreasing Red-tailed Hawk wintering and migration counts in southern regions and increasing winter counts in northern regions were consistent with other observations indicating changes in migratory strategy; an increasing number of Red-tailed Hawks do not migrate, or migrate shorter distances than they did in the past. Further, Red-tailed Hawk populations have been stable or increasing across much of North America. However, we found strong negative count trends at the northernmost migration sites on the eastern flyway, suggesting possible breeding-population declines in the central and eastern Canadian provinces. Our findings demonstrate the benefit of using appropriate data from multiple seasons of the annual cycle to provide insight into shifting avian migration strategies and population change.

Keywords: Buteo jamaicensis, Christmas Bird Count, citizen science, migration strategies, population trends, Red-tailed Hawk, RPI

Combinados inviero y conteos migratorios para mejorar el conocimiento de tendencias poblacionales en rapaces

RESUMEN

Un creciente cuerpo de evidencia científica apoya la idea de que muchas especies de aves están cambiando su comportamiento migratorio debido al cambio climático, el cambio de uso de la tierra, o ambos. Evaluamos las tendencias poblacionales de halcón Rojo (Buteo jamaicensis) de dos partes del ciclo anual (migración de otoño e invierno) para comprender mejor las tendencias de la población regional y su relación con los cambios en la migración. Realizamos análisis de tendencias de 10 años, 20 años y 30 años utilizando los recuentos de migración de otoño normalizados pan-norteamericanos y conteos de aves de Navidad. Comparamos cuantitativamente las tendencias de los recuentos estacionales por latitud dentro de las vías migratorias migratorias orientales y occidentales. Nuestro análisis combinado de la migración y los datos de conteo de invernada reveló patrones específicos de la ruta de vuelo en las tendencias de recuento que sugieren que los halcones de cola roja están experimentando cambios sustanciales tanto en el comportamiento migratorio como en el tamaño de la población. La disminución de los índices de invernada y migración de Hawk de cola roja en las regiones del sur y el aumento de los recuentos de invierno en las regiones septentrionales fueron consistentes con otras observaciones que indican cambios en la estrategia migratoria; Algunos halcones de cola roja no emigran cuando solían o emigran distancias más cortas que hicieron en el pasado. Además, las poblaciones de halcones de cola roja han sido estables o en aumento en gran parte de América del Norte. Sin embargo, se encontraron fuertes tendencias negativas de recuento en los sitios de migración de la ruta oriental más al norte, lo que sugiere una posible disminución de la población reproductora en las provincias del centro y este de Canadá. Nuestros hallazgos demuestran el beneficio de usar datos apropiados de varias temporadas del ciclo anual para proporcionar una visión sobre el cambio de las estrategias de migración aviar y el cambio de población.

Palabras clave: Buteo jamaicensis, ciencia ciudadana, Cuenta del Pájaro de la Navidad, estrategias de migración, Gavilán Colirrojo, invierno, RPI, tendencia poblacional

INTRODUCTION

Global climate change has influenced the distribution of many wildlife species (Parmesan and Yohe 2003, Hitch and Leberg 2007, La Sorte and Thompson 2007). Researchers have demonstrated these shifts by modeling future distributions or looking at phenological changes in reproduction and migration (Both et al. 2004, Van Buskirk et al. 2009, Sohl 2014). Other studies have documented changing migratory distance and range shifts in many landbird species worldwide (Doswald et al. 2009, Visser et al. 2009, Paprocki et al. 2014). Both global climate change and land-use change have been suggested as factors influencing changing migratory behavior (Visser et al. 2009, Zuckerberg et al. 2011, Heath et al. 2012). Changes to migration include increased winter residency, shorter migration distances, or both (Visser et al. 2009, Goodrich et al. 2012, Heath et al. 2012). As avian breeding and wintering distributions shift in response to climate and land-use change, and as migratory behavior changes, it will become increasingly important to use data from multiple seasons of the annual cycle to better understand changes in avian populations (Hitch and Leberg 2007, La Sorte and Thompson 2007, Link and Sauer 2007, Link et al. 2008, Visser et al. 2009, Zuckerberg et al. 2011, Heath et al. 2012, Martin et al. 2014, Paprocki et al. 2014).

A variety of continental datasets from different seasons of the annual cycle are available to assess avian populations. At a continental scale, the status of migratory bird populations is often assessed via long-term breeding population trends determined from the Breeding Bird Survey (BBS), North America's largest and longest-running breeding census (Pardieck and Sauer 2007). Some species and regional populations are difficult to monitor on the breeding grounds because of low densities, secretive breeding behavior, or poor coverage by BBS routes (Dunn et al. 2005, Millsap et al. 2013). For these species, migration (Farmer et al. 2007) and wintering data (Sauer and Link 2002) are often important means for assessing population trends.

Diurnal raptors are not well sampled by the BBS, so other seasonal data are often used to assess their status (Dunn et al. 2005). Raptors concentrate during migration, allowing them to be counted at migration sites across North America. These results have been formalized into the biennial Raptor Population Index (RPI; Bildstein et al. 2008b, Brandes et al. 2013). Many raptor species are partial migrants and exhibit plasticity in migratory behavior (Anderson et al. 2016): Not all individuals of a species will migrate, and the proportion that do migrate or the distances they migrate will fluctuate from year to year. For this reason, migration-count trends confound changes in the proportion of individuals that migrate (or the distance they migrate) with the size of source populations (Bildstein et al. 2008a).

Raptors can also concentrate on the wintering grounds, when territorial boundaries are relaxed (Olson 2006, Elliott et al. 2011, Watson et al. 2014). The Christmas Bird Count (CBC) is a long-term, continent-wide, citizen science–based winter bird survey (National Audubon Society 2014) with geographic coverage that considerably overlaps with several raptor species' winter ranges. Many RPI species are regularly counted on the CBC, allowing CBC data to track large-scale, long-term changes in count trends and changes in distribution of wintering raptor species (La Sorte and Thompson 2007, Paprocki et al. 2014). A regionally comprehensive and standardized assessment of migration and wintering data across a range of raptor species could greatly clarify our understanding of raptor population change (Bildstein et al. 2008a). Several assessments of individual raptor species have used both migration and wintering data (Farmer and Smith 2009, Heath et al. 2012, Bolgiano 2013). These studies set the stage for our continent-wide assessment, which offers an improved approach to account for the variability inherent in CBC data.

We assessed the utility of comparing CBC and RPI (hereafter "wintering" and "migration," respectively) count trends to develop a more complete picture of the population status of migratory raptors in North America. We used an abundant North American raptor species, the Red-tailed Hawk (*Buteo jamaicensis*), as a case study. Our primary goals were to (1) analyze long-term trends in wintering and migration counts of Red-tailed Hawk at multiple spatial and temporal scales; and (2) quantitatively compare seasonal Red-tailed Hawk trends by latitude within the eastern and western migratory flyways. We evaluate migration and winter trend results concurrently to interpret trend combinations derived from RPI and CBC (Table 1). For a given region, an increasing or decreasing migration trend could imply different regional population status depending on concurrent winter trends in the same region. Increasing counts during both migration and winter are a strong sign of a growing regional population and that the species being considered might rank as a low conservation priority (Table 1: A). By contrast, decreasing

TABLE 1. Conceptual framework for interpreting regional patterns in concurrent long-term count trends from both fall migration and wintering sites for North American raptors.

	Wintering trend	
Migration trend	Increasing counts	Decreasing counts
Increasing counts	(A) Population increasing (low conservation priority)	(B) Migration or winter counts not accurate; birds counted on migration use alternate wintering area
Decreasing counts	(C) Increasing residency; decreasing migration distances (climate-niche-related range shift)	(D) Breeding-ground declines; wintering farther north (possible conservation priority)

counts during both seasons could be a sign that the species is declining on the breeding grounds, but could also derive from more individuals wintering in regions farther north, independent of the population trend on the breeding grounds (Table 1: D). Several explanations could apply to migration and winter trends that do not correspond (Table 1: B, C). Declining migration counts paired with increasing winter numbers (Table 1: B) suggest a combination of increasingly resident individuals or shorter migration distances (i.e. short-stopping), either of which may be related to a shifting winter climate niche. Increasing migration counts paired with declining winter counts (Table 1: C) could indicate that birds counted during migration are using an alternate wintering area.

METHODS

Study Species

The Red-tailed Hawk is a generalist raptor species with a pan–North American breeding and wintering distribution (Preston and Beane 2009). Northern populations are almost entirely migratory, while mid- and southern-latitude populations can be partially migratory or sedentary or can exhibit reversed migration (Preston and Beane 2009, Bloom et al. 2015). Red-tailed Hawks are generally north–south migrants (Hoffman et al. 2002) but will fly east or west around large bodies of water (Steenhof et al. 1984, Preston and Beane 2009, Bolgiano 2013). The Red-tailed Hawk wintering range considerably overlaps the CBC survey area, although some migrants likely winter south of CBC survey coverage. Numerous studies document Red-tailed Hawks as positively associated with various measures of anthropogenic activity and development (Berry et al. 1998, Schmidt and Bock 2005, Stout et al. 2006, Rullman and Marzluff 2014, Duerr et al. 2015); thus, these anthropogenic affinities may interact with climate change to alter migration strategies and, ultimately, counts at migration sites.

Winter Data

Christmas Bird Count (CBC) data present several statistical challenges, including inconsistent count effort over time (Link and Sauer 1999), nonrandom spatial distribution of count circles, and poor sample sizes for some species (Dunn et al. 2005). For these reasons, CBC data must be filtered and standardized, particularly to correct for inconsistent observer effort and circle location over time. We used CBC data from 1984–2013, 1994–2013, and 2004–2013 (study periods) for our 30 yr, 20 yr, and 10 yr trend analyses, respectively. We used 2013 as our cutoff because the 2013 CBC season (December 2012–January 2013) corresponded to the winter immediately following 2013, the last year for which standardized RPI data are available (Crewe et al. 2013). For the 30 yr study period, we fit a linear regression model for the effect of year on CBC circle latitude and found a significant but weak relationship between year and latitude for all CBC circles counted during 1984–2013 ($r = 0.02$, df $= 50{,}665$, $P < 0.0001$); this suggests that newly created CBC circle locations shifted north over time. We therefore took a conservative approach and modified Paprocki et al.'s (2014) and La Sorte and Thompson's (2007) method of selecting long-term circles surveyed at least once during $\geq$6 of 10 periods of 3 yr (e.g., 1984–1986, 1987–1989, …, 2011–2013) for our 30 yr trend analysis. These criteria allowed us to maximize the CBC data used in the 30 yr analysis and were the break point at which we no longer detected a significant relationship between year and latitude of CBC circles ($r < 0.01$, df $= 44{,}832$, $P = 0.55$). We included all CBC circles surveyed for the 20 yr and 10 yr analyses because we did not detect a significant relationship between year and latitude of CBC circles for these study periods (20 yr: $r = 0.01$, df $= 35{,}996$, $P = 0.28$; 10 yr: $r > -0.01$, df $= 19{,}248$, $P = 0.66$). We removed CBC circles where Red-tailed Hawks were never encountered. We also removed circle data for years when observer effort was missing or recorded as zero ($n = 262$; Peterson 1995). Additional background information on the CBC is detailed in Paprocki et al. (2014) and National Audubon Society (2014).

We assigned CBC circles to 1 of 9 regions based on flyway (eastern, central, and western) and latitude (northern, central, and southern; Figure 1). Our latitudinal boundaries were somewhat arbitrary and were selected on the basis of CBC-circle sample size and migration site location within each region. We used the following

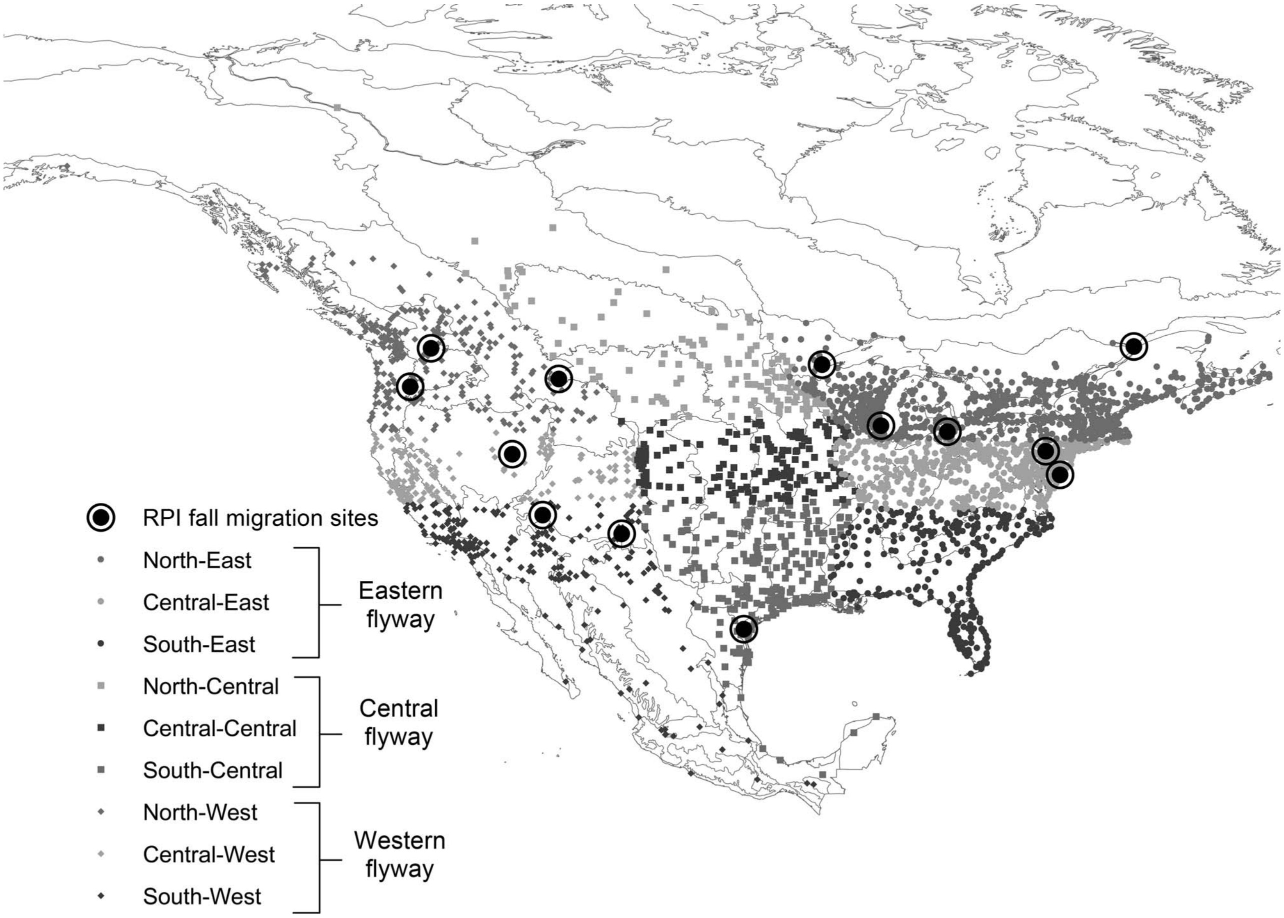

FIGURE 1. Locations of North American Christmas Bird Count circles by region with at least one Red-tailed Hawk detection (small dots, squares, and diamonds) and selected Raptor Population Index (RPI) migration sites (large circles).

latitudes to define our regional boundaries: (1) eastern flyway: 41.4°N and 36.5°N; (2) central flyway: 43.0°N and 37.0°N; and (3) western flyway: 42.0°N and 37.0°N. The boundary between eastern and central flyways was the Mississippi River north to the Manitoba–Ontario border in Canada. The boundary between the central and western flyways was the Rocky Mountain Front Range as defined by Bird Conservation Region (BCR) boundaries (e.g., boundary between Southern Rockies–Colorado Plateau and Shortgrass Prairie) south, following the eastern edge of the Sierra Madre Oriental BCR (Figure 1). These 9 regions allowed for a coarse-scale assessment of wintering trends in discrete latitudinal blocks within flyways.

The CBC was not designed as a true statistical sample, given that count circles have a nonrandom spatial distribution (Link et al. 2006), with disproportionate numbers of circles near population centers and in some regions compared with others (e.g., $n = 87$ in North-Central region vs. $n = 459$ in North-East region). This bias toward population centers is prevalent in migration-count site locations as well, creating a relatively similar bias across our study area and survey types. We acknowledge this limitation but emphasize that we are assessing changes in a count index, and not the population as a whole. We also recognize that our results may be biased toward areas with more CBC circles within regions, but we argue that our comparison of count trends among regions is statistically valid because our model parameter estimates will have greater uncertainty in regions with fewer circles.

For each study period (10 yr, 20 yr, and 30 yr), we tested for an effect of scaled year on annual CBC counts within each region by fitting generalized linear mixed models (R package "glmmADMB") with a negative binomial distribution to correct for overdispersion. We included the number of Red-tailed Hawks counted during each CBC survey as the response variable, scaled year as the predictor variable, and circle ID as a random effect in all models. Because effort is not constant over the history of a CBC circle (Link and Sauer 1999), we assessed the relationship between count and effort and found a quadratic relationship to be the best fit. The quadratic relationship was therefore used as an "offset" term for Red-tailed Hawks for each study period, represented by β1 and β2 (see Supplemental Material Table S1): $\{(\beta 1 \times \text{Effort}_i) + (\beta 2 \times \text{Effort}_i^2)\}$.

We used an information-theoretic approach with Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to evaluate model support within each region and study period by calculating 85% confidence intervals (CIs; Arnold 2010) for parameter estimates from models with the lowest AIC score. We checked, and found little evidence for, residual spatial autocorrelation by creating a spline correlogram (Zuur et al. 2009) of the deviance residuals from regional models for the effect of year on counts. We also checked for residual temporal autocorrelation by plotting the deviance residuals from regional models against year and found no evidence of residual temporal autocorrelation.

Fall Migration Data

Fall raptor-migration watch sites are located across North America but are concentrated within the eastern and western flyways (Farmer et al. 2008, Smith et al. 2008). We selected fall migration sites meeting the 2013 Red-tailed Hawk RPI analysis criteria of $\geq$10 yr of hourly count data from 2002 to 2012 ($n = 32$; Crewe et al. 2013). Some regions of North America, such as the Northeast, had a high density of fall migration sites that were potentially redundant in that they may monitor similar breeding populations. We selected a subset of RPI sites within each flyway to maximize potentially unique flight corridors and minimize redundancy in monitoring. In addition to geographic uniqueness, we selected a subset of RPI sites for our final migration analysis on the basis of several criteria, including (1) long-term survey consistency from 1983 to 2012 and (2) counts of $\geq$100 Red-tailed Hawks yr^{-1}. Our final subset of fall migration sites included 13 sites across the 3 major flyways ($n = 6$ in eastern flyway, $n = 1$ in central flyway, $n = 6$ in western flyway; Figures 1 and 2A). We included western Great Lakes migration sites (i.e. Hawk Ridge and Illinois Beach State Park) in our eastern-flyway analysis because winter band-encounter data of Red-tailed Hawks from these 2 areas were found mainly along and east of the Mississippi River, which we used as our border between the eastern and central flyways (see Bolgiano 2013: fig. 3).

We used annual population indices calculated for each migration site as our Red-tailed Hawk abundance estimate (Crewe et al. 2013). Annual population indices represent the mean of hourly counts each year as predicted by a smoothing function of day of year and hour of day weighted by the ratio of observation length ($\leq$1 hr) to the total number of observation hours each year (Crewe et al. 2013: eq. 1). We then fit separate linear regression models (R package "stats") with a Gaussian distribution for the effect of scaled year on annual population index for the 30 yr, 20 yr, and 10 yr study periods at each migration site. Similar to our wintering analyses, we used an information-theoretic approach to evaluate model support by calculating 85% CIs from models with the lowest AIC score within a set. Only 6 migration sites approached 30 yr of data collection (Figure 2A). We analyzed trends in counts at each site for the 30 yr, 20 yr, and 10 yr study periods by rounding overall site duration to the nearest study-period decade. For example, Corpus Christi conducted 16 yr of migration monitoring during the 20 yr migration study period of 1993–2012, and therefore trends were calculated for the 20 yr and 10 yr study periods (Supplemental Material Table S1). Using fewer years of data from sites like Corpus Christi is not likely to have a significant influence on long-term trends because those particular sites (Figure 2A) did not have count trends changing in a strong nonlinear fashion.

Seasonal Trends by Migratory Flyway

To assess whether trends varied with season (i.e. wintering or migration) and by latitude, we created flyway-specific linear regression models, in which trend was the dependent variable and season (winter or migration), latitude, the interaction between season and latitude, and study period (30 yr, 20 yr, or 10 yr) were predictor variables. Using an AIC model-selection approach, we compared this global model to models that assumed that trends (1) varied independently by season and latitude (i.e. no interaction between season and latitude), (2) varied only by season, or (3) varied only by latitude. When the interaction between season and latitude was the top model, suggesting that latitudinal effects on trends differed by season, we used separate models for each season to predict count trends. When the interaction between season and latitude was not the top model, we combined both seasons to predict count trends from the top model. For each region, we compared models using AIC$_c$, ΔAIC, and Akaike weight (w_i; Burnham and Anderson 2002). We used the top-ranked model for each region to predict Red-tailed Hawk count trends using parameter estimates (β) and 85% CIs (Arnold 2010). We considered covariates with 85% CIs from top models that did not overlap zero as biologically informative. All statistical analyses were run with software from the R Development Core Team (2015).

RESULTS

Fall Migration and Wintering Trends

Annual Red-tailed Hawk counts at individual fall migration sites and wintering regions varied widely, from 119 to 6,947 birds yr^{-1} in migration and from 485 to 13,929 birds yr^{-1} in winter (see Supplemental Material Table S1). We found evidence for declining counts in 43% of migration trends (13 of 30) across all study periods and migration sites used in our analyses (Figure 2A). We also found

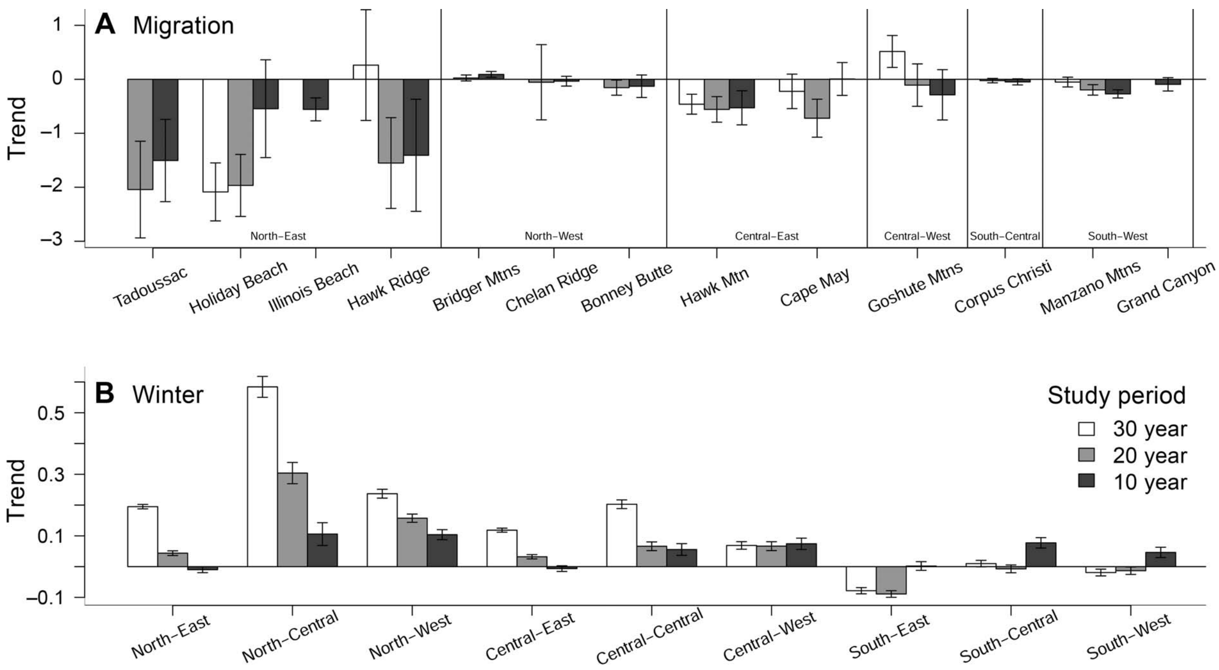

FIGURE 2. Red-tailed Hawk (**A**) migration and (**B**) wintering population trends by region and study period as inferred from migration and Christmas Bird Count data. Migration sites are grouped by their location within winter regions. Whiskers on bars represent 85% confidence intervals around parameter estimates.

evidence for increasing counts in 7% of migration trends (2 of 30), in the Bridger Mountains and Goshute Mountains in the western flyway (Figure 2A). By contrast, we found evidence for declining winter counts in only 19% (5 of 27) of trends, compared to 67% (18 of 27) showing increases, across all study periods and regions (Figure 2B and Supplemental Material Table S2). The direction of wintering trends within regions was relatively consistent across the 3 study periods (30 yr, 20 yr, or 10 yr); however, the trend magnitude was usually greatest during the 30 yr study period. The direction of migration trends was also consistent but did not differ in magnitude across the 3 study periods.

Seasonal Trends by Migratory Flyway

Red-tailed Hawk count trends varied by latitude, season, and flyway (Figure 3). Count trends across the 3 study periods within the eastern flyway differed by latitude and between seasons (Figure 3). Winter count trends were positively associated with latitude ($w_i = 0.91$, $\beta = 0.01$, 85% CI: 0.01–0.02), being generally positive in northern regions and negative in southern regions (Figures 2B and 3), whereas migration count trends were negatively associated with latitude ($w_i = 0.55$, $\beta = -0.11$, 85% CI: –0.19 to –0.04), being more negative in northern regions and less negative in southern regions (Figures 2A and 3). Count trends within the western flyway were positively associated with latitude ($w_i = 0.59$, $\beta = 0.01$, 85% CI: 0.00–0.02) but did not differ by season (Figure 3 and Supplemental Material Table S2), being generally positive in northern regions and negative in southern regions during both seasons (Figures 2 and 3). For complete AIC results for all analyses, see Supplemental Material Table S2.

DISCUSSION

Our results make a strong case for evaluating seasonal population trends within the context of similar trends from different stages of the annual cycle. Concurrent assessment of trends from different seasons has the potential to more clearly illuminate the conservation status of regional wildlife populations than trends from any single season. When viewed alone, fall migration count data, particularly along the eastern flyway of North America, suggest declining Red-tailed Hawk populations. However, when considered in conjunction with increasing wintering populations of Red-tailed Hawks in northern regions, a picture emerges of a stable to increasing Red-tailed Hawk population across much of North America, coupled with substantial changes in migration strategy.

Decreasing Red-tailed Hawk migration counts in southern regions and increasing winter counts in northern regions are consistent with other research on avian range shifts and changing migration ecology (La Sorte and Thompson 2007, Goodrich et al. 2012, Heath et al. 2012, Martin et al. 2014, Paprocki et al. 2014). Raptors in

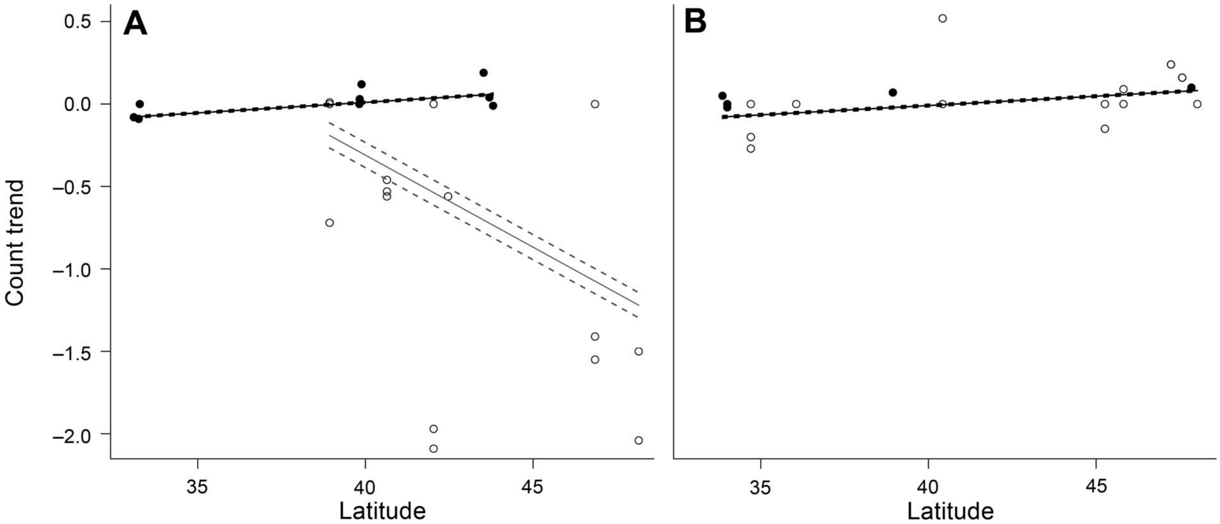

FIGURE 3. Red-tailed Hawk migration and wintering count trends with season (winter or migration) and latitude as predictor variables, and study period as a fixed variable for the (**A**) eastern and (**B**) western flyways of North America. When an interaction was present between latitude and season, open gray circles and lines represent migration sites, and closed black circles and lines represent winter regions. When an interaction was not present, solitary black lines represent migration and winter combined. The 85% confidence intervals (dashed lines) indicate there was a predictive relationship between latitude and count trend.

particular are known to respond to climate change by wintering farther north during warmer winters (Olson and Arsenault 2000, Kim et al. 2008), which can lead to long-term, climate-induced northward range shifts tracking climate niches (Tingley et al. 2009, Visser et al. 2009). Documented range shifts of raptors have also been predictive of local population changes (Paprocki et al. 2014). As species decrease migration distances and increase winter residency (Heath et al. 2012), fewer raptors may pass by mid-latitude long-term migration count sites, instead remaining on more northern wintering grounds. The European Common Buzzard (*Buteo buteo*), a species with a similar life history to the Red-tailed Hawk, has also experienced declining fall migration counts. Martin et al. (2014) provided strong evidence, based on banding data, that linked count declines to a reduction in migratory propensity and decreasing migration distances, while breeding and wintering populations continued to increase. Similarly, research on the American Kestrel (*Falco sparverius*) has shown declining counts at many migration sites, shorter migration distances, and increasing counts at some wintering areas over a similar period (Farmer and Smith 2009, Heath et al. 2012, Paprocki et al. 2014, 2015). Comparable to the Red-tailed Hawk, the Common Buzzard and American Kestrel exhibit population-specific migratory propensity, with northern breeders being migratory and southern breeders being more sedentary (Smallwood and Bird 2002, Martin et al. 2014). Given the life-history similarities and our results, we propose that a similar change is likely occurring in Red-tailed Hawks in North America.

Within all migratory flyways, wintering count trends were consistent with our migratory short-stopping and increased-residency hypothesis (Table 1: B), and this relationship was strongest within the 30 yr study period (Figure 2B). Northern and central wintering regions show stable to increasing counts, while several southern regions show decreasing counts. This strong latitudinal signal in regional trends suggests that an increasing number of Red-tailed Hawks are wintering farther north, consistent with previous research in this species that documented northward winter range shifts of 5.65 km yr^{-1} from 1975 to 2011 in western North America (Paprocki et al. 2014) and migratory short-stopping in eastern North America (Morrison and Baird 2016). In contrast with the migratory short-stopping and increased-residency hypothesis, and with results from the western flyway, eastern migration count trends had a negative relationship with latitude. We found more pronounced negative count trends at northern migration sites such as Hawk Ridge and Observatoire d'oiseaux de Tadoussac than at migration sites to the south. Both of these migration sites are at or near the northern limit of the Red-tailed Hawk wintering range. Fall migrants that pass by these 2 sites likely originate from the central and eastern Canadian provinces, and declining count trends may indicate a declining breeding population originating from these regions (Table 1: D). Indeed, Kirk and Hyslop (1998) found some evidence for breeding population declines in southern Ontario using BBS data, although few BBS routes were surveyed north of Hawk Ridge and Observatoire d'oiseaux de Tadoussac (see Kirk and Hyslop 1998: fig. 1). The BBS sampling protocol was not designed to detect raptor species, and its use for raptor population monitoring is debatable because trend estimates have very low precision (Dunn et al. 2005). Breeding-season monitoring of Red-tailed Hawk occupancy and reproductive success within central and eastern Canadian provinces should be considered a high priority for understanding the status of northern Red-tailed Hawk populations. Another strong research priority highlighted by our analyses is the need for a better understanding of raptor migration ecology in the central flyway. This could come from conventional monitoring at new sites or continuing sites such as the Hitchcock Nature Center in western Iowa, which just missed the criteria for the 2013 RPI analysis. Improved tracking technology, such as an expanded network of automated VHF telemetry receivers to track radio-tagged birds, would also be especially useful in the central flyway (Crysler et al. 2016).

Another factor that may be contributing to changing Red-tailed Hawk migration ecology is adaptation to urban environments (Berry et al. 1998, Schmidt and Bock 2005, Stout et al. 2006, Rullman and Marzluff 2014, Duerr et al. 2015). If Red-tailed Hawks are being subsidized to a certain degree by human activity, such as increased food abundance and access (Duerr et al. 2015), then this may explain their apparent ability to succeed in urban environments. If this change is driving increasing wintering counts, then (1) individuals will be more likely to winter farther north and/or not migrate from breeding grounds around urban areas as compared with natural or rural areas, and (2) increasing wintering counts and declining migration counts will be more apparent in urban areas than in natural or rural areas. Future studies exploring migration strategies and wintering trends between natural or rural and urban areas could test these hypotheses.

Migration data are counts of migrating animals and are a sample that may or may not reflect fluctuations in the underlying population being monitored. Use of these counts to monitor populations assumes that the proportion of the population detected does not vary, or varies randomly, over time (Dunn 2005). Further, the exact breeding origin of most migrating raptors is generally not known; this has been a consistent criticism of raptor migration data (reviewed in Dunn 2005). However, data from band recoveries (Hoffman et al. 2002, Goodrich and Smith 2008, Bolgiano 2013) and, more recently, innovations in satellite/GPS tracking technology and stable isotopes (McIntyre et al. 2008, Bloom et al. 2015, Nelson et al. 2015) have greatly improved our understanding of raptor migratory connectivity and source populations. Emerging genetic techniques previously used on songbirds may also improve our understanding of source populations (Ruegg et al. 2014). Improved understanding of population-specific migratory connectivity between breeding and wintering grounds will greatly enhance interpretation of migration and wintering count data, as well as our ability to recognize declining breeding populations that may warrant conservation action, particularly those that are logistically challenging to monitor. Future avian migration studies should prioritize understanding of population-specific connectivity.

While appropriate for the Red-tailed Hawk because of a large sample size in both datasets (see Supplemental Material Table S1), the degree to which our approach can be applied to other species will vary according to each species' life history and the representativeness of migratory and wintering counts. This approach will likely work well for other partial or short-distance migrants, although there are several long-distance migrants or resident populations in which migration or wintering data alone may still be the most effective way to track population changes. When using concurrent wintering and migration data to inform population trends for raptors or other birds, we recommend a careful species-by-species (and even regional, population-by-population) approach.

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LITERATURE CITED

Anderson, A. M., S. J. Novak, J. F. Smith, K. Steenhof, and J. A. Heath (2016). Nesting phenology, mate choice, and genetic divergence within a partially migratory population of

American Kestrels. The Auk: Ornithological Advances 133:99–109.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Berry, M. E., C. E. Bock, and S. L. Haire (1998). Abundance of diurnal raptors on open space grasslands in an urbanized landscape. The Condor 100:601–608.

Bildstein, K. L., J. P. Smith, and E. Ruelas I. (2008a). The future of raptor-migration monitoring. In State of North America's Birds of Prey (K. L. Bildstein, J. P. Smith, E. Ruelas I., and Veit, R. R. Editors). Nuttall Ornithological Club, Cambridge, MA, and American Ornithologists' Union, Washington, DC, USA.

Bildstein, K. L., J. P. Smith, E. Ruelas I., and R. R. Veit (Editors) (2008b). State of North America's Birds of Prey. Nuttall Ornithological Club, Cambridge, MA, and American Ornithologists' Union, Washington, DC, USA.

Bloom, P. H., M. D. McCrary, J. M. Scott, J. M. Papp, K. J. Sernka, S. E. Thomas, J. W. Kidd, E. H. Henckel, J. L. Henckel, and M. J. Gibson (2015). Northward summer migration of Red-tailed Hawks fledged from southern latitudes. Journal of Raptor Research 49:1–17.

Bolgiano, N. (2013). Evidence for changed migration of Red-tailed Hawks in eastern North America. Hawk Migration Studies 38(2):16–24.

Both, C., A. V. Artemyev, B. Blaauw, R. J. Cowie, A. J. Dekhuijzen, T. Eeva, A. Enemar, L. Gustafsson, E. V. Ivankina, A. Järvinen, N. B. Metcalfe, et al. (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proceedings of the Royal Society of London, Series B 271: 1657–1662.

Brandes, D., D. Oleyar, S. Hoffman, and L. Goodrich (2013). The Raptor Population Index, 2013 Regional Trend Summaries and Conservation Assessments. http://rpi-project.org/2013/assessments2013.php

Burnham K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer, New York, NY, USA.

Crewe, T., P. Taylor, D. Lepage, L. Goodrich, J. Brown, and J. Sodergren (2013). The Raptor Population Index, 2013 Analysis Methods and Trend Results. http://rpi-project.org/2013/

Crysler, Z. J., R. A. Ronconi, and P. D. Taylor (2016). Differential fall migratory routes of adult and juvenile Ipswich Sparrows (*Passerculus sandwichensis princeps*). Movement Ecology 4:3.

Doswald, N., S. G. Willis, Y. C. Collingham, D. J. Pain, R. E. Green, and B. Huntley (2009). Potential impacts of climate change on the breeding and non-breeding ranges and migration distance of European *Sylvia* warblers. Journal of Biogeography 36:1194–1208.

Duerr, A. E., T. A. Miller, K. L. C. Duerr, M. J. Lanzone, A. Fesnock, and T. E. Katzner (2015). Landscape-scale distribution and density of raptor populations wintering in anthropogenic-dominated desert landscapes. Biodiversity and Conservation 24:2365–2381.

Dunn, E. H. (2005). Counting migrants to monitor bird populations: State of the art. USDA Forest Service General Technical Report PSW-GTR-191.

Dunn, E. H., B. L. Altman, J. Bart, C. J. Beardmore, H., H. Berlanga, P. J. Blancher, G. S. Butcher, D. W. Demarest, R. Dettmers, W. C. Hunter, E. E. Iñigo-Elias, et al. (2005). High priority needs for range-wide monitoring of North American landbirds. Partners in Flight Technical Series 2. http://www.partnersinflight.org/

Elliott, K. H., J. E. Elliott, L. K. Wilson, I. Jones, and K. Stenerson (2011). Density-dependence in the survival and reproduction of Bald Eagles: Linkages to chum salmon. Journal of Wildlife Management 75:1688–1699.

Farmer, C. J., R. J. Bell, B. Drolet, L. J. Goodrich, E. Greenstone, D. Grove, D. J. T. Hussell, D. Mizrahi, F. J. Nicoletti, and J. Sodergren (2008). Trends in autumn counts of migratory raptors in northeastern North America, 1974–2004. In State of North America's Birds of Prey (K. L. Bildstein, J. P. Smith, E. Ruelas I., and Veit, R. R. Editors). Nuttall Ornithological Club, Cambridge, MA, and American Ornithologists' Union, Washington, DC, USA.

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

Farmer, C. J., and J. P. Smith (2009). Migration monitoring indicates widespread declines of American Kestrels (*Falco sparverius*) in North America. Journal of Raptor Research 43: 263–273.

Goodrich, L. J., C. J. Farmer, D. R. Barber, and K. L. Bildstein (2012). What banding tells us about the movement ecology of raptors. Journal of Raptor Research 46:27–35.

Goodrich, L. J., and J. P. Smith (2008). Raptor migration in North America. In State of North America's Birds of Prey (K. L. Bildstein, J. P. Smith, E. Ruelas I., and Veit, R. R. Editors). Nuttall Ornithological Club, Cambridge, MA, and American Ornithologists' Union, Washington, DC, USA.

Heath, J. A., K. Steenhof, and M. A. Foster (2012). Shorter migration distances associated with higher winter temperatures suggest a mechanism for advancing nesting phenology of American Kestrels *Falco sparverius*. Journal of Avian Biology 43:376–384.

Hitch, A. T., and P. L. Leberg (2007). Breeding distributions of North American bird species moving north as a result of climate change. Conservation Biology 21:534–539.

Hoffman, S. W., J. P. Smith, and T. D. Meehan (2002). Breeding grounds, winter ranges, and migratory routes of raptors in the mountain west. Journal of Raptor Research 36:97–110.

Kim, D. H., R. D. Slack, and F. Chavez-Ramirez (2008). Impacts of El Niño–Southern Oscillation events on the distribution of wintering raptors. Journal of Wildlife Management 72:231–239.

Kirk, D. A., and C. Hyslop (1998). Population status and recent trends in Canadian raptors: A review. Biological Conservation 83:91–118.

La Sorte, F. A., and F. R. Thompson III (2007). Poleward shifts in winter ranges of North American birds. Ecology 88:1803–1812.

Link, W. A., and J. R. Sauer (1999). Controlling for varying effort in count surveys—an analysis of Christmas Bird Count data. Journal of Agricultural, Biological, and Environmental Statistics 4:116–125.

Link, W. A., and J. R. Sauer (2007). Seasonal components of avian population change: Joint analysis of two large-scale monitoring programs. Ecology 88:49–55.

Link, W. A., J. R. Sauer, and D. K. Niven (2006). A hierarchical model for regional analysis of population change using Christmas Bird Count data, with application to the American Black Duck. The Condor 108:13–24.

Link, W. A., J. R. Sauer, and D. K. Niven (2008). Combining Breeding Bird Survey and Christmas Bird Count data to evaluate seasonal components of population change in Northern Bobwhite. Journal of Wildlife Management 72:44–51.

Martin, B., A. Onrubia, and M. A. Ferrer (2014). Effects of climate change on the migratory behavior of the Common Buzzard *Buteo buteo*. Climate Research 60:187–197.

McIntyre, C. L., D. C. Douglas, and M. W. Collopy (2008). Movements of Golden Eagles (*Aquila chrysaetos*) from interior Alaska during their first year of independence. The Auk 125: 214–224.

Millsap, B. A., G. S. Zimmerman, J. R. Sauer, R. M. Nielson, M. Otto, E. Bjerre, and R. Murphy (2013). Golden Eagle population trends in the western United States: 1968–2010. Journal of Wildlife Management 77:1436–1448.

Morrison, J. L., and J. M. Baird (2016). Using banding and encounter data to investigate movements of Red-tailed Hawks in the northeastern United States. Journal of Raptor Research 50:161–175.

National Audubon Society (2014). Christmas Bird Count historical results. http://www.christmasbirdcount.org

Nelson, D. M., M. Braham, T. A. Miller, A. E. Duerr, J. Cooper, M. Lanzone, J. Lemaître, and T. Katzner (2015). Stable hydrogen isotopes identify leapfrog migration, degree of connectivity, and summer distribution of Golden Eagles in eastern North America. The Condor: Ornithological Applications 117:414–429.

Olson, C. V. (2006). Ecology and roosting behavior of Rough-legged Hawks (*Buteo lagopus*) wintering in the Mission Valley of northwestern Montana. Master's thesis, University of Montana, Missoula, MT, USA.

Olson, C. V., and D. P. Arsenault (2000). Differential winter distribution of Rough-legged Hawks (*Buteo lagopus*) by sex in western North America. Journal of Raptor Research 34:157–166.

Paprocki, N., N. F. Glenn, E. C. Atkinson, K. M. Strickler, C. Watson, and J. A. Heath (2015). Changing habitat use associated with distributional shifts of wintering raptors. The Journal of Wildlife Management 79:402–412.

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.

Pardieck, K. L., and J. R. Sauer (2007). The 1999–2003 summary of the North American Breeding Bird Survey. Bird Populations 8: 28–45.

Parmesan, C., and G. Yohe (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Peterson, A. P. (1995). Erroneous party-hour data and a proposed method of correcting observer effort in Christmas Bird Counts. Journal of Field Ornithology 66:385–390.

Preston, C. R., and R. D. Beane (2009). Red-tailed Hawk (*Buteo jamaicensis*). In Birds of North America Online (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/052

R Development Core Team (2015). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ruegg, K. C., E. C. Anderson, K. L. Paxton, V. Apkenas, S. Lao, R. B. Siegel, D. F. DeSante, F. Moore, and T. B. Smith (2014). Mapping migration in a songbird using high-resolution genetic markers. Molecular Ecology 23:5726–5739.

Rullman, S., and J. M. Marzluff (2014). Raptor presence along an urban–wildland gradient: Influences of prey abundance and land cover. Journal of Raptor Research 48:257–272.

Sauer, J. R., and W. A. Link (2002). Using Christmas Bird Count data in analysis of population change. American Birds (The 102nd Christmas Bird Count). National Audubon Society. pp. 10–14. http://web4.audubon.org/bird/cbc/pdf/american_birds102A.pdf

Schmidt, E., and C. E. Bock (2005). Habitat associations and population trends of two hawks in an urbanizing grassland region in Colorado. Landscape Ecology 20:469–478.

Smallwood, J. A., and D. M. Bird (2002). American Kestrel (*Falco sparverius*). In Birds of North America Online (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/602

Smith, J. P., C. J. Farmer, S. W. Hoffman, G. S. Kaltenecker, K. Z. Woodruff, and P. F. Sherrington (2008). Raptor migration in North America. In State of North America's Birds of Prey (K. L. Bildstein, J. P. Smith, E. Ruelas I., and Veit, R. R. Editors). Nuttall Ornithological Club, Cambridge, MA, and American Ornithologists' Union, Washington, DC, USA.

Sohl, T. L. (2014). The relative impacts of climate change and land-use change on conterminous United States bird species from 2001 to 2075. PLoS ONE 9:e112251.

Steenhof, K., M. N. Kochert, and M. Q. Moritsch (1984). Dispersal and migration of southwestern Idaho raptors. Journal of Field Ornithology 55:357–368.

Stout, W. E., S. A. Temple, and J. M. Papp (2006). Landscape correlates of reproductive success for an urban–suburban Red-tailed Hawk population. The Journal of Wildlife Management 70:989–997.

Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz (2009). Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences USA 106:19637–19643.

Van Buskirk, J., R. S. Mulvihill, and R. C. Leberman (2009). Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. Global Change Biology 15:760–771.

Visser, M. E., A. C. Perdeck, J. H. van Balen, and C. Both (2009). Climate change leads to decreasing bird migration distances. Global Change Biology 15:1859–1865.

Watson, J. W., A. A. Duff, and R. W. Davies (2014). Home range and resource selection by GPS-monitored adult Golden Eagles in the Columbia Plateau Ecoregion: Implications for wind power development. The Journal of Wildlife Management 78:1012–1021.

Zuckerberg, B., D. N. Bonter, W. M. Hochachka, W. D. Koenig, A. T. DeGaetano, and J. L. Dickinson (2011). Climatic constraints on wintering bird distributions are modified by urbanization and weather. Journal of Animal Ecology 80:403–413.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith (2009). Mixed Effects Models and Extensions in Ecology with R. Springer, New York, NY, USA.