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CHANGES IN SURVEY EFFORT CAN INFLUENCE CONCLUSIONS ABOUT MIGRATION PHENOLOGY

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ABSTRACT.—Changes in autumn raptor migration phenology have been documented at hawk count sites across North America. Delays in autumn migration are the most common shift reported, but these changes vary by species. We examined autumn raptor phenology and changes in count effort for 14 raptor species over 46 yr at Hawk Ridge in Duluth, Minnesota, USA, using mean passage date. Among the 14 raptors, six species showed significant shifts in migration phenology; four toward later migration and two toward earlier migration. Our results suggest fewer species are shifting toward later phenology than previously reported at Hawk Ridge and that some previously reported changes in phenology may be explained by changes in survey effort. This study highlights the importance of controlling for count effort when analyzing migration phenology, emphasizing the need for consistent effort in the future.

KEY WORDS: *climate change, Hawk Ridge, migration, phenology, raptors, survey effort.*

LOS CAMBIOS EN EL ESFUERZO DE MUESTREO PUEDEN INFLUIR LAS CONCLUSIONES SOBRE LA FENOLOGÍA MIGRATORIA

RESUMEN.—En los sitios de conteo de aves rapaces en Norteamérica se han observado cambios en la fenología migratoria otoñal. El retraso en la migración otoñal es el cambio más comúnmente observado, si bien estos cambios varían según la especie. Examinamos la fenología de las aves rapaces durante el otoño y los cambios en el esfuerzo de muestreo para 14 especies de aves rapaces durante 46 años en Hawk Ridge, Duluth, Minnesota, EEUU, utilizando la fecha promedio de paso migratorio. De las 14 especies de rapaces, seis especies mostraron cambios significativos en la fenología migratoria; cuatro hacia una migración tardía y dos hacia una migración anticipada. Nuestros resultados sugieren que hay un menor número de especies retrasando su fenología migratoria comparado a lo que se informó anteriormente en esta localidad. Algunos

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cambios reportados previamente en la fenología migratoria podrían ser explicados por cambios en el esfuerzo de muestreo. Este estudio destaca la importancia de controlar el esfuerzo de muestreo al analizar la fenología migratoria, enfatizando la necesidad de un esfuerzo estable en el futuro.

[Traducción del equipo editorial]

INTRODUCTION

There is substantial evidence that climate change has altered the timing of important events in the lifecycle of many temperate bird species (Cotton 2003, Crick 2004, Gordo 2007, Knudsen et al. 2011, Horton et al. 2019). Advanced spring migration has occurred in passerines (Jonzen et al. 2006, Altwegg et al. 2012, Hurlbert and Liang 2012, Bussiere et al. 2015), waterbirds (Hazra et al. 2012, Guillemain et al. 2015), and large soaring birds such as raptors and storks (Jaffré et al. 2013, Sullivan et al. 2016, Therrien et al. 2017). Earlier spring migration in these taxa often results in advanced breeding phenology (Crick 2004).

Compared to spring, autumn phenology is understudied and less understood (Gallinat et al. 2019). Shifts in fall migration phenology often vary among taxa and similar species may have opposing autumn phenological shifts (Scholer et al. 2016). For many species, early spring migration and breeding result in an early departure for the wintering grounds in autumn (Sokolov and Payevsky 1998, Gordo 2007, Horton et al. 2019). In contrast, some diurnal raptors, other large soaring birds, and waterfowl have been found to delay fall migration (Jaffré et al. 2013, Sullivan et al. 2016, Therrien et al. 2017, Thurber et al. 2020) and thus, extend their time on the breeding grounds. Christmas bird count data suggest that raptors are wintering closer to their breeding grounds than in the past (Paprocki et al. 2014).

The statistical methodology for studying phenological data varies greatly between studies (Moussus et al. 2010, Gallinat et al. 2019). Statistics used to analyze phenology have included extreme dates (e.g., first passage date or date of peak abundance), methods that partition data (including a wide variety of quantiles), and mean passage date, which integrates the complete distribution of the migration period (see Table 1 in Knudsen et al. 2007, DeLeon et al. 2011, Therrien et al. 2017, Thurber et al. 2020). Recent studies have recommended the use of statistical methods that treat phenological data as multiple-day events rather than a single date (Gallinat et al. 2019). Methods that integrate across the complete distribution of the data, such as mean

passage date, have been shown to be more accurate and robust than other methodologies (Moussus et al. 2010).

Some of the most valuable data sets for phenological study are long-term count data or banding data from bird observatories (Knudsen et al. 2007). Visible migration counts, such as at hawk watch sites, provide detailed accounts of the timing and magnitude of migration at a given site (Goodrich and Smith 2008). Systematic counts of migrating raptor numbers at Hawk Ridge, Duluth, Minnesota, USA, have been collected since 1972. Autumn migration phenology analyses have been done on this data set using a single species (Rosenfield et al. 2011), across species at Hawk Ridge (Van Buskirk 2012), and as a part of a larger study with other migration sites (Therrien et al. 2017). These studies have primarily found delays in autumn migration.

Although long-term data sets from bird observatories represent valuable data sets for phenological research because they use consistent methodologies, changes in effort do sometimes occur. Statistical methodologies such as mean passage date should be robust to some changes in effort, such as missed days due to weather (Moussus et al. 2010), but changes to effort, such as adding days to the beginning or end of the season that greatly increase the number of birds counted are more likely to lead to biased results. It is therefore important to consider effort in all phenological studies to determine whether the results are due to sampling effects or if they represent a “true” shift in phenology (Knudsen et al. 2007).

At Hawk Ridge, the final day of the hawk count was extended from the end of October to the end of November in the early 1990s, which represents a change in effort that could impact the results of a phenological study, particularly for late migrating species. The most recent publication on migration phenology solely at Hawk Ridge (Van Buskirk 2012) did not take this change in effort into consideration and found migration to be delayed in many species, with the most extreme delays occurring in late migrating species. Van Buskirk (2012) analyzed migration phenology using quantiles, which may not be as robust to changes in effort as mean passage

date. In the present investigation, we studied autumn raptor phenology at Hawk Ridge using mean passage date to analyze migration phenology while controlling for changes in effort across the years of the count.

METHODS

Study Site, Field Methods, and Data. Hawk Ridge is located in Duluth, Minnesota, USA, on a ridge that runs parallel to the shore of Lake Superior. Systematic hawk counts began at Hawk Ridge in 1972 and are now managed by Hawk Ridge Bird Observatory (HRBO) (Hofslund 1966, Peterson et al. 2015). Effort was not consistent in the first two years of the count (Rosenfield et al. 2011), but from 1974–1990 raptors were counted daily from 15 August to 31 October. To better count late migrating species, the count was extended into November in the early 1990s, and in 1997, was standardized to end on November 30. At minimum, migratory raptors are counted on all days without precipitation from the mid-morning to mid-afternoon (HRBO 2019), and counters follow protocols established by the Hawk Migration Association of North America (HMANA 2018). However, additional hours are sometimes added to the hawk count if the hawk flight continues into the evening, or to document passerine migration at dawn during the appropriate season. All data are summarized hourly and submitted to HMANA where they are available to interested parties, with appropriate permission, at www.hawkcount.org. Although this data was proofed for errors prior to being uploaded to HMANA, the data for these analyses were further examined using outlier analysis and any unusual counts were cross-referenced with the original field data.

Statistical Analysis. Following Rosenfield et al. (2011), we dropped the data from 1972 and 1973 from this analysis because of low and inconsistent count effort. Before analyzing migration phenology, we considered the dates between which the majority of the individuals of a species are counted at Hawk Ridge (the passage window). Species for which at least 95% of all observations occurred before 1 November (even after the field season was extended) were analyzed using a data set from 1974 through 2019 and from 15 August through 1 November (hereafter “early migrant data set”). Species for which >5% of all observations occurred after 1 November were analyzed using a data set from 1997 through 2019 and from 15 August through 30 November (hereafter “late migrant data

set”). We used the mean passage date over the appropriate passage window (i.e., early or late migrant data set) as a phenological estimator for 14 raptor species. This method was chosen because it should be more robust to missed days or hours due to inclement weather than other methodologies that could be used to analyze phenological data (Mousus et al. 2010). Species analyzed using the early migrant data set included Turkey Vulture (*Cathartes aura*), Osprey (*Pandion haliaetus*), Northern Harrier (*Circus hudsonius*), Sharp-shinned Hawk (*Accipiter striatus*), Cooper’s Hawk (*Accipiter cooperii*), Broad-winged Hawk (*Buteo platypterus*), American Kestrel (*Falco sparverius*), Merlin (*Falco columbarius*), and Peregrine Falcon (*Falco peregrinus*). Species analyzed using the late migrant data set included Bald Eagle (*Haliaeetus leucocephalus*), Northern Goshawk (*Accipiter gentilis*), Red-tailed Hawk (*Buteo jamaicensis*), Rough-legged Hawk (*Buteo lagopus*), and Golden Eagle (*Aquila chrysaetos*).

From 1974 through 2019 count effort was quantified in two ways: (1) by the number of hours in which raptors were counted in a season, and (2) by the number of days raptors were counted, regardless of the hours counted each day. Similar to our calculations of migration phenology, we calculated the mean count day (hereafter “count days”) and the date on which the mean count hour occurred (hereafter “count hours”) for the data set using ordinal dates. The set of count days was defined as a list of days, within the species’ passage window, on which raptors were counted. Mean count day was defined as the average date of the set of count days. Mean count hour was similarly defined, but with units of hours since the start of the window, rather than days. This variable helps control for systematic declines in the number of effort hours/d as both the season and the time series progress.

To analyze the influence of changing effort on the phenology of a given species, linear regression models were developed using the mean passage date as the response variable with three covariates as explanatory variables included individually in turn; the two measures of effort described above (count days and count hours) and year. The strength of these three univariate models in explaining the phenological trend was evaluated using the standard correction to Akaike’s Information Criterion (AIC_c) for each species to compare year against these two measures of effort. Support for each model was compared using AIC_c weights (w_i ; Burnham and Anderson 2002). These models were also run on the

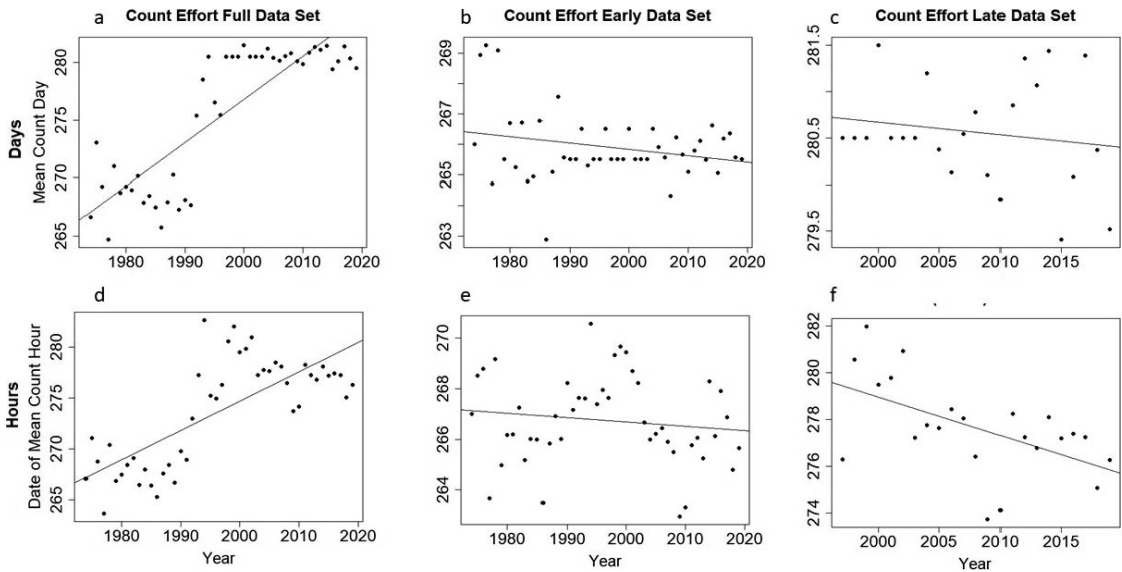


Figure 1. Timing of the two metrics of count effort at Hawk Ridge, Duluth, Minnesota: mean count day and ordinal date of the mean count hour. (A) Mean count days using the full data set ($\beta = 0.37 \pm 0.08$, $P < 0.01$); (B) Mean count days using the truncated early migrant data set ($\beta = -0.02 \pm 0.02$, $P = 0.10$); (C) Mean count days using the truncated late migrant data set ($\beta = -0.01 \pm 0.04$, $P = 0.47$); (D) Mean count hours using the full data set ($\beta = 0.29 \pm 0.08$, $P < 0.01$); (E) Mean count hours using the truncated early migrant data set ($\beta = -0.02 \pm 0.04$, $P = 0.37$); and (F) Mean count hours using the truncated late migrant data set ($\beta = -0.16 \pm 0.11$, $P < 0.01$).

full data set for species in the late migrant data set for comparison with the models run on the truncated data set that had been corrected for effort. We considered a phenological shift significant if the 95% confidence limit on the estimated slope coefficient for year (β) did not include zero. We concluded that the effort models were superior to the year model only if they were at least 2 AIC_c units better than the year model (Arnold 2010). All analyses were completed in R (R Core Team 2018).

RESULTS

Survey Effort. When analyzing the full data set before truncation, we found that the timing of effort has shifted later for both count days ($\beta = 0.37 \pm 0.08$, $P < 0.01$) and count hours ($\beta = 0.29 \pm 0.08$, $P < 0.01$) due to the addition of November counts starting in the 1990s (Fig. 1, all estimates ± 2 SE). When November counts were not included for the early migrant data set, the timing of effort remained consistent across all years for both count days ($\beta = -0.02 \pm 0.02$, $P = 0.10$) and count hours ($\beta = -0.02 \pm 0.04$, $P = 0.37$). For the late migrant data set, effort remained consistent for count days ($\beta = -0.01 \pm 0.04$, $P = 0.47$) but count hours significantly

decreased over the years included in the data set ($\beta = -0.16 \pm 0.11$, $P < 0.01$). This significant decrease in count hours is due to hawk counters at the start of the data set continuing the count all day regardless of migration activity and counters later in the data set leaving early on November days with little migration activity.

Raptor Phenology. Five of the fourteen species analyzed showed significant shifts in migration phenology (Table 1, Fig. 2, Fig. 3). Four species had significantly later shifts in migration phenology, including Turkey Vulture ($\beta = 0.14 \pm 0.06$, $P < 0.01$), Northern Harrier ($\beta = 0.10 \pm 0.09$, $P = 0.04$), Sharp-shinned Hawk ($\beta = 0.18 \pm 0.06$, $P < 0.01$), and American Kestrel ($\beta = 0.17 \pm 0.07$, $P < 0.01$). Bald Eagle had significantly earlier shifts in migration phenology ($\beta = -0.83 \pm 0.29$, $P < 0.01$). Year explained the shift in phenology better than metrics of effort in all species with significant shifts except for Northern Harrier which was best explained by the timing of count hours (Table 2). In this case, the model including year ($AIC_c w_i = 0.42$) was very competitive with the model for count hours ($AIC_c w_i = 0.53$).

Table 1. The 95% confidence interval of the slope (β) for year, the significance of the slope (P), the explained variation (R^2) of the phenology shift by year, and the number of days shifted per decade for the autumn migration phenology of the 14 raptor species regularly counted at Hawk Ridge. Bold font indicates species with significant shifts. Results from Therrien et al. 2017 added for comparison of phenological shift magnitudes.

| SPECIES | β (95% CI) | P | R^2 | DAYS/DECADE | THERRIEN ET AL. 2017 β (95% CI) |
|--------------------|-----------------------------|-----------------|-------------|--------------|---------------------------------------|
| Turkey Vulture | 0.14 (0.08, 0.20) | <0.01 | 0.30 | 1.35 | 0.12 (0.04, 0.19) |
| Osprey | -0.03 (-0.08, 0.02) | 0.22 | 0.01 | -0.30 | -0.02 (-0.07, 0.03) |
| Bald Eagle | -0.83 (-1.11, -0.54) | <0.01 | 0.59 | -8.27 | -0.09 (-0.22, 0.03) |
| Northern Harrier | 0.10 (0.01, 0.20) | 0.04 | 0.08 | 1.01 | 0.08 (0.00, 0.17) |
| Sharp-shinned Hawk | 0.18 (0.12, 0.23) | <0.01 | 0.48 | 1.78 | 0.20 (0.15, 0.25) |
| Cooper's Hawk | -0.02 (-0.16, 0.12) | 0.79 | -0.02 | -0.19 | 0.07 (0.00, 0.13) |
| Northern Goshawk | -0.25 (-0.43, 0.09) | 0.21 | 0.03 | -1.73 | 0.21 (0.04, 0.38) |
| Broad-winged Hawk | 0.03 (-0.02, 0.08) | 0.26 | 0.01 | 0.30 | 0.03 (-0.01, 0.08) |
| Red-tailed Hawk | -0.07 (-0.17, 0.31) | 0.56 | -0.03 | 0.72 | 0.01 (-0.06, 0.09) |
| Rough-legged Hawk | 0.04 (-0.36, 0.44) | 0.84 | -0.05 | 0.42 | 0.18 (0.00, 0.35) |
| Golden Eagle | -0.09 (-0.35, 0.16) | 0.49 | -0.02 | -0.94 | 0.16 (0.04, 0.28) |
| American Kestrel | 0.17 (0.10, 0.25) | <0.01 | 0.32 | 1.74 | 0.08 (0.02, 0.14) |
| Merlin | 0.07 (-0.02, 0.16) | 0.12 | 0.03 | 0.70 | 0.09 (0.00, 0.17) |
| Peregrine Falcon | -0.04 (-0.12, 0.04) | 0.33 | -0.001 | -0.40 | 0.05 (-0.05, 0.14) |

DISCUSSION

Our estimated shifts in raptor phenology at Hawk Ridge agree with previous research that most species were migrating later in the fall, but fewer species showed significant shifts than in previous studies. Each of our five species with significant phenology

trends also had a similar trend calculated by Therrien et al. (2017; Table 1), and in the case of Sharp-shinned Hawk, also by Rosenfield et al. (2011). However, Therrien et al. (2017) found the Cooper's Hawk, Northern Goshawk, Rough-legged Hawk, Golden Eagle, and Merlin all showed significant trends toward later migration, while we did not find significant shifts in these species after correcting for effort. This may be due to inherent differences between Hawk Ridge, the westernmost study site, and the other eastern USA sites used in the Therrien et al. (2017) analysis. We suggest that counts at Hawk Ridge represent a different population or region than most, if not all, of more easterly hawk count sites. Further, we suggest that the more eastern populations of raptors may be showing a different response to climate change than the birds of a more midwestern origin counted at Hawk Ridge.

There has been much speculation on the reasons for migration phenology shifts (Gordo 2007). Most of the species with significant migration phenology shifts in our study are exhibiting later migration, which likely indicates a prolonged stay on their breeding grounds. This is further supported by earlier spring migration by Turkey Vulture, Sharp-shinned Hawk, and American Kestrel (Therrien et al. 2017) and migratory short-stopping by Sharp-shinned Hawk (Duncan 1996), Northern Harrier, and American Kestrel (Paprocki et al. 2014). Warmer temperatures and later snowfall may be extending the window in which these four raptor

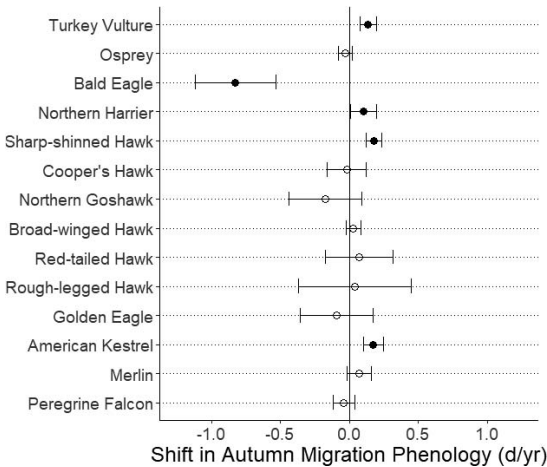


Figure 2. Autumn migration phenology shifts (β = slope of regression of lognormal mean migration date) for 14 raptor species at Hawk Ridge. Species for which $P < 0.05$ and that have a confidence interval not crossing zero are considered to have a statistically significant shift in migration phenology and are marked with solid circles. Species for which $P > 0.05$ and that had a confidence interval that crossed zero are marked with open circles.

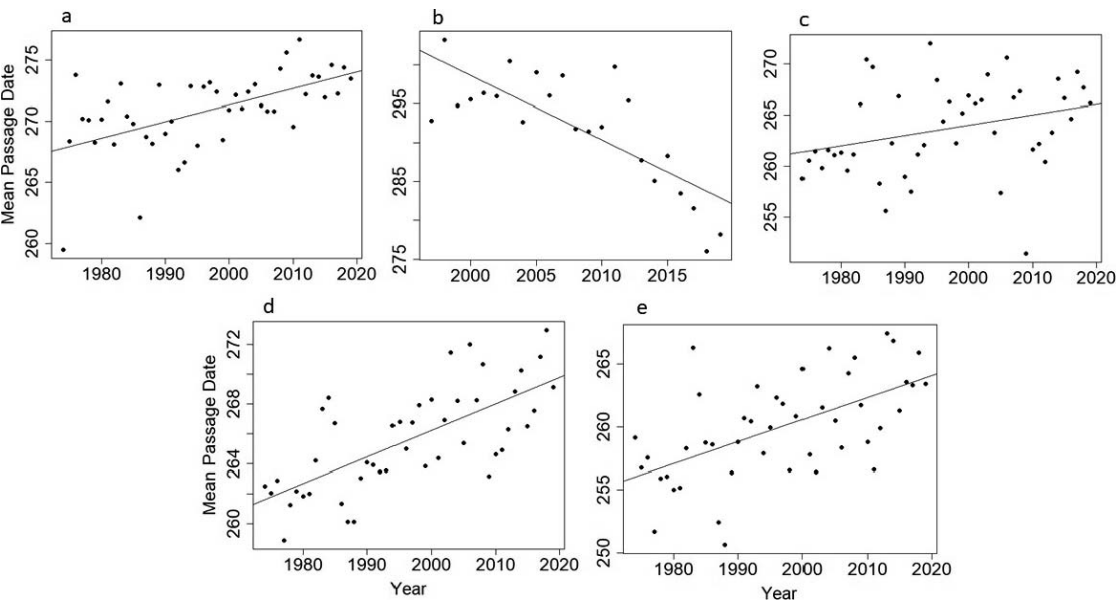


Figure 3. Autumn migration phenology for six species with significant shifts. (A) Turkey Vulture ($\beta = 0.14 \pm 0.06$, $P < 0.01$); (B) Bald Eagle ($\beta = -0.82 \pm 0.29$, $P < 0.01$); (C) Northern Harrier ($\beta = 0.10 \pm 0.09$, $P = 0.04$); (D) Sharp-shinned Hawk ($\beta = 0.18 \pm 0.06$, $P < 0.01$); and (E) American Kestrel ($\beta = 0.17 \pm 0.07$, $P < 0.01$).

species can access the abundant resources on their breeding grounds. Furthermore, two of these species, Sharp-shinned Hawk and American Kestrel, may also be timing their migration to align with the migrations of their prey sources. Sharp-shinned Hawks primarily hunt passerines, which show some evidence of delayed migration in some species (Smith and Patton 2011, Ellwood et al. 2015). At Hawk Ridge, American Kestrels have frequently been observed eating dragonflies while migrating (Hofslund 1973) and a correlation between large flights of migratory dragonflies and kestrels has been reported (Nicoletti 1996). Data on the timing of dragonfly migration phenology is sparse but delayed

emergence has been observed in Japan and has been linked to increased temperature (Doi 2008). If this delayed emergence also occurs in the boreal forests of North America, then the timing of the migration of dragonflies could explain the shift in American Kestrel migration.

The shift toward earlier migration by Bald Eagle is more difficult to explain, as the water bodies they hunt are freezing later rather than earlier. However, Bald Eagles have shown large increases in population in many parts of their range (Brandes et al. 2016, United States Fish and Wildlife Service 2020), including in Minnesota (Pfannmuller et al. 2017). This increase in population may increase the

Table 2. The ΔAIC_c score and w_i for models comparing the mean passage date for five species with statistically significant phenological shifts against year and the two measures-of-effort (mean count day and the date of the mean count hour). Phenological shifts calculated using early and late migrant data sets that have been truncated to account for effort.

| SPECIES | YEAR | | COUNT DAYS | | COUNT HOURS | |
|--------------------|----------------|-------|----------------|-------|----------------|-------|
| | ΔAIC_c | w_i | ΔAIC_c | w_i | ΔAIC_c | w_i |
| Turkey Vulture | 0.000 | 1 | 16.352 | 0 | 17.406 | 0 |
| Bald Eagle | 0.000 | 1 | 20.772 | 0 | 15.406 | 0 |
| Northern Harrier | 0.467 | 0.42 | 5.060 | 0.04 | 0.000 | 0.53 |
| Sharp-shinned Hawk | 0.000 | 1 | 30.260 | 0 | 30.365 | 0 |
| American Kestrel | 0.000 | 1 | 16.906 | 0 | 18.585 | 0 |

Table 3. Comparison of results of phenological analyses for late migrating species when using the truncated late migrant data set (1997–2019) and the full data set (1974–2019) that does not take effort into consideration. Included are the 95% confidence interval of the slope (β), the significance of the slope (p), and the ΔAIC_c comparison between year and the two measures of effort. Bold font indicates species with significant shifts.

| SPECIES | DATA SET | ΔAIC_c | | | | |
|-------------------|-----------|-----------------------------|-----------------|---------------|---------------|---------------|
| | | β (95% CI) | P | YEAR | COUNT DAYS | COUNT HOURS |
| Bald Eagle | Truncated | −0.83 (−1.11, −0.54) | <0.01 | 0.000 | 20.772 | 15.406 |
| | Full | 0.22 (0.02, 0.42) | 0.03 | 21.142 | 9.816 | 0.000 |
| Northern Goshawk | Truncated | −0.17 (−0.43, 0.09) | 0.21 | 0.000 | 0.649 | 0.769 |
| | Full | 0.27 (0.12, 0.41) | <0.01 | 17.997 | 5.254 | 0.000 |
| Red-tailed Hawk | Truncated | 0.07 (−0.17, 0.31) | 0.56 | 1.228 | 0.000 | 1.591 |
| | Full | 0.18 (0.07, 0.29) | <0.01 | 4.238 | 1.999 | 0.000 |
| Rough-legged Hawk | Truncated | 0.04 (−0.36, 0.44) | 0.84 | 0.986 | 0.996 | 0.000 |
| | Full | 0.38 (0.22, 0.53) | <0.01 | 10.750 | 3.643 | 0.000 |
| Golden Eagle | Truncated | −0.09 (−0.35, 0.16) | 0.48 | 3.130 | 3.117 | 0.000 |
| | Full | 0.48 (0.37, 0.60) | <0.01 | 22.728 | 3.533 | 0.000 |

competition for food on northern lakes both with other eagles and with Ospreys. This increased pressure for food in the northern latitudes may be driving Bald Eagles to migrate south earlier. Interestingly, Ospreys also show a trend toward earlier migration, although it is not significant.

Alternatively, the increase in the numbers of Bald Eagles could explain the shift in their migration in another way. Bald Eagles breed in two separate populations: northern breeders that breed during the summer across the northern portion of the species’ range, and southern breeders that breed during the winter in the southeastern part of the USA (Wheeler 2003, Wright 2016). The southern breeding population migrates north during the summer to spend its nonbreeding season in the northern USA and Canada (Broley 1947, Mabie et al. 1994, Smith et al. 2017). Both of these populations would therefore migrate by Hawk Ridge in the fall. If the southern breeding population migrates south earlier than its northern breeding counterpart, a disproportionate increase in the southern breeding eagle population could result in what appears to be a shift toward earlier migration. Further research is needed to find the causes for shifts in migration phenology.

Our study also demonstrated the importance of considering effort when analyzing phenology data. This is best illustrated by the disparity in results between this study and that of Van Buskirk (2012), particularly for late migrating species. In his analysis, late migrating species, particularly Bald Eagle, Golden Eagle, and Rough-legged Hawk, appeared to be showing the greatest shifts in migration

phenology; however, we found none of these species showed a shift toward later migration and Bald Eagle showed a shift toward earlier migration. When analyzed from 1974 through 2019 without accounting for the change in effort, these late migrants appeared to show a dramatic shift toward late migration (Table 3, Fig. 4), but this shift seems better explained by the changes in effort than by year.

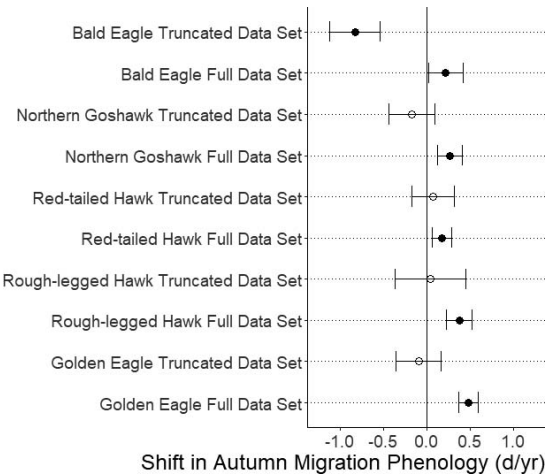


Figure 4. Autumn migration phenology shifts (β = slope of regression of lognormal mean migration date) for five late migrating raptor species comparing the truncated late migrant data set and the full data set. Species for which $P < 0.05$ and that have a confidence interval not crossing zero are considered to have a statistically significant shift in migration phenology and are marked with solid circles. Species for which $P > 0.05$ and that had a confidence interval that crossed zero are marked with open circles.

Our study demonstrated that rigorous adherence to standardizing effort is essential in longitudinal studies of migration counts. Future studies of migration phenology should ensure variation in effort has not influenced their results. Analyses need to be completed on a site-by-site basis, and in studies including multiple locations, each location may need to be examined separately. Bednarz et al. (1990) and Hussell and Ruelas Inzunza (2008) have previously emphasized the importance of maintaining consistent effort through time at count sites. If we want to better understand phenological shifts in raptor migration, it is critical to count raptors through their entire migration cycle. Moreover, if some raptors are migrating earlier and some later, earlier and extended count periods will be necessary to properly document these shifts.

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