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Does migration phenology of Northern Saw-whet Owls (*Aegolius acadicus*) vary over time?

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ABSTRACT—Ongoing climate change can affect migration phenology in a variety of species. We assessed autumn migration phenology of Northern Saw-whet Owls (*Aegolius acadicus*) using 25 years of banding data from 7 sites throughout eastern North America. Using a linear mixed model, we found a significant trend toward a later passage for the median passage date. Phenological changes in migration could be a way to cope with changing environmental conditions. *Received 16 May 2022. Accepted 31 May 2023.*

Key words: aggregation, distribution, point pattern data, spatial ecology.

Est-ce que la phénologie de la migration des Petites Nyctales (*Aegolius acadicus*) varie au fil du temps?

RÉSUMÉ (French)—Le changement climatique peut affecter la phénologie de la migration chez une variété d'espèces. Nous évaluâmes la phénologie de la migration automnale de la Petite Nyctale (*Aegolius acadicus*) en utilisant 25 années de données de baguage provenant de sept sites répartis dans l'est de l'Amérique du Nord. En utilisant un modèle mixte linéaire, nous trouvâmes une tendance significative à un passage plus tard pour la date de passage médiane. Les changements phénologiques de la migration pourraient être une façon de faire face aux conditions environnementales variables.

Mots clés: changement climatique, date de passage, migration automnale.

Besides range shifts, changes in phenology are one of the most observed and investigated responses of species to climate warming (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Visser and Both 2005). Understanding changes in phenology is important because they can generate ecological mismatches (asynchrony in timing between life cycles of organisms; Visser and Gienapp 2019) and have potential effects on life history traits, such as body condition, survival, and ultimately on population trends of many species (Parmesan and Yohe 2003, Parmesan 2006, Mayor et al. 2017, Cohen et al. 2018, Horton et al. 2020). Changes in phenology are broadly studied within migratory birds, as the timing of arrival at the breeding or wintering grounds can be a crucial determinant of their reproductive success and overall fitness (Cotton 2003, Carey 2009, Mayor et al. 2017).

Over the past decades, several studies observed a trend toward earlier spring arrival of birds at their breeding grounds in Europe and North America (Butler 2003, Root et al. 2003, Gordo 2007, Mayor et al. 2017, Horton et al. 2020). In many cases, the advanced spring arrivals of birds have been attributed to climate change and more specifically to warmer spring temperatures (Butler 2003, Cotton 2003, Root et al. 2003, Knudsen et al. 2007, Sullivan et al. 2016, Haest et al. 2018). In contrast to spring migration phenology, observed changes in autumn migration phenology are less uniform, with indications of both delays and

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advances in autumn passage dates (Cotton 2003, Jenni and Kéry 2003, Gordo 2007, Gallinat et al. 2015, Haest et al. 2019). The timing of autumn migration to the wintering grounds seems to be species-specific and highly different in long- vs. short-distance migrants (Jenni and Kéry 2003, Gordo 2007). Whereas long-distance migrants generally advance their autumn passage dates, short-distance migrants tend to delay them (Jenni and Kéry 2003, Van Buskirk et al. 2009). This apparent distinction in autumn migration trends may be caused by climate change and the contrasting effects of weather variables (Haest et al. 2019).

In diurnal birds of prey, studies in North America and Europe found an overall delay in autumn migration passage dates (Van Buskirk 2012, Jaffré et al. 2013). The overall delay in the autumn migration timing of diurnal raptors is coupled with an overall advancement of their spring migration. Both phenological adjustments result in increases in breeding area residence time (Thorup et al. 2007) and follow a pattern consistent with climate change (Van Buskirk 2012, Jaffré et al. 2013, Sullivan et al. 2016, Therrien et al. 2017).

To our knowledge, phenological changes in the migration of owls (Strigidae) in relation to climate change have not yet been investigated. Most studies on migration phenology of owls focus on differences between age or sex classes, such as those reported for Eurasian Pygmy-Owls (*Glaucidium passerinum*) and Northern Saw-whet Owls (*Aegolius acadicus*; Lehikoinen et al. 2011, Brittain and Jones 2014). The Northern Saw-whet Owl (hereinafter NSWO) has been extensively trapped and banded since the 1990s in eastern North America (Wall et al. 2020) and is therefore an excellent study species for investigating changes in migration phenology over time.

The NSWO is a common owl that inhabits the boreal and eastern temperate forests across North America (Rasmussen et al. 2020). Annually, during the autumn, many individuals move south of their breeding range to overwinter in the mixed forests of the United States (Rasmussen et al. 2020). Although common and widespread throughout North America, NSWOs are not easily observed because of their small size, highly nocturnal behavior, and use of dense habitats as diurnal roosts (Rasmussen et al. 2020). A recent study of NSWO population trends in eastern North America suggests that its populations have been relatively stable since 1992, despite revealing a negative trend over the years 2001–2017 (Wall et al. 2020). This negative trend may be an early warning that population numbers are decreasing, potentially related to habitat loss and/or climate change (Udvardy and Farrand 1994, Hinam and St. Clair 2008, Domahidi et al. 2019).

In this study, we aim to assess whether NSWO migration phenology has shifted over time, potentially related to ongoing climate change. We hypothesize that, as a short-distance migrant, the NSWO is responding to global warming by delaying its autumn migration. If so, we further hypothesize a latitudinal gradient in the phenological adjustment, with sites farther north showing a stronger delay in migration timing.

Methods

NSWOs were captured and banded at 7 sites throughout eastern North America from 1992 to 2020 (Fig. 1). The location and years of operation for the 7 banding sites are presented in Table 1. Data were collected by Project Owlnet volunteers, guided by experts, at all 7 banding stations throughout the study period. Owls were captured during their fall migration using mist nets and audio lures according to standardized protocols (Erdman and Brinker 1997).

We used 60 mm mesh mist nets with a length of 9–12 m. Nets were set in exactly the same location every year, arranged in either a single line, an L-shaped array, or multiple lines separated by a distance of 2–4 m. At the center of the net array we installed an audio lure, broadcasting a male NSWO solicitation call at 80–100 dB. Details of the lure design can be found in Brinker et al. (1997). Banding stations operated from September/October to November/December depending on the site (Table 1). Depending on the site, mist nets were open daily from dusk to midnight/dawn, unless closing early or not opening due to severe weather conditions (consistent snow or rainfall, strong winds $>$30 km/h, or dense fog). During a banding night, all captures after midnight were attributed to the previous banding date.

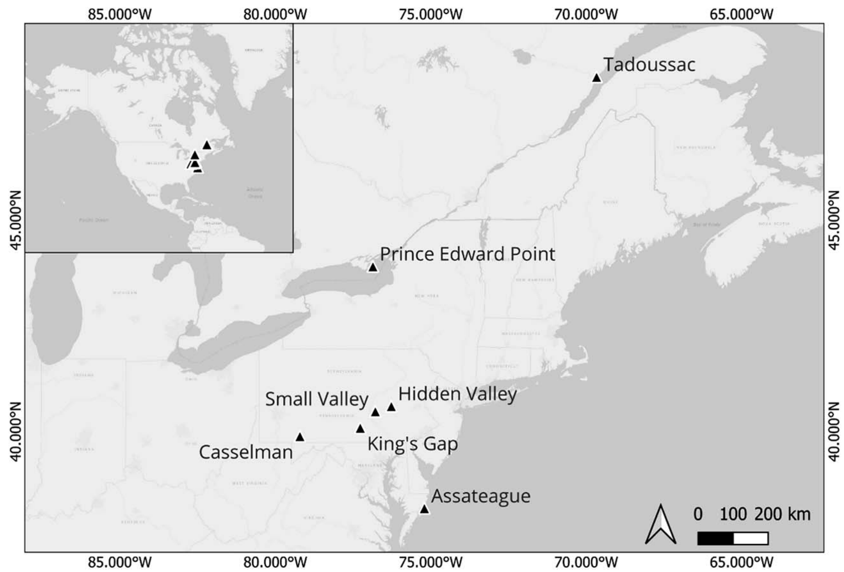

Figure 1. Location of the 7 Northern Saw-whet Owl (*Aegolius acadicus*) banding sites selected for this study.

Statistical analyses

For each site, we calculated median annual passage dates (hereinafter 50% passage date) as the date at which 50% of the total number of NSWOs that were captured on that year and converted those calendar dates to Julian dates. We chose to work with median passage dates because this phenological estimator is less sensitive to sampling effort and population size compared with other estimators such as first appearance dates (Miller-Rushing et al. 2008, Moussus et al. 2010). We ran a linear mixed model with year as a fixed effect and site as a random factor to assess whether the passage date is getting later over time, using R 3.6.3 (R Core Team 2020) and package *lme4* 1.1.21 (Bates et al. 2015). We chose to run a linear mixed model because of the flexible specification of the covariance structure of the model (Knudsen et al. 2007), which is required to investigate if there is a phenological adjustment for the overall geographical range covered here. Secondly, to test for a latitudinal effect in the phenological adjustment, we ran a general linear model with the 50% passage dates as the response variable and an interaction of Year and Latitude as predictor variables.

Climate data were obtained from NOAA National Centers for Environmental information using our study sites (https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/global/time-series). We acquired mean temperature anomalies for the months of September–December (when banding stations operated), with temperature anomalies in respect to the mean temperature over the period 1991–2020 (Fig. 2).

Results

We detected a delay in average passage date of NSWO (slope $= 0.10 \pm 0.05$; $P < 0.05$; $F_{1,147} = 3.92$; $R^2_{\mathrm{GLMM(c)}} = 0.93$) during autumn migration (Fig. 3). Specifically, the 50% passage dates displayed a delay of 0.98 d/decade over the 25-year study period. For the random effect site, the variance among sites is estimated at 223.42 ($\pm$14.95), which is much larger than the estimated residual variance (variation within the same site) of 16.51 ($\pm$4.06). The low estimated residual variance indicates that the model explains most of the variation in the data, with a lot of the variability described by the differences among sites. This is also reflected in the R^2 values of the mixed model ($R^2_{\mathrm{GLMM(c)}} = 0.93$ and $R^2_{\mathrm{GLMM(m)}} = 0.002$): the conditional R^2,

Table 1. Location and years of operation for the 7 Northern Saw-whet Owl (*Aegolius acadicus*) banding sites in eastern North America selected for this study.

Site	Location	Latitude	Longitude	Years of operation	Total number of owls banded
Tadoussac	Québec, Canada	48.1572	−69.6656	1997–2020	3,914
Prince Edward Point	Ontario, Canada	43.9397	−76.8614	2001–2018	12,307
Hidden Valley	Pennsylvania, USA	40.6206	−76.2686	1999–2020	3,668
Small Valley	Pennsylvania, USA	40.4939	−76.7836	2002–2020	2,645
King's Gap	Pennsylvania, USA	40.0922	−77.2683	2001–2020	2,040
Casselman	Pennsylvania, USA	39.8863	−79.2110	1992–2017	3,665
Assateague	Maryland, USA	38.0917	−75.2056	1992–2017	2,282

which is the proportion of the total variance explained through both the fixed and random effects (93%), is remarkably high compared to the marginal R^2, the proportion of the total variance explained by the fixed factor alone (0.2%). We did not detect a latitudinal gradient in the observed delay (interaction Year*Latitude: $P = 0.37$) nor for the main effects Year ($P = 0.27$) and Latitude ($P = 0.45$).

Discussion

Our results suggest that NSWOs are delaying their autumn migration. The observed magnitude (1 d/decade) is similar to what has been measured in diurnal raptors (Van Buskirk 2012, Jaffré et al. 2013, Therrien et al. 2017) and other migrating birds (Lehikoinen et al. 2004, Brisson-Curadeau et al. 2020). Ongoing global climate changes seem to be a potential explanation for the phenomenon. Autumn temperatures have significantly increased in our study area over the last decades and may explain the observed delay in autumn migration as it is thought that short-distance migrants, such as NSWOs, postpone their departure from the breeding grounds when temperatures are higher (Brisson-Curadeau et al. 2020). Future climate scenarios predict milder conditions in northern latitudes (Masson-Delmotte et al. 2021), which can benefit migrants that delay migration from the breeding grounds through the opportunity of having successful second broods (Gordo 2007, Van Buskirk 2012).

The effects of increasing temperatures on NSWO migration phenology are likely indirect, acting through complex food web interactions, and changes in temperatures at various times of the year in addition to data on prey species will be needed to assess the causal mechanism. Moreover, increasing temperatures are only one among several possible hypotheses explaining a delay in migration phenology. Slower migration speeds could explain a delay in autumn migration as for instance unfavorable winds can impact migration speed by forcing birds to reduce flight speed or make stopovers (Therrien et al. 2017, Brisson-Curadeau et al. 2020). Furthermore, abiotic and biotic variables, including precipitation regime (Gordo 2007; Haest et al. 2018, 2019), food availability (Therrien et al. 2017), and/or changes in age-class ratios (Brittain and Jones 2014) could all be at play.

Even though we observed a delay in NSWO median passage dates over time, the marginal R^2 value indicates the effect to be rather small. This is likely because the effect is indirect and because of the noisy nature of our dataset. In addition, it is possible that strong differences between sites mask the overall effect size as the delay might not be present in all sites or can be more pronounced in some sites than others.

For diurnal raptors, the overall delay in autumn migration is coupled with an earlier spring arrival on the breeding grounds, both linked to increasing temperatures, resulting in increased residency time (Tøttrup et al. 2006, Therrien et al. 2017). Not much is known about NSWO spring migration phenology, but it is possible that spring passage dates could be advancing, and that this species also spends more time on the breeding grounds. Preliminary observations of NSWO spring migration suggest a correlation between

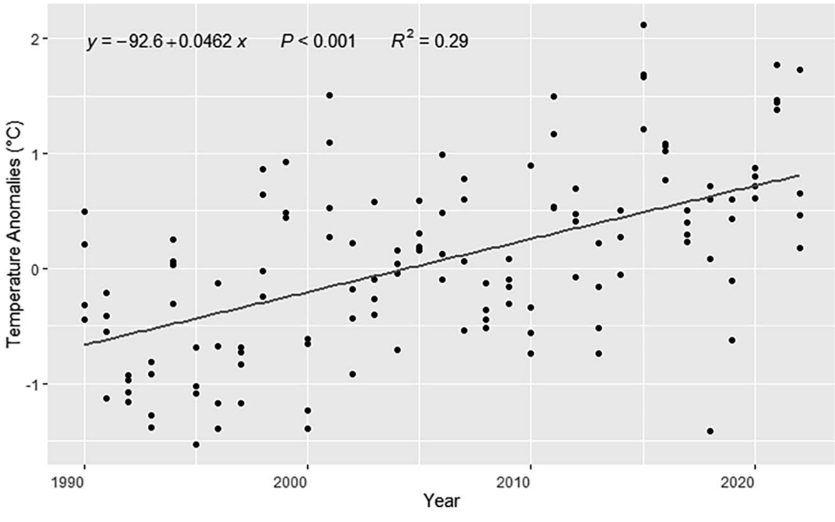

Figure 2. Annual September–December temperature anomalies with respect to the 1991–2020 average for all our study sites. Data obtained from NOAA National Centers for Environmental Information, Climate at a Glance: Global Time Series, retrieved on 15 March 2023 (https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/global/time-series).

the timing of migration and year-to-year variance in temperature and snow cover, with NSWO migrating north earlier in milder years (S. Weidensaul, unpubl. data).

Delayed autumn departure could be beneficial for NSWOs if it allows individuals to produce second broods, or extend the post-breeding period to reach a better condition prior to southward migration (Jenni and Kéry 2003, Mills 2005, Van Buskirk 2012, Brisson-Curadeau et al. 2020, Youngflesh et al. 2021). However, since the recent study of Wall et al. (2020) revealed a negative population trend—and considering that the current delay of only 1 d/decade hardly allows much room for individuals to have a second brooding attempt—it seems unlikely that NSWO produce more second broods. A delayed migration might also impact NSWOs negatively if it would create

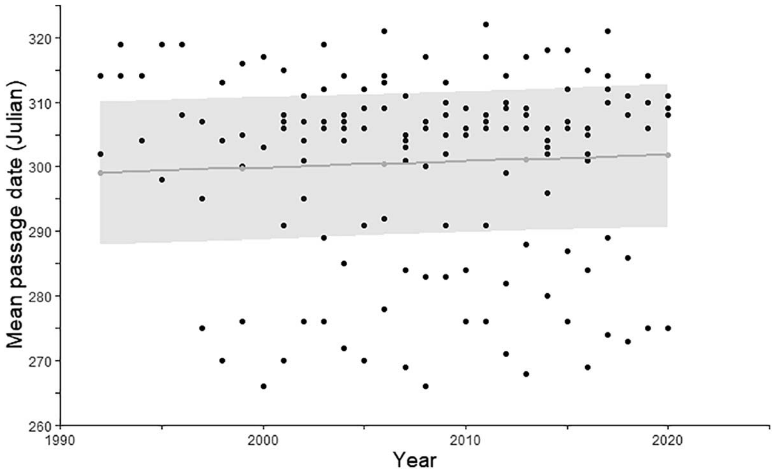

Figure 3. Mixed model estimates of the fixed effect “Year” (gray dots) on the median passage dates of Northern Saw-whet Owls (*Aegolius acadicus*), with 95% confidence interval, plotted on top of the actual data (black dots).

a mismatch with resources and in turn reduce survival during migration and on the wintering grounds (Van Buskirk 2012).

Even though we covered a relatively broad geographical gradient, we did not detect any latitudinal effect in phenological adjustment of autumn migration over time. As all sites are located within the Atlantic Flyway, it is possible that once NSWO start moving, they keep moving at the same rate to reach lower latitudes and so there is simply no latitudinal effect detectable within our study system. More power could be obtained by adding sites to the analysis for underrepresented latitudes as well as elsewhere outside of the Atlantic Flyway.

Our results show that changes in autumn migration phenology occur in NSWO in a manner similar to diurnal raptors, and might be related to a changing climate. More research is needed to determine if similar changes are occurring in the migration phenology of other owl species. Future research should specifically test for the effect of climatic variables and investigate if the phenological adjustment could trigger population dynamic trends. Moreover, studies should assess if phenological changes differ between juvenile and adult NSWOs.

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