The Wilson Journal of Ornithology 129(2):360–364, 2017

Increase in Numbers and Potential Phenological Adjustment of Ruby-throated Hummingbirds (*Archilochus colubris*) during Autumn Migration at Hawk Mountain Sanctuary, Eastern Pennsylvania, 1990–2014

Jennifer C. Probst,[1] Jean-François Therrien,[1,2] Laurie J. Goodrich,[1] and Keith L. Bildstein[1]

ABSTRACT.—Global change can affect several aspects of bird biology, including population size and migration timing. We used count data collected during 25 years (1990–2014) at Hawk Mountain Sanctuary, a raptor migration watch-site in eastern Pennsylvania, to investigate population changes in Ruby-throated Hummingbirds (*Archilochus colubris*) and the timing of their autumn migration, in light of ongoing climate change. Hummingbird numbers increased significantly from 1990–2014. The first 5%-, 50%-, 95%- and average passage dates of hummingbirds over this time indicated an earlier passage, with the first 5% passage-date shifting earlier significantly. Passage duration (number of days between 5% and 95% of the flight) remained relatively constant from 1990–2014. In light of similar shifts in timing of spring passage of this species, our results suggest that Ruby-throated Hummingbirds may be shifting the timing of their migratory cycle. *Received 23 January 2016. Accepted 24 July 2016.*

Key words: *Archilochus colubris*, autumn migration, migration counts, Ruby-throated Hummingbird, timing.

As temperatures and precipitation regimes are altered worldwide (Hartmann et al. 2013), many biological aspects of living organisms are influenced. Indeed, many plants and insects have been recorded emerging earlier from winter dormancy, with higher temperatures allowing some plants to flower earlier (Sparks et al. 2000, Fitter and Fitter 2002). Impacts of climate change also have been shown to delay but also potentially hasten autumn senescence in several plant species (e.g., Estiarte and Peñuelas 2015), phenomena likely to affect food availability in bird populations. In response to those ongoing changes, we are witnessing changes in distribution as well as population size for several bird species across various taxa (Møller et al. 2008). Many bird species have also adjusted the timing of key events such as migration (Parmesan and Yohe 2003, Root et al. 2003, Thackeray et al. 2010, Charmantier and Gienapp 2014). Adjustments in migration phenology seem especially noticeable for species feeding on resources such as plants and insects.

Among the growing number of studies looking at migration phenology adjustments, autumn seems to have been neglected, and several authors are now advocating for a better understanding of how species might be affected by global changes during that particular season (Gallinat et al. 2015). Even with the limited knowledge available on phenological adjustments, ongoing climate change has been shown to advance as well as to delay autumn migration in birds (Jenni and Kéry 2003, Van Buskirk et al. 2009). Such phenological changes are likely to affect several aspects of the birds' biology including body condition, survival, and reproductive success.

Ruby-throated Hummingbirds (*Archilochus colubris*) migrate from breeding grounds in eastern Canada to the Gulf of Mexico to wintering grounds in southern Florida, Mexico, Central America, and the Caribbean Islands (Weidensaul et al. 2013). During migration monitoring in autumn, Ruby-throated Hummingbirds are counted as they pass Hawk Mountain (Willimont et al. 1988), in the central Appalachian Mountains of southeastern Pennsylvania (see Therrien et al. 2012 for details). This provides a useful source of information regarding population changes for Ruby-throated Hummingbirds in eastern North America, complementing other databases such as Breeding Bird Surveys. Because of low detectability of Ruby-throated Hummingbirds, it is difficult to determine their population trends using breeding surveys (Sauer et al. 2014), but migration counts

[1] Hawk Mountain Sanctuary, Acopian Center for Conservation Learning, 410 Summer Valley Road, Orwigsburg, PA 17961, USA.

[2] Corresponding author; e-mail: therrien@hawkmountain.org

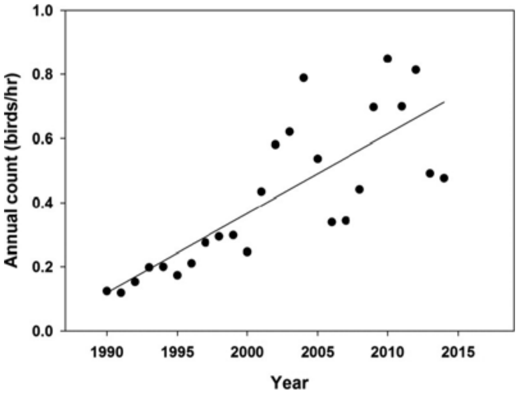

FIG. 1. Annual counts of Ruby-throated Hummingbirds at Hawk Mountain Sanctuary, Pennsylvania, 1990–2014.

at individual watch sites have been demonstrated to reflect population changes in sparse and inconspicuous species (e.g., Bednarz et al. 1990, Hill and Hagan 1991, Dunn and Hussell 1995, Farmer et al. 2010). Moreover, this monitoring allows us to assess how the timing of the hummingbird autumn flight has changed during a 25-year period.

METHODS

Study Area.—Counts were made at Hawk Mountain Sanctuary's North Lookout, on the Kittatinny Ridge in the central Appalachians of eastern Pennsylvania (40° N, 75° W; Willimont et al. 1988, Bednarz et al. 1990).

Counts.—Counts were made daily, weather permitting, from August 15 to December 15, annually starting in 1990. Daily counts typically began at 08:00 hrs and ended at 17:00 hrs, Eastern Time. Count protocol and daily observation duration have been consistent throughout the study period (for more details on the procedure, see Therrien et al. 2012). The number of migrating hummingbirds per day was recorded by one or two experienced counters. No classifications regarding age and sex of hummingbirds were made.

Statistical Analyses.—Similarly to most bird migration studies using a number of individuals recorded per unit of time (e.g., Bednarz et al. 1990, Hill and Hagan 1991, Allen et al. 1996, Farmer et al. 2007), we computed mean annual passage rates by dividing the total number of individual hummingbirds counted each year by the number of hrs spent at the lookout from 15 August to 23 October, the period when the hummingbird flight occurred. We evaluated the population trend for 25 years (1990–2014). We used annual counts of Ruby-throated Hummingbirds to evaluate the timing of passage. Although first appearance dates are still frequently used as indexes of phenological variation, it has been shown that percentile values are more reliable (Moussus et al. 2010). We thus calculated dates when the first 5%, 50% and 95% of the individuals passed annually. We also determined the average passage date for each year and an average passage date over all years. We defined the passage window as the length (in days) of the period of passage per year between the 5%- and 95%- passage dates. We calculated all trends using linear regressions in SigmaPlot software (version 11.0; Systat Software Inc., San Jose, CA, USA).

RESULTS

A total of 6,766 individuals were counted during the study period. Annual counts ranged from 69 individuals in 1991 to 574 individuals in 2012. Mean annual passage rates of Ruby-throated Hummingbirds increased between 1990 and 2014 (slope = 0.02, $P < 0.001$, $r^2 = 0.63$; Fig. 1), averaging 8% annually.

The 5%-passage date exhibited a significant trend for earlier passage with an advancement of 1.3 days per decade (slope = –0.13, $P = 0.041$, $r^2 = 0.17$; Fig. 2a). The timing of the 95%-passage date also exhibited a trend for an earlier passage, although this was not significant (slope = –0.19, $P = 0.10$, $r^2 = 0.11$; Fig. 2b). The median (slope = –0.03, $P = 0.63$, $r^2 = 0.01$) and average passage dates (slope = –0.07, $P = 0.19$, $r^2 = 0.07$) both tend toward an earlier passage, although neither varied significantly over time. Average passage date over all years was 2 September ± 1.9 days. The passage window remained unchanged throughout the study period (average = 27.8 ± 5.1 days, slope = –0.06, $P = 0.68$, $r^2 = 0.01$) but shifted in timing from 21 August through 19 September in 1990 to 18 August through 14 September in 2014.

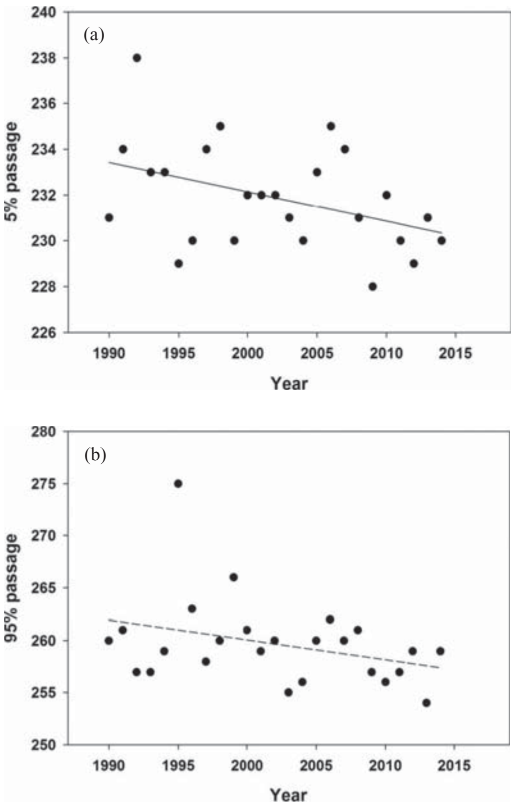

FIG. 2. Timing of Ruby-throated Hummingbirds during autumn migration at Hawk Mountain Sanctuary, Pennsylvania, from 1990–2014 showing the day of the year (y-axis) for (a) first 5%-passage dates and (b) first 95%-passage dates.

DISCUSSION

The increase in numbers of Ruby-throated Hummingbirds we observed agrees with other monitoring schemes including the Breeding Bird Survey, which have seen a 2%-increase annually in the populations between 1966 and 2013 in New England and the mid-Arctic (Sauer et al. 2014), and the Christmas Bird Counts, which also show a steady increase in numbers from 1990–2014 across the United States (National Audubon Society 2010).

Our results suggest that passage dates of hummingbirds in autumn might have been advancing during the 1990–2014 period. Both observations, an apparent increase in numbers, and an apparent earlier autumn migratory passage in Ruby-throated Hummingbirds, may be linked. An increase in the number of migrants from the northern regions, as suggested by eBird (eBird 2012) and the Breeding Bird Surveys (Sauer et al. 2014), could explain, in part, the apparent observed advance in migration timing that we observed in the present study, especially evident for the date at which 5% of the individuals have passed. In most species, populations from the latitudinal limit of the species' range are known to migrate earlier in autumn than populations from lower latitudes (e.g., Fransson 1995, Kelly et al. 2002). The observed pattern could thus be the result of an increase in numbers, and especially in the northern portion of the species' breeding range.

In Ruby-throated Hummingbirds, adult males apparently precede females in both spring and autumn migrations while juveniles tend to lag behind, at least during autumn (Robinson et al. 1996). Although speculative, adult males from the northern portion of this species' range could thus contribute a large proportion of the early migrants seen during autumn migration and could be in part responsible for the advancement observed in the 5% passage date. By migrating somewhat later, adult females and especially juveniles would contribute in keeping the median and average passage dates unchanged. Assessing sex, age, and origin of migrating hummingbirds remains a challenge, and we did not have that information for our analyses. More research is needed to assess if early migrants in Ruby-throated Hummingbirds are over-represented by adult males coming from the northern portion of the species' range.

A previous study has suggested that the external cue for autumn migration in hummingbirds is the seasonal decline in the length of daylight (Williamson 2001). This cue is obviously not affected by climate change. However, food abundance, which is likely connected with the length of daylight could act as an additional cue triggering autumn migration. Migration of Ruby-throated Hummingbirds in autumn was found to be nearly synchronous with peak flowering of jewelweed (*Impatiens capensis*; Bertin 1982, Willimont et al. 1988), one of the major food sources of Ruby-throated Hummingbirds (Weidensaul et al. 2013). And this cue is likely to be affected by climate change, as many plants respond to increasing temperatures with earlier flowering onset (Sparks et al. 2000, Fitter and Fitter 2002). This phenomenon could result in a temporal shift in the

//titan/Production/w/wils/live_jobs/wils-129/wils-129-02/tail-ins/wils-129-02-13_30.3d ■ 2 May 2017 ■ 7:23 pm ■ Allen Press, Inc. Page 362

availability of food sources to which hummingbirds could be adapting by shifting the timing of their migrations. Courter et al. (2013), for example, reported an advancement in spring migration timing of Ruby-throated Hummingbirds over all latitudes in North America which also corresponds with warmer winters and springs in the region.

As both spring and autumn migration show signs of advancement and the autumn passage window remained stable over the observed period, it is possible that the annual cycle of Ruby-throated Hummingbirds is shifting. Additional research is needed to assess the underlying causes.

ACKNOWLEDGMENTS

We thank Hawk Mountain Sanctuary scientists, educators, and volunteers for collecting and compiling the data set. J. C. Probst was a conservation science trainee at Hawk Mountain Sanctuary in autumn 2015 when this paper was written. This is Hawk Mountain Sanctuary contribution to conservation science number 277.

LITERATURE CITED

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

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

Bertin, R. I. 1982. The Ruby-throated Hummingbird and its major food plants: ranges, flowering phenology, and migration. Canadian Journal of Zoology 60:210–219.

Charmantier, A. and P. Gienapp. 2014. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. Evolutionary Applications 7:15–28.

Courter, J. R., R. J. Johnson, W. C. Bridges, and K. G. Hubbard. 2013. Assessing migration of Ruby-throated Hummingbirds (*Archilochus colubris*) at broad spatial and temporal scales. Auk 130:107–117.

Dunn, E. H. and D. J. T. Hussell. 1995. Using migration counts to monitor landbird populations: review and evaluation of current status. Current Ornithology 12:43–88.

eBird. 2012. eBird: an online database of bird distribution and abundance. eBird, Cornell Lab of Ornithology, Ithaca, New York, USA. www.ebird.org (accessed 10 Nov 2015).

Estiarte, M. and J. Peñuelas. 2015. Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: effects on nutrient proficiency. Global Change Biology 21:1,005–1,017.

Farmer, C. J., D. J. T. Hussell, and D. Mizrahi. 2007. Detecting population trends in migratory birds of prey. Auk 124:1,047–1,062.

Farmer, C. J., K. Safi, D. R. Barber, I. Newton, M. Martell, and K. L. Bildstein. 2010. Efficacy of migration counts for monitoring continental populations of raptors: an example using the Osprey (*Pandion haliaetus*). Auk 127:863–870.

Fitter, A. H. and R. S. R. Fitter. 2002. Rapid changes in flowering time in British plants. Science 296:1,689–1,691.

Fransson, T. 1995. Timing and speed of migration in north and west European populations of *Sylvia* warblers. Journal of Avian Biology 26:39–48.

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

Hartmann, D. L., A. M. G. Klein Tank, M. Rusticucci, L. V. Alexander, S. Brönnimann, Y. A.-R. Charabi, F. J. Dentener, E. J. Dlugokencky, D. R. Easterling, A. Kaplan, B. J. Soden, P. W. Thorne, M. Wild, and P. M. Zhai. 2013. Observations: atmosphere and surface. Pages 159–254 *in* Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change (T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, Editors). Cambridge University Press, Cambridge, United Kingdom.

Hill, N. P. and J. M. Hagan III. 1991. Population trends of some northeastern North American landbirds: a half-century of data. Wilson Bulletin 103:165–182.

Jenni, L. and M. Kéry. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. Proceedings of the Royal Society of London, Series B 270:1,467–1,471.

Kelly, J. F., V. Atudorei, Z. D. Sharp, and D. M. Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216–221.

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences of the USA 105:16,195–16,200.

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

National Audubon Society. 2010. The Christmas Bird Count historical results. www.christmasbirdcount.org (accessed 20 Oct 2015).

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

Robinson, T. R., R. R. Sargent, and M. B. Sargent. 1996. Ruby-throated Hummingbird (*Archilochus colubris*). The birds of North America. Number 204.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski Jr., and W. A. Link. 2014. The North American Breeding Bird Survey, results and analysis 1966–2013. Version 01.30.2015. USDI, Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Sparks, T. H., E. P. Jeffree, and C. E. Jeffree. 2000. An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. International Journal of Biometeorology 44:82–87.

Thackeray, S. J., T. H. Sparks, M. Frederiksen, S. Burthe, P. J. Bacon, J. R. Bell, M. S. Botham, T. M. Brereton, P. W. Bright, L. Carvalho, T. Clutton-Brock, A. Dawson, M. Edwards, J. M. Elliott, R. Harrington, D. Johns, I. D. Jones, J. T. Jones, D. I. Leech, D. B. Roy, W. A. Scott, M. Smith, R. J. Smithers, I. J. Winfield, and S. Wanless. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology 16:3,304–3,313.

Therrien, J.-F., L. J. Goodrich, D. R. Barber, and K. L. Bildstein. 2012. A long-term database on raptor migration at Hawk Mountain Sanctuary, northeastern United States. Ecology 93:1,979.

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.

Weidensaul, S., T. R. Robinson, R. R. Sargent, and M. B. Sargent. 2013. Ruby-throated Hummingbird (*Archilochus colubris*). The birds of North America online. Number 204.

Williamson, S. L. 2001. Natural history of North American hummingbirds. Pages 8–32 *in* A field guide to hummingbirds of North America. Houghton Mifflin Co., New York, USA.

Willimont, L. A., S. E. Senner, and L. J. Goodrich. 1988. Fall migration of Ruby-throated Hummingbirds in the northeastern United States. Wilson Bulletin 100:482–488.

Queries for wils-129-02-13_30

This manuscript/text has been typeset from the submitted material. Please check this proof carefully to make sure there have been no font conversion errors or inadvertent formatting errors. Allen Press.