

PHENOLOGICAL ASYNCHRONY IN POPULATIONS OF MIGRATORY BIRDS AS A CONSEQUENCE OF CLIMATE CHANGE:

A Literature Review



Wildlife Conservation Society
Adirondack Program Technical Paper No. 6
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January 2015

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Suggested Citation

Technical Paper

Rubenstein, M.A., and M.J. Glennon. 2015. Phenological asynchrony in populations of migratory birds as a consequence of climate change: a literature review. Wildlife Conservation Society, Adirondack Program Technical Paper #6.

Photo credit: Lawrence Master

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ACKNOWLEDGEMENTS

This project was made possible through support provided by Joseph and Joan Cullman Conservation Grants Program of Northern New York Audubon and the Yale University School of Forestry and Environmental Studies. The content and opinions expressed herein are those of the authors and do not necessarily reflect the position or the policy of Northern New York Audubon or the School of Forestry and Environmental Studies, and no official endorsement should be inferred.

FOREWORD

The Wildlife Conservation Society's (WCS) Adirondack Program has been working since 2003 to understand the status and distribution of lowland boreal birds in the Adirondack Park. The Adirondack Park represents the southern range extent for several species of boreal forest birds within eastern North America. The habitats of these boreal specialists are thought to be particularly vulnerable to climate change, especially in the Adirondacks where they represent disjunct and isolated fragments of the "true boreal" to the north. In a recent publication, I explored occupancy patterns over time for 8 species (black-backed woodpecker, boreal chickadee, gray jay, Lincoln's sparrow, olive-sided flycatcher, palm warbler, rusty blackbird, yellow-bellied flycatcher) in lowland boreal forest wetlands (Glennon 2014). I found that dynamic patterns of species occurrence in boreal wetlands indicated that these birds function as metapopulations in the Adirondacks and that area and connectedness of their wetland habitats, as well as nearby human infrastructure, are controlling factors, with birds much more likely to experience local extinction from smaller, isolated wetlands that are in close proximity to development. The paper notes declining occupancy trends for several target species, and data collected since the conclusion of the study indicate additional species declines (Glennon, unpublished data); palm warbler appears to be the only species increasing in the Adirondack landscape. For some, these declines are relatively minor, but for others they are steep and troubling. Furthermore, they do not appear to match predictions of vulnerability to climate change according to several vulnerability indices which predict that resident birds should be less vulnerable than the migrant species targets. Declines for 2 resident species – black-backed woodpecker and gray jay – are of similar or greater magnitude than several migratory species.

We expect these birds to be sensitive to climate change because of their association with a vulnerable habitat type (Hilke and Galbraith 2013). Although the evidence for northward or upward shifts in occupancy patterns was not clear (Glennon 2014), we expect that climate change will influence these species and serve to exacerbate other stressors they may face in the park. There are several characteristics shared among these target species that may make them vulnerable to climate change, including dependence on a boreal habitat type expected to decline as a result of warming temperatures (Pastor et al. 1998), dependence on a habitat type with important hydrological regimes that may change, a restricted diet for some species (i.e., insectivores vs more generalist omnivores), and potential phenological mismatch of insect/plant prey availability and timing of breeding (Parmesan and Yohe 2003). It is thought that resident species may be less sensitive to such mismatches because they are always present and better able to track available resources. The problem of mismatch may not be prevalent in all habitats because habitats likely differ in the penalties of being late depending on the seasonality of food availability (Both et al. 2009b). Though the species we are monitoring are tied to boreal habitats in general, some of them are more closely associated with forest habitats and others more closely associated with open peatlands. Similarly, several target species are insectivores (e.g., olive-sided flycatcher) while others make use of a more varied diet (i.e., gray jay, boreal chickadee). These differences in habitat and food associations may moderate the potential negative consequences of altered seasonality in food resources.

We wished to investigate the potential for phenological mismatch between birds and their food sources as it relates to expected and observed climate changes in the park and observed declines among these species. Through a supporting grant from Northern New York Audubon and the Joseph and Joan Cullman Foundation, we partnered with Madeleine Rubenstein from the graduate program of the Yale School of Forestry and Environmental Studies to help us provide a

foundation for potential future research. Madeleine worked with us in 2014 to complete a literature review of phenological asynchrony in migratory species and to document cases of phenological mismatch in avian communities and the life history characteristics of species in which such mismatches have been demonstrated. This report is the result of her extensive review.

Michale Glennon, Ph.D.
Science Director
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ABOUT THE AUTHORS

As a Master's student at the Yale University School of Forestry and Environmental Studies, Madeleine Rubenstein has used both coursework and independent research to explore the application of terrestrial ecosystem ecology to wildlife conservation. Through her Master's research project, she investigated the links between community structure and ecosystem function, using the response of wood-rot fungal communities to climate change as a study system. While at Yale, her studies emphasized statistical ecology, quantitative modeling of ecological systems, and the integration of ecological research into conservation management. During her work with WCS and other projects, she aims to use rigorous, policy-relevant natural science research to help inform the management and conservation of wildlife and wild landscapes. Before coming to Yale, she worked with the Smithsonian Environmental Research Center to research the distribution and conservation status of native orchids in the mid-Atlantic, and volunteered with a community conservation project in Guassa, Ethiopia. She currently lives in New Haven, CT with her husband, Joseph.

As the Science Director for WCS's Adirondack Program, Dr. Michale Glennon serves a leading role in the ecological research conducted in the Adirondacks. Her research interests lie primarily at the intersection between land use management and ecological integrity, with a number of projects ranging from the impacts of low density, exurban development on wildlife to the potential changes to Adirondack lowland boreal communities resulting from climate change. Michale joined WCS in 2003 after completing a Ph.D. at the State University of New York, College of Environmental Science and Forestry where she explored the effects of land use management on bird and small mammal communities in the Adirondacks. She has also worked on the potential impacts of ski area development on Bicknell's thrush, a Neotropical migrant of high conservation priority in the east, and on a project to understand the rapidly expanding moose population in the Adirondacks and its relatedness to nearby populations in neighboring states and provinces. In addition to her exurban development work, Michale is currently working to understand the potential impacts of recreation on wildlife communities. She serves on advisory committees for the Shingle Shanty Preserve and Research Station, the Adirondack Park Agency, the New York State Department of Environmental Conservation, the Adirondack All-Taxa Biodiversity Inventory, and the Paul Smiths College Fisheries and Wildlife Science Program. Dr. Glennon is widely published and holds an adjunct position at SUNY-ESF. She grew up in Lake Placid, NY, in the Adirondack Park, graduated from Lake Placid High School and lives in Ray Brook with her husband, Scott van Laer – a New York State Forest Ranger, children Phoebe and Clancy, one cat, and three horses.

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INTRODUCTION

Temperature is an important determining factor in the phenology of many organisms, including in the migration and reproduction of birds. Phenological events are therefore likely to change in response to climate change, and differing responses across species, geographic regions, and trophic levels are likely. Phenological mismatch, where previously synchronized events become desynchronized, may result from such unequal responses to warming (Schwartzberg et al., 2014). The degree to which a species may advance or delay a phenological event depends on several factors, including phenotypic plasticity; the influence of other non-temperature related factors (i.e., photoperiod); and the penalty of asynchrony. This literature review presents an overview of the state of knowledge of phenological asynchrony in migratory birds, with a focus on birds that breed in North America and Europe, and a summary of documented cases of phenological asynchrony.

Theory and Overview

Phenological asynchrony in migratory birds can be understood as the unequal phenological response of birds and their food sources to temperature change (Visser, Holleman, & Gienapp, 2006). It is unlikely that all levels of the food chain will exhibit similar phenological responses to warming, leading previously synchronized events to fall out of step (Visser, Both, & Lambrechts, 2004). Phenological mismatch has the potential to decrease fitness: if birds are unable to advance their reproduction sufficiently to match the phenology of their food sources, their reproductive success will suffer as a result. The severity of the threat posed by phenological asynchrony depends on several factors, including the difference between birds' phenological responses and that of their food source; migratory distance; temperature conditions along the migration route; and the seasonality of food availability in breeding-ground habitat (Both et al, 2009b; Hüppop & Winkel, 2006; Visser, Both, & Lambrechts, 2004).

Migratory birds are generally thought to time their migration based primarily on endogenous cues, such as photoperiod, and other climatic factors not directly related to the local temperature regime of the breeding ground (i.e., North Atlantic Oscillation or Southern Oscillation; Wilson (2007) and Both & Visser (2001)). Since factors such as photoperiod are unrelated to climate change, these endogenous signals may limit birds' ability to adjust their migration in the face of rising temperature and advancing phenology of lower trophic levels (i.e., trees and insects).

As lower trophic levels on the breeding grounds advance their phenology, avian communities will face increasingly unfavorable conditions for their reproduction if they remain static in the timing of their arrival and breeding. Scientific literature on the subject has not yet produced a clear assessment of how static these phenological events truly are: many studies reviewed below argue that birds are able to respond, at least somewhat, to advances in their food source's phenology and that they therefore do not experience any reduced fitness as a result of phenological mismatch. In addition, several papers find evidence that while endogenous cues such as photoperiod are important for timing of bird migration, birds do also respond directly to temperature, especially along the migration corridor (Visser, Both, & Lambrechts, 2004; Ahola et al., 2004; Both and te Marvelde, 2007). While these studies would suggest that phenological asynchrony is therefore not a significant threat to migratory birds in a warming climate, other studies have linked declining population levels to an increasing mismatch between the phenology of migratory birds and their food sources.

Restrictions on Phenological Adaptation

Spatial Variation

Spatial unevenness in temperature rise is a primary limitation on birds' ability to adapt their phenological events sufficiently to mirror changes in their food sources. Temperature changes in breeding grounds may not be reflected in wintering grounds, meaning that long-distance migrants cannot be informed by relevant conditions before they begin migration. Several studies found that long-distance migrants were less likely to sufficiently advance their reproductive phenology than short-distance migrants or resident birds; in large part, this is likely due to the fact that the warming experienced in breeding grounds is not the same as the warming experienced in wintering grounds. Both and te Marvelde (2007) find that the pied flycatcher (a long-distance migrant to Europe) advanced its lay date by only 1.57 days for each 1°C temperature rise between 1980 and 2004, while the European starling (a short-distance migrant) advanced its lay date by 2.03 days. This uneven warming across the globe between breeding and wintering ground is especially pronounced at high latitudes. Because ecosystems at high latitudes have experienced particularly large increases in spring temperatures, Dunn and Winkler (2010) propose that species which breed at these high latitudes (especially above 50°N) may be more sensitive to phenological asynchrony than other similar species which breed in more southerly grounds.

In addition, uneven warming along the migratory corridor means that birds do not experience consistent warming trends as they move from wintering to breeding grounds. This can lead to potential miscalculations as the birds work their way towards breeding habitat (Both & te Marvelde, 2007). Hüppop and Winkel (2006) found that between 1960 and 2002, points along the migration route of pied flycatchers have experienced less warming than their breeding grounds, effectively resulting in a "climatic barrier" that prevents birds from sufficiently advancing their arrival. Similarly, Strobe (2003) found that eight species of wood warblers experience substantial spatial variation in warming along their migration corridor: while spring has arrived earlier between 1960-2002 in Minnesota, points in Illinois have experienced the opposite trend. Strobe argues that this prevents migratory birds from experiencing strongly directional pressure in favor of earlier migration, and narrows the window of available time to migrate, refuel, and breed by up to 20 days.

Temporal Variation

In addition to variation in warming across space, there can be substantial temporal variation within and across years. In both breeding and wintering grounds, there can be substantial inter-annual temperature variation. Townsend et al. (2013) found that years with warmer springs were associated with earlier breeding dates for black-throated blue warblers, suggesting that this yearly variation in warming requires regular adaptation from these migratory birds. In this particular case, however, the authors found that selection for earlier breeders was not stronger in warmer springs, suggesting that this population had been able to adequately adjust their mean lay date in order to match inter-annual variations in warming.

In addition to variation between years, there can be substantial variation in warming within a single season. The degree of temperature rise above average can change significantly over the course of several months: in some years, the majority of warming occurs early in the season, while in other years the majority of warming occurs later in the spring. If warming is concentrated in the later part of spring, birds may not sufficiently advance egg laying and be unable to track advances in food sources (Both & Visser, 2001). Because the gestation period for birds is relatively inflexible, it would be impossible for birds to rapidly respond to a late spring increase in temperatures. Their insect food sources, however, are able to rapidly adjust to localized temperature changes, potentially resulting in asynchrony (Both et al., 2009a).



Impacts of Phenological Asynchrony

Phenological asynchrony in response to warming is expected to have a variety of impacts on individual bird populations; interspecific interactions between bird species; and trophic dynamics between birds, their predators, and their food sources.

Individual Populations

The most direct impact of phenological asynchrony is likely to be a decline in population levels or reproductive success due to mismatch in timing between bird arrival and/or reproduction and food sources. Both et al. (2009b) found that warming-induced asynchrony contributed to a significant decline in populations of forest-dwelling long-distance migratory birds in the Netherlands. The authors hypothesized that long distance migrants are more susceptible to phenological asynchrony because the timing of their migration is less informed by local conditions at breeding sites; and that the most significant effects will be for bird species occupying highly seasonal habitats with narrow peaks in food availability (i.e. deciduous forests) due to the severe penalty for late arrival. Indeed, the authors found that populations of forest dwelling, long-distance migrants declined by 38%, while neither residents nor short-distance migrants

experienced population decline. They find that declines in habitat quality cannot explain declines in populations of migratory birds, since resident populations did not decline. In addition, they found that migrants to less seasonal habitats with less pronounced and broader food peaks (i.e. marshes and coniferous forests) declined less than migrants to more seasonal habitats with narrower food peaks (i.e. deciduous forests).

A larger study of more than 100 species of migratory European birds found that species that had failed to advance the timing of their spring migration experienced a greater population decline than species that had significantly advanced their migration (Moller, Rubolini, & Lehikoinen, 2008). Indeed, between the period 1990-2000, advancement in spring migration was the only significant predictor of whether populations declined, remained stable, or increased. Breeding habitat type, breeding latitude, and wintering habitat were not significant predictors of population decline during the 1990-2000 period, although these variables were significant predictors during 1970-1990. This implies that the climate-induced effects of phenological mismatch have recently grown more prominent.

Reed et al. (2013) provide an interesting counter example to the effect that phenological mismatch can have on a single population of migratory birds. In a population of great tits in the Netherlands, the authors found that climate change had indeed led to phenological mismatch between the birds and their primary food source, caterpillars. For each 1°C rise, the mismatch grew by almost 3 days and resulted in increasing directional selection for earlier laying dates. Although it was clear that females were not adequately advancing their reproduction to track changes in caterpillar phenology, this did not result in any measurable population decline. In fact, the magnitude of phenological mismatch in any given year was not a statistically significant predictor of population growth. The authors propose that this could be due to the density dependence of recruitment: because juvenile survival is strongly density dependent, a low number of fledgling survivors in strongly mismatched years will not necessarily result in fewer successful recruits the next year as compared to highly successful fledgling years. This effect of density-dependent buffering may explain why certain populations do not suffer ill effects of phenological asynchrony, even when the mismatch is strong.

Interspecific Interactions

Ahola et al. (2007) found that changes in bird arrival dates contributed to altered resource competition dynamics between resident and migratory birds. Using data from 1953-2005, the authors studied nest-hole competition between the great tit (a resident species over most of its range in Europe) and pied flycatchers (a long-distance migrant). The authors quantified competition dynamics by measuring the number of successful takeovers of great tit nests by pied flycatchers, and number of unsuccessful takeovers that result in pied flycatcher death. The study finds that as the interval between the laying dates of these two species decreases, fatal competition increases. While the authors did not observe any significant trend in laying date over the study period, inter-annual variation in the interspecific laying date interval proved to be a significant predictor of fatal nest takeover attempts by pied flycatchers. The authors conclude that warming-induced phenological changes have the potential to alter the competitive balance between residents and migrants in avian communities.

Schaefer et al (2006) studied the breeding period of two similar migratory birds, the reed warbler and great reed warbler, in northern Bavaria from 1973-2003. The study found that although these species have similar life history characteristics, the reed warbler advanced its breeding season by 15 days, while the great reed warbler did not significantly change its phenology. The authors propose that the observed changes in reed warbler breeding phenology is due to their greater

reliance on the growth of marsh reeds, in which it conceals its nest; an advance in reed growth therefore allows the reed warbler to advance its nesting. The great reed warbler, on the other hand, does not rely on reed growth for nest concealment, and is therefore less dependent on the phenology of reeds. Reed warbler breeding is affected by population size of the great reed warbler: a decline in great reed warbler population appeared to result in competitive release, allowing reed warblers to expand in number and to lengthen their breeding season. These results serve as another example of how unequal phenological response to temperature changes can alter intraspecific dynamics, including competition.



Trophic Interactions

Several studies have found that different trophic levels show different phenological responses to temperature rise, with lower trophic levels (i.e., plants, insects) generally demonstrating greater adaptability. Marra et al (2005) find that while lilac budburst had advanced by 3.2 days per 1°C temperature rise, few species of the 43 neotropical migratory birds surveyed in their study demonstrated any advances.

Both et al. (2009a) studied differing phenological responses to rising temperatures across four trophic groups (trees, herbivorous insects, insectivorous passerines, and avian predators) and found that consumer responses are consistently weaker than that of their food sources. The authors propose that this may be explained by relative costs and benefits of phenological response: lower trophic levels experience a greater benefit by advancing their phenology if their predators do not, because they can escape predation. Consumers in higher trophic levels, however, generally rely on diverse food sources and so therefore do not experience as severe a penalty for mistimed phenology. In addition, differing ability to time gestation in response to rapid changes in temperature can explain some of this differing response: caterpillars readily respond to

temperature change, whereas passerines and the avian predator spend 20+ and 50+ days in gestation, respectively. This means that the avian predator is significantly less flexible in the timing of its reproduction and less able to respond quickly to local changes in temperature than passerines or insects. By demonstrating the effects of phenological asynchrony on trophic interactions, this study in particular highlighted the most significant aspect of climate change's impact on phenology—changes to the timing and strength of trophic dynamics.

Vulnerable Species

Migratory Distance

Long-distance migrants are thought to be more vulnerable to phenological mismatch, given that their wintering grounds likely do not experience the same warming as breeding grounds (Both et al., 2009b). Most papers reviewed here present evidence that long-distance migrants are more vulnerable than short-distance migrants or residents because of the relatively inflexible timing of their arrival. Generally, this is demonstrated by a smaller advance in arrival date by long-distance migrants than by short-distance migrants, or a greater decline in populations of long-distance migrants than short-distance migrants (see (Both & te Marvelde, 2007; Both et al., 2009b; Butler, 2003; Miller-Rushing et al., 2008). However, Jones and Cresswell (2010) suggest that long-distance migrants may simply be more vulnerable to population decline because they face environmental change or potential habitat degradation in both wintering and breeding grounds. Jonzen et al. (2006) found that long-distance migrants to Scandinavia in fact advanced their arrival date by *more* than short-distance migrants between 1980-2004. This stands in contrast to the majority of findings presented here, which collectively suggest that long-distance migrants are more vulnerable to phenological asynchrony.

Diet: Diversity and Seasonality of Food Source

Another important factor is the seasonality of the bird's habitat and food sources. Migratory birds dependent on habitats with a limited, short peak in food supply (i.e. deciduous forests) are likely more vulnerable to phenological mismatch than birds in less seasonal habitats (i.e., coniferous forests or marshes). For birds arriving to seasonal habitats, the cost of late arrival is high, while birds arriving to less seasonal habitats experience a broader peak in food supply and therefore do not face a heavy "penalty" for late arrival. This would logically make birds breeding in seasonal habitats more vulnerable to phenological mismatch, unless they demonstrate a greater responsiveness to temperature rise by advancing their arrival or breeding date (Both et al., 2009b). Indeed, Wilson (2012) finds that birds relying on food sources with a short, narrow peak (including leaf-gleaners) showed the largest advance in arrival date when compared to other species dependent on less seasonal food sources. Visser, Both, & Lambrechts (2004) find that populations of Dutch flycatchers in deciduous forests declined significantly in the last several decades, whereas those populations in mixed and coniferous forests did not. The seasonality of food sources is therefore an important determinant of vulnerability to phenological mismatch.

The type and diversity of food sources consumed by birds also appears to be an important factor in determining vulnerability to phenological mismatch. Winkler, Dunn, & McCulloch (2002) argue that insectivorous birds with a greater diversity of food sources will be the least affected by warming-induced phenological mismatch, since insects display a wide range of phenological responses to temperature rise and their broad diet thus ensures that sufficient food will be available at any given time. Dunn and Winkler (2010) suggest that because plants and insects likely advance their phenology faster than vertebrates, herbivorous or insectivorous birds will need to advance their reproduction more than birds which feed on vertebrates (e.g. fish) in order to avoid asynchrony. Torti and Dunn (2005) found results to support this idea: they observed that

song sparrows, which are less dependent on arthropods than other species of similar North American birds, advanced their reproduction less than other comparable species. These authors also present evidence that birds with larger body mass are less sensitive to temperature change and therefore less likely to advance their breeding phenology than smaller bodied birds.

Brood Number

Townsend et al. (2013) hypothesize that the number of broods a species produces in a single season could be a determining factor in their successful adaptation to climate-induced phenological mismatch. Their study found that early breeders of black-throated blue warblers were more likely to attempt a second brood, and that both double brooding and early lay dates were positively linked to overall reproductive success. This conclusion therefore suggests that species which brood twice in a season are perhaps likely to be more resilient in the face of warming-induced changes to the phenologies of their food sources. The authors recognize, however, that the tendency to brood twice in a single season is poorly documented for many species, and that further research is therefore needed to determine which species might be impacted by this aspect of phenological asynchrony.

Fall Migration

Phenological changes in autumn migration spurred by rising temperatures and delayed autumns are expected to be complex. Unlike in spring migrations, there is not a strong relationship between the timing of autumn migration and reproductive success, and so it can be difficult to make clear predictions about how autumn migrations may be impacted by rising temperatures. Mills (2005) proposes several potential outcomes: birds may exhibit no change in timing of autumn migration, because timing is linked to non-climate factors, such as endogenous cues or predator avoidance. Secondly, birds may delay migration to take advantage of a longer summer season at their breeding grounds by having a second brood or protecting territory for next year's breeding. Finally, birds facing competitive habitats in wintering grounds may migrate earlier (having already bred earlier due to advancing springs) in order to better compete for limited wintering territories. Mills found that between 1975-2000, five of thirteen species delayed their autumnal migration from Ontario, whereas two of thirteen advanced migration. Mills' study is the only paper presented in this literature review to address autumn migration.

Sources of Uncertainty: Attribution and Measurements

Attributing changes in bird phenology or declines in reproductive rates to climate change is complex, as it can be difficult to distinguish the effects of multiple environmental variables. Indeed, climate change is one of many anthropogenic influences on bird populations and their habitats, making attribution of any specific trend to climate change difficult. In order to distinguish the effects of climate change from other anthropogenic influences, such as habitat loss, Both et al. (2004) studied the populations and egg lay date of migratory birds across Europe between 1990-2002, when there has been significant variability in the degree of spring warming. The authors observed that there has been greater advancement of lay dates in areas with higher spring temperatures, suggesting that climate change does indeed play a role in earlier lay dates, independent of other environmental variables. Both et al. (2009b) found that while populations of long-distance migrants have declined substantially, populations of resident birds and short-distance migrants in the same habitats have not declined at all. This eliminates the possibility that habitat degradation is responsible for population declines. While this suggests that long-distance migrants may be more sensitive to phenological asynchrony, it does not eliminate the possibility that some other variable is affecting the fitness of long-distance migrants (such as habitat

degradation or environmental change in their wintering habitats, as proposed by Jones and Cresswell (2010)).

Another problem affecting the study of phenological asynchrony is the use of first arrival date (FAD) as the main indicator of phenological response to rising temperatures. Although it is widely employed, this metric is problematic as it does not (by definition) reflect the majority of the population, and because it is sensitive to changes in population size and observer effort (Miller-Rushing et al., 2008). If population declines or if observer effort decreases, this could decrease the likelihood of observing first arrivals. Similarly, if populations grow or if more and more observers participate, the likelihood of observing the first arrivals also increases (Vitale & Schlesinger, 2011). In addition, Mills (2005) finds that FAD is problematic because it generally describes male arrivals, and so cannot account for changes in female migration.

Several studies have attempted to quantify the effect of changes in population size and observer effort on the reliability of FAD. Vitale and Schlesinger (2011) find that controlling for this effect does not affect results, and conclude that FAD is a generally reliable measurement. Butler (2003) also controlled for number of observers and found no effect on results. Miller-Rushing et al. (2008), on the other hand, find that cohort size greatly affects FAD and that mean arrival date is a more robust measurement. Mills (2005) suggests that FAD may reflect a few vanguard individuals who respond atypically to rising temperatures, and may not reflect broader trends in the entire migratory cohort. Butler (2003) acknowledges that FAD may be subject to observer bias, but argues that it can still be a useful metric: in his study, he found that short-distance migrants advanced their arrival date more than twice as much as long-distance migrants, and argues that an increase in observer effort would not account for this difference.



DOCUMENTED CASES OF PHENOLOGICAL ASYNCHRONY AND ADAPTATION

This section reviews documented cases of phenological mismatch resulting from climate warming in European and North American birds. To be considered an example of phenological asynchrony, the phenological response of migratory birds to warming (i.e., an advancement in arrival date or lay date) must be insufficient to track the phenological response of their food source. In addition, this resulting mismatch must have some negative effect on the birds' reproductive success. While definitively proving that a decline in reproductive success or population levels is directly attributable to phenological asynchrony is extremely difficult, the following papers have documented cases where phenological asynchrony is very likely a contributor to declines in the target species.

Phenological Asynchrony

Both and Visser (2001) find that long-distance migratory pied flycatchers in Europe have failed to advance their laying date sufficiently to track advancing spring temperatures and advancing peaks in insect abundance between 1980-2000. Although this population of flycatchers did advance its breeding date somewhat, demonstrating that females are able to employ individual plasticity in laying date, this population did *not* advance its arrival date, resulting in a narrower window between arrival and egg laying date. This narrow window ultimately restricts the birds' ability to sufficiently advance lay date. Continued selection over the study period in favor of earlier breeders demonstrates that lay date has not advanced sufficiently to track advancing springs.

Sanz et al. (2003) find that the laying date of the Spanish pied flycatcher has not advanced between 1984 and 2000, despite a significant increase in May temperatures and an advance in the phenology of oak trees (which host their primary food source, caterpillars). They find that this resulting phenological mismatch has led to a measurable decline in fitness of the flycatchers, resulting in a decline in breeding success, a decrease in fledgling body mass, and an increase in nestling mortality. In addition, the authors find that adult body mass declined over time, suggesting that adult's subsequent survival may be compromised by mistimed reproduction.

Visser, Holleman, & Gienapp (2006) measured peak caterpillar biomass and the laying date of great tits in the Netherlands between 1955-2004. The authors found that while peak caterpillar biomass advanced by 0.74 days, bird lay date did not advance sufficiently to track this change. Indeed, the authors found that lay date only advanced 0.3 days for every day advance in peak caterpillar biomass. In addition, the authors measured reproductive success as correlated with peak caterpillar biomass: they found that the number of successfully fledged young is strongly determined by both brood size and timing relative to peak biomass. Clutches raised before or after peak biomass fledged fewer chicks, suggesting that the observed mismatch between avian reproduction and peak food availability has important implications for reproductive fitness.

Moller, Rubolini, & Lehikoinen (2008) studied more than 100 species of migratory European birds between 1960-2000, and found that species that had failed to advance the timing of their spring migration experienced a greater population decline than species that had significantly advanced their migration. Between 1970-1990, variables such as breeding habitat type, breeding latitude, and winter range proved to be significant predictors of population levels (with birds wintering in Africa and species breeding in agricultural habitats demonstrating the greatest declines). And yet between 1990-2000, these variables ceased to have a significant effect on population level, and the timing of migration became the sole significant variable. This suggests

that phenological asynchrony has become an increasingly important factor in determining the viability of migratory bird populations.

Both et al. (2009a) conducted a comprehensive review of phenological synchronization across four trophic levels in the Netherlands between 1988 and 2005. The authors measured the timing of tree budburst; peak biomass of herbivorous insects; reproduction of insectivorous passerines; and reproduction of one avian predator. The results showed that consumers demonstrate a weaker phenological response to warming than their food source, resulting in potential phenological asynchronies at multiple points along the food chain. The four species of insectivorous passerines (blue tits, coal tits, great tits, and pied flycatchers) did not advance lay date sufficiently to track peak caterpillar biomass, while the avian predator did not demonstrate any significant advance in hatching date at all.

McKinney et al. (2012) find that Broad-tailed Hummingbirds have not sufficiently advanced their arrival date to track the advancing phenology of their primary nectar sources, *E. grandiflorum* and *D. nuttallianum*, in Arizona and Colorado from 1975-2011. While the FAD of these birds did increase over the study period, it was not sufficient to account for larger advancements in the first and peak flowerings of these plants. While the authors did not document declines in fitness, the current low reproductive output of this species (2 eggs per clutch, one clutch per season in mountain sites) makes any phenological mismatch likely to have a significantly negative effect on future population stability.

Schwartzberg et al. (2014) conducted an experimental study to examine the effects of temperature rise on the phenology of tree budburst and herbivorous insects. Using a field-based free air warming experiment in Minnesota, the authors measured the effect of temperature rise of 1.7 and 3.4 °C on the timing of tent caterpillar reproduction and budburst in beech and poplar trees. The study found that after two years, tree phenology had advanced more than insect reproduction: in the 3.4 °C plot, tree budburst advanced by 10-15 days, while caterpillar larvae emerged 8-9 days earlier. The results support the findings of Both et al. (2009a), showing that consumers demonstrate weaker phenological responses to warming than their food sources.

Synchronous Adaptation

The following papers review cases where bird populations appear to have sufficiently adapted their breeding phenology to mirror phenological changes in their food sources. Because the communities in these examples appear to be able to adapt to changing climate conditions and therefore avoid a mismatch with their food sources, these cases stand as counterexamples to the previous section and suggest that some bird populations may be able to avoid the negative effects of phenological asynchrony.

Charmantier et al. (2008) find that great tits in the United Kingdom have advanced their lay date by approximately 47 days between 1961 and 2007, closely tracking the peak biomass of their primary food source, caterpillar. Indeed, the birds laying date and caterpillar biomass peak are similarly correlated with temperature; both phenological events changed over the years at a similar rate. This case therefore represents an example not of phenological asynchrony, but of synchronous adaptation across trophic levels.

Townsend et al. (2013) found that black-throated blue warblers in New Hampshire were able to adequately track inter-annual variations in temperature from 1986-2010. While there was no strong warming trend in spring temperatures during the entire study period (and therefore no significant advance in mean lay date), the authors did find that birds advanced their breeding

in warmer springs. Selection favored earlier breeders, but as noted above, the strength of selection did not increase in warmer years, suggesting that the birds were adequately advancing their breeding each year to track temperature changes. As in Charmantier et al. (2008), this study suggests synchronous adaptation instead of phenological asynchrony. Although the phenology of lower trophic levels was not addressed in this paper, the reproductive trends observed in this study suggest that black-throated blue warblers may not suffer the same fitness declines as observed in other European studies.



DOCUMENTED CASES OF ADVANCED MIGRATION IN NORTH AMERICA

The papers described above examine phenological synchrony *per se*, with an emphasis on different phenological responses across trophic levels and resulting impacts on fitness. Much of the literature on North American birds, however, focuses instead on the timing of arrival in breeding grounds. While this is an important component of predicting phenological asynchrony, arrival date is not in itself a measure of phenological mismatch: documented cases of phenological mismatch need to show that bird *reproduction* has come out of sync with lower trophic levels to an extent that fitness is reduced (Visser, Both, & Lambrechts, 2004) . Moreover, changes of bird migration in response to temperature rise may in fact indicate adaptation to climate change and therefore a decreased vulnerability to climate change-induced phenological asynchrony. Nevertheless, the ability of various species to advance their arrival is an important part of understanding avian vulnerability to phenological asynchrony. The table below presents a summary of species that have advanced their arrival in North America; further details of the cases can be found in the text above.

Table 1. Summary of documented cases of advanced arrival dates in North America (First Arrival Date, FAD; Median Arrival, MA; Mean Arrival Date, MAD).

Species	Time Period	Metric	Advance	Source
Turkey vulture	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Blue-winged teal	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Virginia rail	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Killdeer	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Common snipe	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
American woodcock	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Chimney swift	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Yellow-bellied sapsucker	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Eastern wood-pewee	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Purple martin	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Tree swallow	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Northern rough-winged swallow	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Bank swallow	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Barn swallow	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Wood thrush	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003
Brown thrasher	1903-1993	FAD	Significant advance over study period (P <0.05)	Butler, 2003

Blue-winged warbler	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Tennessee warbler	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Nashville warbler	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Yellow-rumped warbler	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Northern waterthrush	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Field sparrow	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Fox sparrow	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Lincoln's sparrow	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
White-crowned sparrow	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Indigo Bunting	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Bobolink	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Brown-headed cowbird	1903-1993	FAD	Significant advance over study period ($P < 0.05$)	Butler, 2003
Ruby-crowned kinglet	1975-2000	FAD	Significant advance over study period ($P < 0.05$)	Mills, 2005
White-throated sparrow	1975-2000	FAD	Significant advance over study period ($P < 0.05$)	Mills, 2005
Yellow warbler	1975-2000	FAD	Significant advance over study period ($P < 0.05$)	Mills, 2005
Common yellowthroat	1975-2000	FAD	Significant advance over study period ($P < 0.05$)	Mills, 2005
Common grackle	1994-2005	MA	Significant relationship with NAO Index ($P < 0.01$) in all 3 quantiles (0.1, 0.25, 0.5)	Wilson, 2007 ⁺
Northern parula	1994-2005	MA	Significant relationship with temperature ($P < 0.01$) in all 3 quantiles (0.1, 0.25, 0.5)	Wilson, 2007
Red-winged blackbird	1994-2005	MA	Significant relationship with temperature ($P < 0.01$) in all 3 quantiles (0.1, 0.25, 0.5)	Wilson, 2007
Ruby-crowned kinglet	1994-2005	MA	Significant relationship with temperature and NAO Index ($P < 0.01$) in all 3 quantiles (0.1, 0.25, 0.5)	Wilson, 2007
Warbling vireo	1994-2005	MA	Significant relationship with temperature ($P < 0.05$) in all 3 quantiles (0.1, 0.25, 0.5)	Wilson, 2007
American kestrel	1994-2005	MA	Significant relationship with NAO Index ($P < 0.01$) in all 3 quantiles (0.1, 0.25, 0.5)	Wilson, 2007
American woodcock	1994-2005	MA	Significant relationship with NAO Index ($P < 0.01$) in all 3 quantiles (0.1, 0.25, 0.5)	Wilson, 2007
Belted kingfisher	1994-2005	MA	Significant relationship with	Wilson, 2007

Eastern phoebe	1994-2005	MA	NAO Index (P <0.01) in all 3 quantiles (0.1, 0.25, 0.5) Significant relationship with NAO Index (P <0.01) in all 3 quantiles (0.1, 0.25, 0.5)	Wilson, 2007
Tree swallow	1994-2005	MA	Significant relationship with NAO Index (P <0.01) in all 3 quantiles (0.1, 0.25, 0.5)	Wilson, 2007
Trail's flycatcher*	1970-2002	MAD	Significant advance over study period (P <0.05)	Miller-Rushing et al, 2008
Blue jay	1970-2002	MAD	Significant advance over study period (P <0.05)	Miller-Rushing et al, 2008
Grey catbird	1970-2002	MAD	Significant advance over study period (P <0.05)	Miller-Rushing et al, 2008
Northern parula	1970-2002	MAD	Significant advance over study period (P <0.05)	Miller-Rushing et al, 2008
Magnolia warbler	1970-2002	MAD	Significant advance over study period (P <0.05)	Miller-Rushing et al, 2008
Ovenbird	1970-2002	MAD	Significant advance over study period (P <0.05)	Miller-Rushing et al, 2008
Eastern towhee	1970-2002	MAD	Significant advance over study period (P <0.05)	Miller-Rushing et al, 2008
Swamp sparrow	1970-2002	MAD	Significant advance over study period (P <0.05)	Miller-Rushing et al, 2008

* Willow and alder flycatchers (*Empidonax alnorum* and *Empidonax traillii*) were combined as Traill's flycatcher.

* Significant regressions in Wilson (2007) do not necessarily indicate statistically significant advance in arrival date over study period, but that the independent climate variable (either temperature or NAO Index) is a significant predictor of arrival date.



CONCLUSION

Of the many effects that anthropogenic climate change may have on avian communities, phenological asynchrony is perhaps one of the most complex. By definition, this phenomenon describes a mismatch in timing between birds and their food sources, and therefore must involve changes to several trophic levels. In addition, it is likely only to be observed over multiple generations and decades: in order to diagnose phenological asynchrony, we must observe consistent declines in fitness associated with a mismatch between birds' reproductive phenology and the availability of their food sources. Disentangling the effects of other determinants of bird migration and reproduction, other environmental changes, and natural variability in bird population levels and reproductive rates is no easy feat. Superimposed on these confounding factors is the inherent unevenness of warming trends over both space and time, which makes detecting strong, consistent signals a challenge.

Despite these complexities, there is a strong theoretical framework and abundant observational evidence to suggest that phenological asynchrony may be a reality for many bird species as our climate warms. Although some species, including several in North America, have demonstrated the ability to advance their arrival, breeding, and/or lay date, the literature demonstrates that many species have not. Long-distance migrants, those dependent on highly seasonal food sources or with restricted diets, and high-latitude species are thought to be the most sensitive to these phenological changes.

Although only mitigation of anthropogenic climate change through emission reductions can directly address the root causes of climate-induced phenological asynchrony, there are a number of conservation measures that can be taken to improve the resilience of avian communities in the face of this pressure. Primary among these is the active conservation and stewardship of both breeding and wintering grounds, and of stopover locations along migration corridors. By reducing pressures from habitat loss, degradation, and other threats, conservation managers can help to ensure that the effects of phenological asynchrony are as minimal as possible.

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