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The impact of climate change on the mistiming of bird-resource phenologies

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Abstract

As the climate continues to warm, phenologies of organisms across a variety of taxa are continuing to change. These changes are resulting in potential mismatches in resource acquisition. Specifically, migratory birds are experiencing population declines as a result of their food resources emerging at different times in their breeding grounds. I have shown how these food-timing mismatches are resulting in population declines in a range of migratory bird species, from passerines to shorebirds to hummingbirds. A failure to match their migration timing with resource availability in breeding grounds could result in significant population declines in migratory birds.

Introduction

Climate change can contribute to population declines in a variety of ways. More specifically, warming presents a potential issue for migratory bird populations, and those that do not change their migration timing to match their resources available are at a significant disadvantage (Burger et al., 2012). This is the topic I will closely address in this review. Nonetheless, the warming climate and changes in precipitation are causing shifts in the phenologies of both plants and animals, and is one consequence of climate change that can be attributed to declining populations. These alterations in phenologies are occurring across trophic levels (Cahill et al., 2012). As climate change progresses, we are seeing earlier breeding and first singing in birds, early arrival of migrant birds, earlier appearance of butterflies, earlier choruses of amphibians, and earlier shooting and flowering of plants (Walther et al., 2002). At the plant level, studies have shown that flowering and reproductive timing in flowers is significantly affected by local environmental conditions, including temperature and precipitation (Galloway & Burgess, 2012). Insect emergence has also begun to vary widely from the norm (Ellwood et al., 2012). As a result of these modifications in plant and insect phenologies, plant-animal interactions are taking a blow. These interactions, such as pollination services, are integral to the rest of the ecosystem as they provide valuable food services (Gilman, Fabina, Abbott, & Rafferty, 2012). Timings in migratory bird patterns are also starting to change. In particular, the song thrush has been advancing its spring migration in response to climate change (Sinelschikova, Kosarev, Panov, & Baushev, 2007).

Due to these shifts in so many ecosystem dynamics, such as flower timing, herbivore interactions, and seasonal breeding, climate change is causing a large shift in the possibilities of population trajectories for migratory bird populations (Johansson & Jonzén, 2012). All of the aforementioned implications of climate change can have significant effects across trophic levels. Therefore I will ask, do phenological shifts due to climate change cause a mistiming between bird migrations (including optimal breeding times) and food availability? I will show how accounting for this potential mismatch is critical in migratory birds across taxons.

Population declines in birds that do not shift phenologies

Møller et al. (2008) used a long-term data set of 100 migratory bird species in Europe to determine any population declines due to mistiming of bird phenologies with their food sources. They collected 289 estimates of changes in mean/median spring migration dates in birds from 1960-2006. They coupled this information with bird population trends during two periods: 1970-1990 and 1990-2000. They then used a model to predict what factors most influenced population stability or declines in these 100 migratory bird species.

When the authors analyzed population trends from 1970-1990, they found that the most important variables for population trends were body mass and farmland breeding habitat. Migration date was not a significant predictor of population trends for this time period. However, when they focused on population trends from 1990-2000 the only significant factor affecting population trends was change in migration date. The data showed that populations that accelerated their spring migration showed stable population trends, while those that did not accelerate their spring migration timing experienced declines in populations.

These population declines are due to the inability of later-migrating birds to capitalize on spring food resources. Birds that arrive sooner have a greater chance of acquiring necessary food resources than those that arrive later. Furthermore, birds that arrive sooner were also found to have larger clutch sizes than those that arrived later. This is most likely due to the fact that birds that arrived sooner had a longer time to acclimate to the environment of their breeding site, including climate and resource availability. Therefore, birds that do not alter their spring migration time to coincide with the changing climate will not fare well in the future. The most notable result, however, was that migration date was not a significant predictor of population trends for the 1970-1990 period, but migration date was the only significant predictor for the 1990-2000 period. The authors noted that this is clear evidence that climate-mediated changes in phenology in European migratory birds have intensified in recent years.

Phenological plasticity acts to buffer population declines

More recently, Salido et al. (2012) conducted a similar study to that of Møller et al. (2008), using a long-term data set to study population trends in migratory birds from 1994 to 2007. Salido et al. (2012) used a data set of UK passerines to investigate the flexibility of phenology of these migratory birds. They obtained population data from the BTO/JNCC/RSPB Breeding Bird

Survey. Data for laying dates and first clutch laying periods were obtained from the Nest Record Scheme. A model was then used to compare species-specific traits and population trends.

Predictors that best explained variation in population growth rates included both life history, and phenological and resource traits. The final model retained mean change in arrival date, average laying date and the average first clutch laying period, citing these as the most important predictors. Diet type was also significant in the model.

Similar to the findings of Møller et al. (2008), Salido et al. (2012) attributed life history traits, phenology, migration and resource use to long-term population trends in UK passerines. Though Møller et al. (2008) studied 100 migratory bird species in Europe and Salido et al. (2012) focused on UK passerines, the results can certainly be extrapolated. These findings again show that earlier migration can contribute to more stable population sizes, and Salido et al. (2012) even take it a step further to claim that early migration acts as a buffer to population declines. Individuals that migrate earlier have the opportunity to obtain resources whose phenologies have also advanced due to climate change. With the earlier acquisition of these resources comes the ability to have earlier egg laying dates, and larger clutch sizes. Salido and colleagues (2012) note that in addition to earlier migration, birds that are capable of taking advantage of a variety of food resources also fare better. The combination of earlier migration and a more generalized diet create optimum conditions to maintain stable population sizes and buffer against population decline. Some additional food sources (those not initially favored) may be more available at optimal times and the ability to take advantage of these resources is highly favorable.

Salido et al. (2012), again similarly to Møller et al. (2008), also found that earlier migrants had increased clutch sizes and a longer laying period. A longer laying period allows for relaying eggs in the event that eggs do not hatch or hatchlings do not survive in the first attempt. The authors also found that a second clutch is often not necessary for birds that migrate sooner, and will instead invest energy in having one large clutch. This large clutch can be easily cared for due to a large amount of available food following earlier migration dates. Birds that migrate later often have multiple, smaller clutches as a result of an inability to adequately provide food for their hatchlings. Again, Salido et al. (2012) has shown the problems associated with a failure of birds to match their migration timing with the emergence of food resources.

Phenological adjustments in blue and great tits

The studies by Møller et al. (2008) and Salido et al. (2012) have documented that some migratory birds are adjusting their migration timing to account for the changing climate, while others are not. Matthysen et al. (2011) identified instances in which blue and great tits have adjusted their migration schedules to coincide with the changing phenologies of their resources.

Matthysen and colleagues (2011) conducted their study in a forest near Antwerp, Belgium. The investigators set up nest boxes and monitored the boxes for breeding phenology between the years of 1979 and 2007. The authors identified first egg dates by the first observation of a partially laid clutch. They also observed the number of clutches laid with laying interruptions, the number of clutches (first clutches, replacement clutches, and second clutches), and clutch size.

Over the course of the 29-year study, both species advanced their egg-laying dates by 11.5 and 11.7 days. Fledging dates of first clutches also advanced by 0.50 and 0.52 days per year. Yet, fledging dates of all nests increased by 0.55 and 0.66 days per year in blue and great tits respectively. Mean fledging date was also highly correlated with prelaying temperature.

Prelaying temperatures, and the mean temperatures during laying and incubation periods all increased over time. In blue tits incubation periods were shorter in warm years. Other phenological parameters that correlated highly with temperature included: first-egg date, date of large nestling size, and total nest time.

In addition to advancements in bird phenology, food peak times advanced significantly. This advancement was 0.55 days per year, or 0.72 days per year, depending on the estimate measure used. Thus, due to advancements in bird phenologies, the interval between the peak in food demand and the peak in food availability did not change significantly over time.

The study by Salido et al. (2012) concluded that birds that exhibit an advancement in migration and breeding phenologies are less likely to have multiple clutches. This study by Matthysen et al. (2011) had similar findings. Blue and great tits have advanced their breeding phenologies, and have grown less likely to have multiple clutches. Matthysen and colleagues (2011) contribute this to the shortening of the peak food period, therefore making second clutches less likely to succeed and less valuable. Birds benefit more from expending as much energy as possible into one clutch, rather than attempting to raise a later clutch in less than favorable conditions. The clutches of the birds were also found increase in size. Instead of expending energy for multiple clutches, great and blue tits developed a habit of having one large clutch.

Additionally, great and blue tits have managed to maintain synchrony between their breeding times and their food sources. This finding is important for the reductions in the number of clutches, and increase in clutch size. Great and blue tits are continuing to time their first clutch with the optimal feeding times. The lengths of these feeding times are decreasing, and great and blue tits are maximizing their energy expenditure to account for these phenological shifts. Unlike declining populations of migratory birds, great and blue tits have managed to account for the changing climate, and change the timing of their breeding accordingly to correctly match the timings of their food sources.

Phenological mismatch in arctic shorebirds

While the studies of great and blue tits by Matthysen et al. (2011) yielded promising results regarding the correct timing of bird breeding and food availability, other species of migratory birds are not as fortunate. McKinnon et al. (2012) took to the arctic to observe a possible mismatch between food availability and breeding phenology in arctic shorebirds. McKinnon and colleagues (2012) studied the shorebirds on Bylot Island in Canada, which consists of tundra wetland and is a much different ecosystem than that of the Belgian forest studied by Matthysen et al. (2011). Additionally, the shorebirds are dissimilar taxonomically to the tits, which are songbirds. The three bird species observed were the White-rumped Sandpiper, the Baird's Sandpiper and the American Golden Plover.

The investigators monitored nests in the study site from 2005 to 2008, and information on egg measurements, number of eggs and young upon hatch, and incubation stage was collected. The authors also used pitfall traps with modified Malaise traps to catch arthropods to monitor variations in food availability among years. To monitor chick growth the investigators banded chicks at age zero in the nest. The investigators then returned to the sites every two days to recapture and reweigh the chicks.

Throughout the course of the study (2005-2008) proper timing between breeding phenology and food resources availability was only found in one year (2006). In 2006 86% of White-rumped Sandpiper and 92% of Baird's Sandpiper hatch dates fell within the peak food resource availability time. However, when observing all species studied across the 4-year span, timing was asynchronous as a whole between breeding and food resource availability. Furthermore, chicks that were hatched within the ideal hatching period for resource availability had a greater mass than those hatched outside of the ideal period.

McKinnon et al. (2012) assert that breeding must be timed properly with peaks in resource availability for the proper formation of eggs and hatchlings. The authors also concluded that climate change is affecting the breeding times of these shorebirds, particularly with the alterations in snow melt recently from year to year. The findings of Møller et al. (2008) and Salido et al. (2012) indicated that mistiming between breeding and peak food resource availability results in smaller clutch sizes. McKinnon and colleagues (2012) discovered that these food-breeding mismatches have an even further negative impact on migrating bird populations, finding that asynchrony can also result in reduced mass of hatchlings. McKinnon et al. (2012) have shown that this lower mass of hatchlings can prove to have negative implications for the future of the hatchlings, being less prepared for the bird's eventual need to survive and fend for itself. The lower mass of hatchlings can be attributed to the inability of these birds to match the emergence of critical food resources.

Population declines in the pied flycatcher

The last two examples have dealt with clutch sizes, the number of clutches, and hatchling success as a result of synchrony between food resources and breeding, but I will now shift the focus back the population levels. Studies by Both et al. (2006) and Burger et al. (2012) have observed how these mismatches have resulted in population declines in the pied flycatcher. Both et al. (2006) studied populations dynamics of the pied flycatcher in relation to its food source, caterpillars. The researchers studied 10 pied flycatcher populations in an oak-dominated forest in the Netherlands from 1987 to 2003, where they studied populations living in nest boxes during this time period (more than 98% of flycatchers breed in nest boxes in this area). Laying date was also known for six populations from 1980 to 2002, and this data was averaged to find a mean laying date. The authors measured caterpillar biomass by catching caterpillar droppings underneath trees in 2002. Their data was then compared to historical data as well. The investigators also measured the percent of great tits producing second broods, as this is a significant indicator of late caterpillar peak.

Pied flycatcher populations declined about 90% in areas with the earliest food peaks, while populations only declined 10% in areas with the latest food peaks. Flycatcher populations also declined most in areas where great tits did not produce second broods, which designates areas where caterpillars peaked early. Both et al. (2006) state that pied flycatchers are likely not advancing their migration from the wintering grounds soon enough to catch up with the advancement of caterpillar peak times. The authors also conclude that further advancement of peak food availability timing will prove to be even more detrimental to flycatcher populations if these birds do not advance their migration timing.

A more recent study of the pied flycatcher, conducted by Burger et al. (2012) had similar conclusions to those of Both et al. (2006). However, while Both et al. (2006) studied flycatchers in the Netherlands alone, Burger et al. (2012) studied flycatcher populations from nine areas in Europe and Russia, and collected data between 1998 and 2008. The researchers used cameras, video cameras, and neck collars to accumulate data of flycatcher populations, and collected data from deciduous, coniferous, and mixed forest types. The investigators analyzed laying date, clutch size, nestling condition and number of fledglings per nest. Linear mixed models were used to observe the relationship between proportion of caterpillars in the diet and reproductive success, and the effect of temperature on diet.

Fledgling mass was positively correlated with the proportion of caterpillars in the diet. As the proportion of caterpillars in the diet increased, fledgling mass also increased following a logarithmic curve. In oak forests there was a strong decline in caterpillars in diets in warm years, with not as strong of a decline in cold years.

Again, similar to the studies of Both et al. (2006), Burger et al. (2012) found that pied flycatchers are highly reliant on caterpillars for their diet. In warmer years where caterpillars emerge earlier, flycatcher numbers decrease due to a mismatch in migration and food availability. These effects were most pronounced in oak habitats, where caterpillars were more likely to emerge sooner. In coniferous habitats caterpillars were more likely to emerge at later dates. Mixed forest habitats were the most suitable for flycatchers, as caterpillars emerged early on deciduous trees and later on coniferous trees. The authors hypothesized that, given the flycatchers reliance on caterpillars in their diet, habitat selection will shift towards coniferous dominated forests where there is not as pronounced a mismatch between peak caterpillar times and flycatcher migration times. Flycatchers benefit most from breeding earlier in oak dominated forests, and are not nearly as harmed in other habitats. Regardless of these differences in habitat types, both the authors of Both et al. (2006) and Burger et al. (2012) have shown the vulnerability of the pied flycatcher to a changing climate. The pied flycatcher is failing to alter its migration timing to meet the timing of the emergence of its primary food resource, and this mismatch is proving deleterious for pied flycatcher populations.

Latitude determines magnitude of phenological mismatches

The previous two studies regarding the pied flycatchers both took place at higher latitudes. According to McKinney et al. (2012), latitude plays a significant role in the magnitude that phenologies are changing as a result of climate change. McKinney and colleagues (2012) focused their study on Broad-tailed Hummingbirds, which rely on floral nectar as a food source. The authors monitored Broad-tails from 1984 through 2010 in a pine-oak woodland at two sites near Tucson, AZ. Investigators also monitored first and peak flowering times of ocotillo, a nectar resource for Broad-tails. The researchers also observed spring arrival time of Broad-tails and plant phenology in Colorado from 1975 through 2011.

Broad-tail arrival at the Arizona sites did not significantly change throughout the course of the study. Plant flowering times also did not change significantly. However, arrival of Broad-tails at the northern site in Colorado has advanced by 1.5 ± 6.8 days per decade over the last 37 years. Glacier lily peak flowering advanced by 4.6 ± 1.6 days and 2.7 ± 1.4 days per decade. Twolobe larkspur peak flowering advanced by 4.3 ± 1.5 days and 2.8 ± 1.4 days per decade. If these changes continue at the same rate, Broad-tails will arrive after the peak flowering times of glacier lily by 2033 and after the peak flowering times of twolobe larkspur by 2069.

This data suggests that plants at the more northern Colorado site show greater advancement in peak flowering time due to climate change than plants at the more southern Arizona site. This eventual later arrival of Broad-tails is not promising for their future nesting success and population trajectory. However, McKinney et al. (2012) predict that a shift in the breeding grounds may occur towards lower latitudes for the Broad-tails. This data provides interesting conclusions regarding mismatches between bird migrations and food resource availability. Further studies investigating these differences in phenology are important to understand how different species of migratory birds may be affected by latitudinal differences in climate change in varying parts of the world.

Onset of migration

Thus far I have identified how food availability has the potential to create problems for migratory birds when they arrive at their breeding grounds. However, a recent study by Studds and Marra (2011) shows that changes in food availability due to climate change in the wintering grounds of birds has a considerable impact on the onset of migration. Studds and Marra (2011) studied American redstarts in its wintering ground of Jamaica from 2003-2009, which is primarily dominated by white and red mangroves. Redstarts were captured in mist nets, banded and weighed. The investigators sampled arthropods available as redstart prey using a sweep net, and then weighed arthropods of an appropriate size (2-20mm in length). The authors also monitored monthly rainfall from the Jamaican Meteorological Service. Studds and Marra (2011) used a linear mixed model to analyze spring departure schedules.

Arthropod biomass was highest in years when March rainfall was high. Recently, rainfall during this time of the year has been highly variable from year to year, causing variation in arthropod abundance. Redstarts exhibited a 1-day delay in departure from the wintering grounds for every 9.2mg reduction in arthropod biomass. Previously, it was thought that bird migration leaving the wintering grounds was reliant solely on photoperiod, however this study shows that this timing is also dependent on rainfall and food availability. Not only is food availability an important issue for populations of migratory birds at their breeding grounds, but it also is important for the timing of their departure from their wintering grounds. Timing of departure from wintering grounds has the potential to add to mistiming between arrival at breeding grounds and food supply.

Conclusion

As the climate continues to change, phenologies of migratory birds are going to need to change to match the phenologies of their food resources. I have identified reasons for the need of a variety of species of migratory birds to do so. Meta-analyses by Møller et al. (2008) and Salido et al. (2012) have shown that birds that match peak food availability times with their migration and breeding times are far more successful than birds that do not. Birds that fail to make this match experience population declines. Matthysen et al. (2011) proved that great and blue tits are among the species of migratory birds that are making changes in their migratory and breeding timing to match their food resources, and are successful species as a result. Pied flycatchers, on the other hand, are one species that are failing to meet these phenological adjustments, and their populations are on the decline (Both et al., 2006; Burger et al., 2012). Shorebirds on Bylot Island are producing offspring with lower masses due to their inability to match the phenologies of their resources (McKinnon et al., 2012). These mismatches are also accentuated at higher latitudes (McKinney et al., 2012). Finally, migratory birds are also reliant on sufficient food resources in their wintering grounds in order to leave early enough to get to their breeding grounds on time (Studds & Marra, 2011).

If migratory birds fail to meet the phenological fluctuations in their food supply, they may experience dire circumstances in the future. Certainly, future studies are required to fully understand this mismatch between bird migration and food availability. However, there is no doubt that there is sufficient evidence to conclude that this mismatch is a reality, and birds that arrive at their breeding grounds at different times than the peak food availability are negatively impacted.

References

Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. [10.1038/nature04539]. *Nature, 441*(7089), 81-83. doi:

Burger, C., Belskii, E., Eeva, T., Laaksonen, T., Magi, M., Mand, R., . . . Both, C. (2012). Climate change, breeding date and nestling diet: how temperature differentially affects seasonal changes in pied flycatcher diet depending on habitat variation. [Article]. *Journal of Animal Ecology, 81*(4), 926-936.

Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Yeong Ryu, H., . . . Wiens, J. J. (2012). How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*.

Ellwood, E. R., Diez, J. M., Ibanez, I., Primack, R. B., Kobori, H., Higuchi, H., & Silander, J. A. (2012). Disentangling the paradox of insect phenology: are temporal trends reflecting the response to warming? [Article]. *Oecologia, 168*(4), 1161-1171.

Galloway, L. F., & Burgess, K. S. (2012). Artificial selection on flowering time: influence on reproductive phenology across natural light environments. [Article]. *Journal of Ecology, 100*(4), 852-861.

Gilman, R. T., Fabina, N. S., Abbott, K. C., & Rafferty, N. E. (2012). Evolution of plant-pollinator mutualisms in response to climate change. [Review]. *Evolutionary Applications, 5*(1), 2-16.

Johansson, J., & Jonzén, N. (2012). Game theory sheds new light on ecological responses to current climate change when phenology is historically mismatched. *Ecology Letters, 15*(8), 881-888.

Matthysen, E., Adriaensen, F., & Dhondt, A. A. (2011). Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (Cyanistes caeruleus, Parus major). [Article]. *Global Change Biology, 17*(1), 1-16.

McKinney, A. M., CaraDonna, P. J., Inouye, D. W., Barr, B., Bertelsen, C. D., & Waser, N. M. (2012). Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology, 93*(9), 1987-1993.

McKinnon, L., Picotin, M., Bolduc, E., Juillet, C., & Bêty, J. (2012). Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Canadian Journal of Zoology, 90*(8), 961-971.

Møller, A. P., Rubolini, D., & Lehikoinen, E. (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, 105*(42), 16195-16200.

Salido, L., Purse, B. V., Marrs, R., Chamberlain, D. E., & Shultz, S. (2012). Flexibility in phenology and habitat use act as buffers to long-term population declines in UK passerines. [Article]. *Ecography, 35*(7), 604-613.

Sinelschikova, A., Kosarev, V., Panov, I., & Baushev, A. (2007). The influence of wind conditions in Europe on the advance in timing of the spring migration of the song thrush (<i>Turdus philomelos</i>) in the south-east Baltic region. *International Journal of Biometeorology, 51*(5), 431-440.

Studds, C. E., & Marra, P. P. (2011). Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. [Article]. *Proceedings of the Royal Society B-Biological Sciences, 278*(1723), 3437-3443.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., . . . Bairlein, F. (2002). Ecological responses to recent climate change. [10.1038/416389a]. *Nature, 416*(6879), 389-395.