

CHAPTER NINE

Shorebird Migration in the Face of Climate Change*

POTENTIAL SHIFTS IN MIGRATION PHENOLOGY AND RESOURCE AVAILABILITY

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Abstract. Changes in temperature and seasonality resulting from climate change are heterogeneous, potentially altering important sources of natural selection acting on species phenology. Some species have apparently adapted to climate change but the ability of most species to adapt remains unknown. The life history strategies of migratory animals are dictated by seasonal factors, which makes these species particularly vulnerable to heterogeneous changes in climate and phenology. Here, we examine the phenology of migratory shorebirds, their habitats, and primary food resources, and we hypothesize how climate change may affect migrants through predicted changes in phenology. Daily abundance of shorebirds at stopover sites was correlated with local phenology and peaked immediately prior to peaks in invertebrate food resources. A close relationship between migrant and invertebrate phenology

indicates that shorebirds may be vulnerable to changes in seasonality driven by climate change. It is possible that shifts in migrant and invertebrate phenology will be congruent in magnitude and direction, but because migration phenology is dependent on a suite of ecological factors, any response is likely to occur at a larger temporal scale and may lag behind the response of invertebrate food resources. The resulting lack of sufficient access to food at stopover habitats may cause migrants to extend migration and have cascading effects throughout their life cycle. If the heterogeneous nature of climate change results in uneven changes in phenology between migrants and their prey, it may threaten the long-term viability of migratory populations.

Key Words: *Calidris*, climate change, food availability, habitat selection, phenology, stopover habitat.

Global climate change is proceeding at an unprecedented rate, creating known and unknown challenges for conservation and research professionals (IPCC 2007). Climate change is spatially and temporally heterogeneous,

which makes predicting ecological consequences difficult and designing effective mitigation strategies challenging. Spatial and temporal disparity in changes to seasonality, resource availability, and phenology are predicted to have far-reaching

* Stutzman, R. J., and J. J. Fontaine. 2015. Shorebird migration in the face of climate change: potential shifts in migration phenology and resource availability. Pp. 145–159 in E. M. Wood and J. L. Kellermann (editors), *Phenological synchrony and bird migration: changing climate and seasonal resources in North America*. Studies in Avian Biology (no. 47), CRC Press, Boca Raton, FL.

implications for biodiversity (Sala et al. 2000, Thomas et al. 2004, Botkin et al. 2007), particularly for species that occupy large geographic areas and have complex life history strategies such as long-distance migrants (Both and Visser 2001, Robinson et al. 2009, Both et al. 2010). Understanding the degree to which life history events like migration are dependent on intertwined phenological cues such as trees beginning to flower or seasonal insect blooms is essential for wildlife professionals to mitigate the effects of climate change. Seasonality has been important in shaping life history evolution, such as Neotropical songbirds that preferentially forage on trees with more flowers (McGrath et al. 2009) or the apparent ability of some species to adapt to changes in phenology (Walther et al. 2002, Root et al. 2003, Jonzén et al. 2006). Nevertheless, general information concerning the phenological sensitivity and progression for most species is lacking. Addressing the implications of climate change for species phenology is of growing interest, but few studies have considered these relationships in the context of additional sources of anthropogenic change (Opdam and Wascher 2004).

Avian migration is a well-studied life-history event, but our understanding of the phenological cues driving migratory phenology, and the potential for climate change and other sources of anthropogenic change to influence migration behaviors remains limited (Ahola et al. 2004, Gordo 2007, Petersen 2009). Avian species often show preference for stopover habitats with greater food availability (Hutto 1985, Russell et al. 1992, Kelly et al. 2002, van Gils et al. 2005), and variation in food availability at stopover sites affects body condition and, ultimately, individual fitness (Moore et al. 1995, Pfister et al. 1998, Drent et al. 2003, Baker et al. 2004). However, anthropogenic change, be it from climate change or other forces such as land-use changes, can change the cues that predict food resources, the food resources themselves, or both, potentially leading to an ecological trap (Battin 2004, Robertson and Hutto 2006). Moreover, heterogeneity in the rate of climate change across the range of many migratory bird species has the potential to affect habitats and resources differently at various locations throughout the migration cycle (Visser et al. 2004, Fontaine et al. 2009, Jones and Cresswell 2010). Strong selection pressure and a reliance on predictable spatial and temporal relationships

have resulted in stopover events that often occur during optimal resource availability at a single location en route (McGrath et al. 2009), despite the fact that migratory timing is dictated in part by conditions at earlier stages of the migratory cycle and that migrants make local habitat decisions without prior knowledge of habitat conditions (Hutto 1985, Loria and Moore 1990, Moore et al. 1990, Moore and Aborn 2000, Petit 2000).

Some migratory species are flexible in their response to changes in seasonality, with variability in arrival dates among years (Crick et al. 1997, Hüppop and Hüppop 2003, Jenni and Kéry 2003, Lehikoinen et al. 2004, Stervander et al. 2005, Jonzén et al. 2006, Tøttrup et al. 2006, Swanson and Palmer 2009). In other cases, phenological responses are variable and inconsistent among species (Inouye et al. 2000, Both and Visser 2001, Gordo et al. 2005, Weidinger and Král 2007, Wilson 2007, Møller et al. 2008, Both 2010). Given inconsistency among species, it is unknown how most species will respond to changes in food availability or phenology driven by climate change, land-use change, or the interactions among them. However, species that are not able to adapt migratory patterns effectively to changing conditions at stopover sites may experience population declines. Food availability prior to and during migration clearly has the potential to impact the timing and duration of migration (Piersma 1987, Russell et al. 1992, Yong and Moore 1997, Newton 2006). Furthermore, populations that have responded to changes in resource phenology through advanced migration phenology may be less prone to declines than populations unable to advance the timing of their migration (Strode 2003, Møller et al. 2008). Differential responses may result in higher rates of population decline among long-distance migrants than among resident species (Sherry and Holmes 1996, Sanderson et al. 2006, Both et al. 2010). Migratory populations are likely to be affected negatively when migration events and periods of peak resources that were once synchronized become decoupled due to independent changes in phenology (Both 2010, Jones and Cresswell 2010).

Two factors—degree of phenological mismatch and migratory distance—influence the effect that changes in phenology will have on migratory populations (Jones and Cresswell 2010). Decoupling between migrant arrival and availability of resources can occur one of four ways:

changes in migration phenology, changes in resource phenology, changes in cue phenology, or a combination of factors (Jones and Cresswell 2010). For example, it is possible that changes in phenology of resources or cues are occurring in the Prairie Pothole Region of North America as the region is experiencing warmer winters (Swanson and Palmer 2009), which may cause earlier peaks in green-up of vegetation or invertebrate abundance. While resources and cues are dependent on local climatic conditions, migrant arrival at stopover sites is dependent on endogenous and external factors at overwintering locations, previous stopover sites, and predicted phenological conditions at breeding grounds (Gwinner 1996, Yong and Moore 1997, Marra et al. 1998, Ottick and Dierschke 2003, Studds and Marra 2011). Given the heterogeneous nature of climate and climate change, it is possible that migrants will not respond in the same manner to local phenological conditions at one or more stopover locations (Rosenzweig et al. 2008, Fontaine et al. 2009, Both 2010). If there is not a corresponding shift in avian migration, it will likely lead to a mismatch in timing of migration and resource availability that ultimately leads to a decrease in stopover success through reduced fat deposition, prolonged stopover duration, or direct mortality.

Here, we make predictions for how shorebird populations may respond to climate change by examining a number of possible climate change-induced phenological shifts. We then test our predictions with empirical data to examine the influence of local phenological factors on shorebird migration and invertebrate abundance to compare the potential sensitivity of shorebirds and their prey to climate change and other phenological factors.

SCENARIO DEVELOPMENT

We hypothesized patterns between shorebird migration and invertebrate food resources based on changes to the predicted historical relationship given hypothetical changes in phenology (Miller-Rushing et al. 2010). The Prairie Pothole Region's spring temperatures are expected to increase and result in advancing phenology, and all scenarios involve either no change or advances in phenology. Furthermore, our scenarios contain

an invertebrate phenology comparison between agricultural lands with reduced food availability versus grassland wetlands as the assumed historical condition.

Migratory shorebirds are known to select agricultural wetlands during stopover (Elphick and Oring 1998, Niemuth et al. 2006, Taft and Haig 2006) and may even prefer these habitats. However, agricultural wetlands often have lower food availability than grassland wetlands (Euliss and Mushet 1999, but see Taft and Haig 2005). Migrants may be able to buffer against the effects of using novel habitats through behavioral modification, but it is worth exploring how climate change might affect resource and migration phenology at preferred habitats because the degree of behavioral modification and, subsequently, the ability of migrants to adapt to change may be limited.

It is possible that shorebirds and other migrants may adapt to changing conditions brought about by climate change through behavioral modification or dietary flexibility or by making adjustments to migration routes. However, climate change and the corresponding changes in phenology may compound the impacts of land-use changes on shorebird stopover success in the midcontinent region, eventually resulting in population-level effects. If resource phenology shifts to earlier in the migration season and migrants do not adapt, shifts would likely prolong migration through increases in stopover duration and number, and they could delay arrival to the breeding grounds, which can reduce recruitment and lead to population declines (Piersma 1987, Kuenzi et al. 1991, van Eerden et al. 1991, Russell et al. 1992, Moore et al. 1995, Yong and Moore 1997).

Scenario 1: No Change

Here, we show the expected historical relationship between migration and invertebrate phenology with the added effect of migrants using habitats with reduced food availability (Figure 9.1a). Midcontinental migratory shorebirds prefer using agricultural wetlands for stopover, despite the likelihood that they have a lower abundance of benthic invertebrates. We predict this pattern if climate change does not affect the phenology of migrants or invertebrates in our study area.

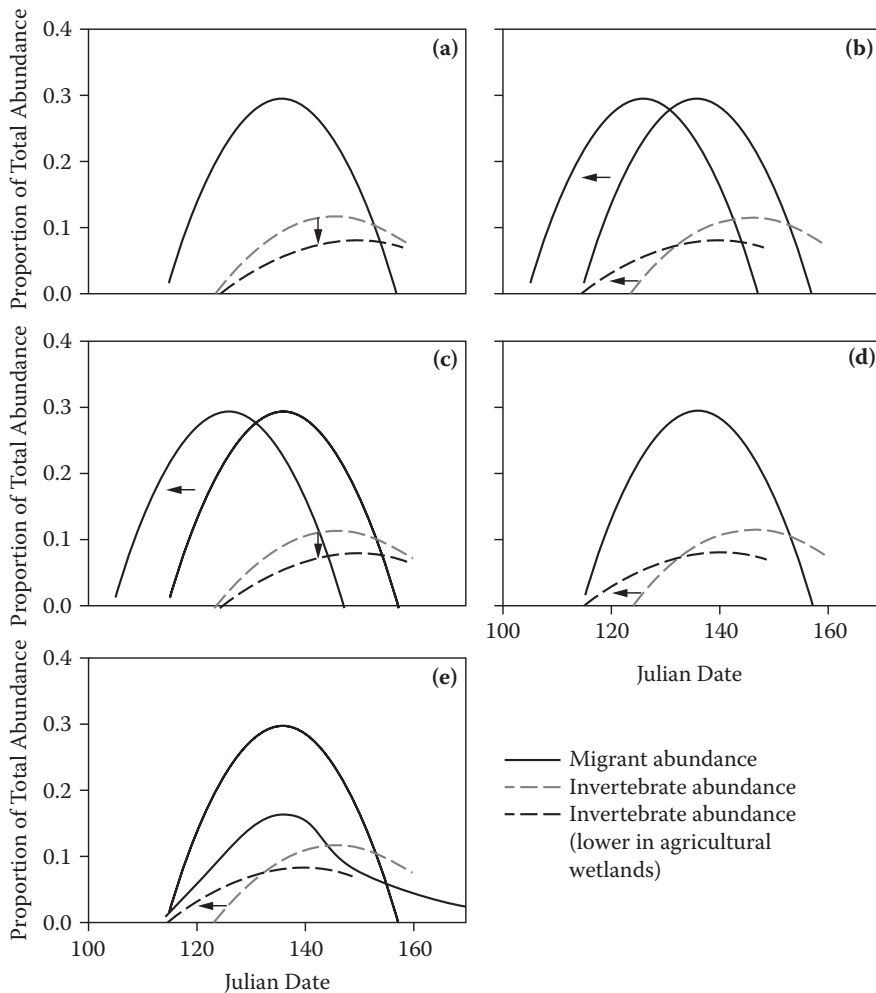


Figure 9.1. (a) Scenario 1: current conditions; available food resources in agricultural fields represented by lower dotted line. (b) Scenario 2: peaks in migration and food resources both occur earlier but the relationship remains unchanged. (c) Scenario 3: peak in migration occurs earlier but invertebrate phenology is unchanged. (d) Scenario 4: peak in migration remains unchanged but invertebrate food resources peak earlier. (e) Scenario 5: peak in migration remains the same but duration is extended. Earlier peak in food resources.

Scenario 2: Matched Advances in Migration and Invertebrate Phenology

Scenario 2 assumes that migration and invertebrate food resources both respond to changing climatic conditions by peaking earlier than under current conditions (Figure 9.1b). Here, invertebrates respond quickly to local changes in wetland conditions and migrants are able to respond at an equal rate. In this scenario, the relationship between migration and invertebrate phenology is unchanged, although migrants still face reduced food availability through a continued preference

for agricultural fields. An additional potentially negative effect of advancing migration phenology is increased exposure to extreme weather events (Moore et al. 1995, 2005; Decker and Conway 2009).

Scenario 3: Advancing Migration Phenology, but No Change in Invertebrate Phenology

Scenario 3 represents the relationship between migrant and invertebrate phenology if only migration advances (Figure 9.1c). This set of circumstances is likely to occur if southern stopover

or overwintering locations warm at a faster rate than stopover sites in the Prairie Pothole Region. The timing of migration is dependent on many complex factors, including endogenous factors, photoperiod, and conditions at overwintering grounds (Gwinner 1996, Marra et al. 1998, Studds and Marra 2011). Still, extreme late-winter warming in the southern latitudes may drive migrants to depart earlier, causing migrants to arrive prior to the peak in food resources.

Scenario 4: No Change in Migration Phenology, but Invertebrate Phenology Advances

Scenario 4 represents the phenological relationship if only invertebrate phenology changes (Figure 9.1d). Given that our study area is expected to experience warmer temperatures, such a response would likely manifest as an earlier peak in food resources (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003). Conversely, because previous stopover sites occur nearer the equator, they may not experience congruent changes in climate (Fontaine et al. 2009). Migration arrival dates are dependent on a suite of ecological conditions (Gwinner 1996, Yong and Moore 1997, Marra et al. 1998, Ottick and Dierschke 2003, Studds and Marra 2011), and any response is likely to occur at a larger temporal scale and may lag behind the response of invertebrate food resources at any one location in the migratory cycle (Jones and Cresswell 2010). Here, migration abundance peaks after the predicted peak in food resources, which may preclude migrants from achieving optimal migratory condition. In this case, migrants face depressed food availability in concert with the potentially negative effects of foraging in agricultural habitats.

Scenario 5: Migration Phenology Is Extended as Migratory Success Is Constrained by Advancing Invertebrate Phenology

Here, we show the same change to invertebrate phenology as in scenario 4, with the peak in food resources occurring earlier (Figure 9.1e). However, because migrants are likely to experience the effects of climate change at each stop during migration, the response to this suite of changing conditions would be cumulative. As a consequence of continuously missing periods of

peak resources at stopover sites, migrants would likely have to extend their stopover duration at each site, leading to a prolonged period of migration for individuals and the population.

METHODS

Study Area

We collected data in the Prairie Pothole Region of north-central North America, specifically McPherson, Edmunds, and Brown Counties in northeast South Dakota (Figure 9.2). This region of north-central North America is characterized by millions of small depressional wetlands left by receding ice sheets in the late Pleistocene and by a seasonal, relatively dry climate punctuated by severe droughts and deluges (Johnson et al. 2005). The region experiences daily average high temperatures between 14.1°C and 21.2°C and receives an average of 11.5 cm of precipitation during the 3-month study period (April–June). The region has high wetland density and diverse land-use practices, including row crops, rangelands, hay fields, and conservation reserve grassland as well as many native prairie remnants. Shorebirds use shallow water for foraging (Skagen and Knopf 1994, Davis and Smith 1998), and sampling was restricted to wetlands with seasonal and temporary hydrologic regimes to avoid sampling of unsuitable habitat (Stewart and Kantrud 1971). All sampling was done from early April through mid-June of 2010 and 2011 to encompass the entire migration period of all northbound migratory shorebirds in the region (Skagen et al. 2008).

Study Species

We limited our surveys of migratory shorebirds to seven species of arctic-nesting sandpipers (*Calidris* spp., Table 9.1). We established sample wetlands along nine road transects within the study area and surveyed shorebirds at 155 and 163 wetlands in 2010 and 2011, respectively, and visited 85% of the wetlands in both years. We selected transects following a systematic random sampling protocol, constrained by logistics like road passability and safety, and all transects were between 15 and 30 km long. We surveyed transects every 7–10 days, as this time exceeds average stopover duration for shorebirds in the region (Skagen and Knopf 1994) and reduces the likelihood of



Figure 9.2. Map of South Dakota, with inset of study area.

TABLE 9.1
*Species of migratory sandpipers and sample size (n) of birds
 observed during Spring migration in South Dakota, 2010 and 2011.*

| Species | | 2010 | 2011 |
|-------------------------------|-----------------------------|------|------|
| Baird's Sandpiper | <i>Calidris bairdii</i> | 46 | 170 |
| Dunlin | <i>Calidris alpina</i> | 1 | 6 |
| Least Sandpiper | <i>Calidris minutilla</i> | 54 | 217 |
| Pectoral Sandpiper | <i>Calidris melanotos</i> | 21 | 231 |
| Semipalmated Sandpiper | <i>Calidris pusilla</i> | 49 | 250 |
| Stilt Sandpiper | <i>Calidris himantopus</i> | 2 | 25 |
| Unknown small <i>Calidris</i> | <i>Calidris</i> spp. | | 254 |
| Unknown large <i>Calidris</i> | <i>Calidris</i> spp. | | 26 |
| White-rumped Sandpiper | <i>Calidris fuscicollis</i> | 258 | 364 |
| Total | | 431 | 1543 |

resampling individuals. To maximize detection of shorebirds, we only sampled wetlands that were located within 150 m of the transect. Wetlands along transects were separated by a minimum of 0.8 km, creating a sample of wetlands randomly distributed in different land-use types. Observers began surveys within an hour of sunrise and did not continue counts after 2 P.M. Using binoculars and a spotting scope, a single observer identified

and enumerated all *Calidris* that were visually detected either on the ground or in the air before alighting at the wetland during a 10-minute sampling window. We used a standardized sampling window in an effort to control for sampling effort and detection probability.

Due to small sample sizes for individual species, we analyzed pooled counts for all *Calidris* spp. Different species had subtle differences in

microhabitat use and foraging technique; however, differences were negligible in the scope of this study because migratory species of *Calidris* shorebirds occupy the same ecological niche whereby they forage in shallow water and mud-flat habitats for benthic invertebrates (Skagen and Oman 1996, Davis and Smith 2001, Skagen 2006). Stopover periods overlap, but do not coincide between species (Skagen et al. 2008), and by including all species in subsequent analysis, we improved the scope of inference of the study.

Migration Phenology

We compared migration phenology with wetland phenology as indicated by local characteristics. Total daily bird abundance across the study area was used as an index of migration phenology. We used generalized linear models (hereafter GLMs) with a Poisson distribution and included date as a covariate to examine the relationship between migration phenology (total daily abundance), mean daily values for green vegetation, invertebrate abundance, and daily minimum water temperature. We did an independent analysis for each year due to high variability in local conditions between years. However, we tested for the influence of green vegetation and water temperature on daily migrant abundance across 2010–2011, using year as a factor. We estimated the proportion of green vegetation of all nonsubmerged vegetation and shore within 10 m of the water's edge for each wetland. Timing of spring green-up is an indicator of wetland phenology and migrating species use vegetative characteristics as a cue to select sites with favorable foraging conditions (McGrath et al. 2009). We measured green vegetation as a potential cue because it changes predictably through the season and we hypothesized that it may indicate food availability.

Food availability is a primary concern for migratory species and is often cited as the limiting resource during stopover (Hutto 1985, Moore et al. 1995, Newton 2006). The relationship between migration phenology and benthic invertebrate abundance is important because the two are influenced by climatological variables at different scales that are not expected to change uniformly with climate (Cresswell and McCleery 2003, Visser et al. 2004, Fontaine et al. 2009, Jones and Cresswell 2010). We included water temperature in the migration phenology model

as a predictor and potential driver of local phenology. Temperature is known to influence the overall phenological progression of invertebrates (Corbet 1964, Wiggins et al. 1980, Hogg and Williams 1996) and may act as a reliable indicator of food potential. Furthermore, invertebrates are expected to be sensitive to changes in temperature associated with climate change (Bale et al. 2002). Both vegetation and temperature have the potential to change in response to climate and create a mismatch in the cue–resource relationship. A key distinction, however, is that migrants are likely responding to vegetation as a cue, whereas the invertebrate community is likely responding to water temperature to assess optimal emergence conditions.

We deployed temperature loggers (HOBO pendant loggers, Onset Instruments) in the water column using a weight and buoy system that ensured that they remain at a consistent depth (2010: $n = 21$; 2011: $n = 51$). Data loggers recorded water temperature every hour and were deployed before migration began (late April) and retrieved after northward migration through the region was completed (late June). We performed all analyses using the minimum mean daily temperature as an indicator of biophenological progression.

Invertebrate Phenology

In 2011, we measured benthic invertebrate availability at 26 wetlands. We resampled each wetland up to three times every 10–14 days or until dry, resulting in 70 wetland sampling visits. Three soil cores were taken within a 3×3 m sample plot to a depth of 5 cm using a 5-cm-diameter corer (Sherfy et al. 2000). We selected three to five plot locations at randomly selected compass bearings from the wetland's center point for a total of 9–15 soil cores per wetland per sampling session. In all cases, we ensured that plots were separated by >10 m. We then washed core samples through a 0.5-mm soil sieve and enumerated invertebrates at the wetland to establish relative abundance. We did not classify benthic invertebrates because *Calidris* sandpipers exhibit high dietary plasticity across invertebrates (Skagen and Oman 1996), allowing individuals to feed opportunistically as they move across latitudes and encounter different communities. Invertebrate biomass may be a better index of total caloric availability, but invertebrate abundance is generally correlated

with biomass and responds similarly to changing conditions (Whiles and Goldowitz 2005, Hamer et al. 2006). We predicted that shorebirds are more likely to forage on larger prey items, which would create a scenario where a lower abundance of individual prey items would result in disproportionately lower biomass available for foraging.

Using data collected in 2011, we compared local conditions with invertebrate abundance using a GLM that included date as a covariate. The importance of food availability to migrants is well documented and invertebrate populations are sensitive to changes in temperature (Wiggins et al. 1980, Bale et al. 2002), creating a potential for the primary resource of migrant shorebirds to undergo relatively rapid changes in phenology that may result in a disparity of the cue–resource relationship. We compared estimates of invertebrate abundance to water temperature values from the wetland data loggers and with estimates of dissolved chlorophyll *a* from wetlands where invertebrates were sampled. We hypothesized that these parameters would influence invertebrate abundance and might be even more sensitive as indicators of changing phenology. Before sampling invertebrates at each wetland, we measured the dissolved chlorophyll *a* fluorescence using an *in vivo* probe (Aquaflor handheld fluorometer, Turner Designs). Water samples were placed in the probe whereby a relative chlorophyll *a* reading is returned. Chlorophyll *a* is an indicator of phytoplankton growth and is a sensitive index of overall wetland productivity (Desortova 1981, Canfield et al. 1984).

RESULTS

Daily abundance of shorebirds was correlated with local conditions in both years. In 2010, migration phenology was significantly correlated with both green vegetation and water temperature (green vegetation: $F_{1,36} = 378.4$, $P < 0.001$; water temperature: $F_{1,36} = 13.3$, $P < 0.001$; date: $F_{1,36} = 104.4$, $P < 0.001$). Data from 2011 produced a similar pattern as all three phenological variables were significant (green vegetation: $F_{1,26} = 523.4$, $P < 0.001$; water temperature: $F_{1,26} = 62.7$, $P < 0.001$; invertebrate abundance: $F_{1,26} = 99.4$, $P < 0.001$; date: $F_{1,26} = 4.5$, $P = 0.035$). Across years, green vegetation and date were significantly correlated with daily migrant abundance (green vegetation: $F_{1,69} = 1743.4$, $P < 0.001$; water temperature:

$F_{1,69} = 14.1$, $P = 0.294$; date: $F_{1,69} = 51.7$, $P < 0.001$; year: $F_{1,69} = 0.7$, $P = 0.41$). Invertebrate abundance was not significantly correlated with either water temperature or dissolved chlorophyll *a* but was significantly correlated with date (water temperature: $F_{1,30} = 0.1$, $P = 0.708$; chlorophyll *a*: $F_{1,30} = 0.2$, $P = 0.644$; date: $F_{1,30} = 5.2$, $P = 0.028$).

In both years, migrant daily abundance was positively correlated with water temperature early in the season before peaking and eventually became negatively correlated (Figure 9.3a). The relationship between green vegetation and daily migrant abundance showed an initial positive correlation in both years, before the peak of migration fell off (Figure 9.3b). Last, the relationship between bird migration and food availability showed that peak shorebird migration occurred immediately prior to peak resource availability (Figure 9.3c).

DISCUSSION

We provide a preliminary examination of the relationships between migratory shorebird phenology and local phenological factors, and we examine a number of scenarios and how they may affect shorebird populations. The potential consequences of climate change and the resulting changes in phenology to migratory shorebirds remain unclear. Migratory shorebirds use widely distributed habitats and the nature of migration requires individuals to make habitat decisions repeatedly in novel environments under temporal constraints (Moore et al. 1990, Moore and Aborn 2000, Petit 2000). Given the nature of the shorebird migratory strategies and their reliance on specialized habitats in midcontinental flyways, shorebirds may be particularly vulnerable to the effects of climate change. Alternatively, because migrants encounter a wide range of habitats and climatic conditions, they may be well suited to adapt to changing conditions. For example, it is well known that shorebirds use agricultural fields (Elphick and Oring 1998, Niemuth et al. 2006, Taft and Haig 2005) and may even prefer these habitats despite lower resource availability (but see Taft and Haig 2005). Thus, even under current conditions (Figures 9.1a and 9.2c), migrants still face the potentially negative effects of using a habitat type with lower food availability. However, migrants have seemingly adapted to a new suite of conditions by compensating for the limited

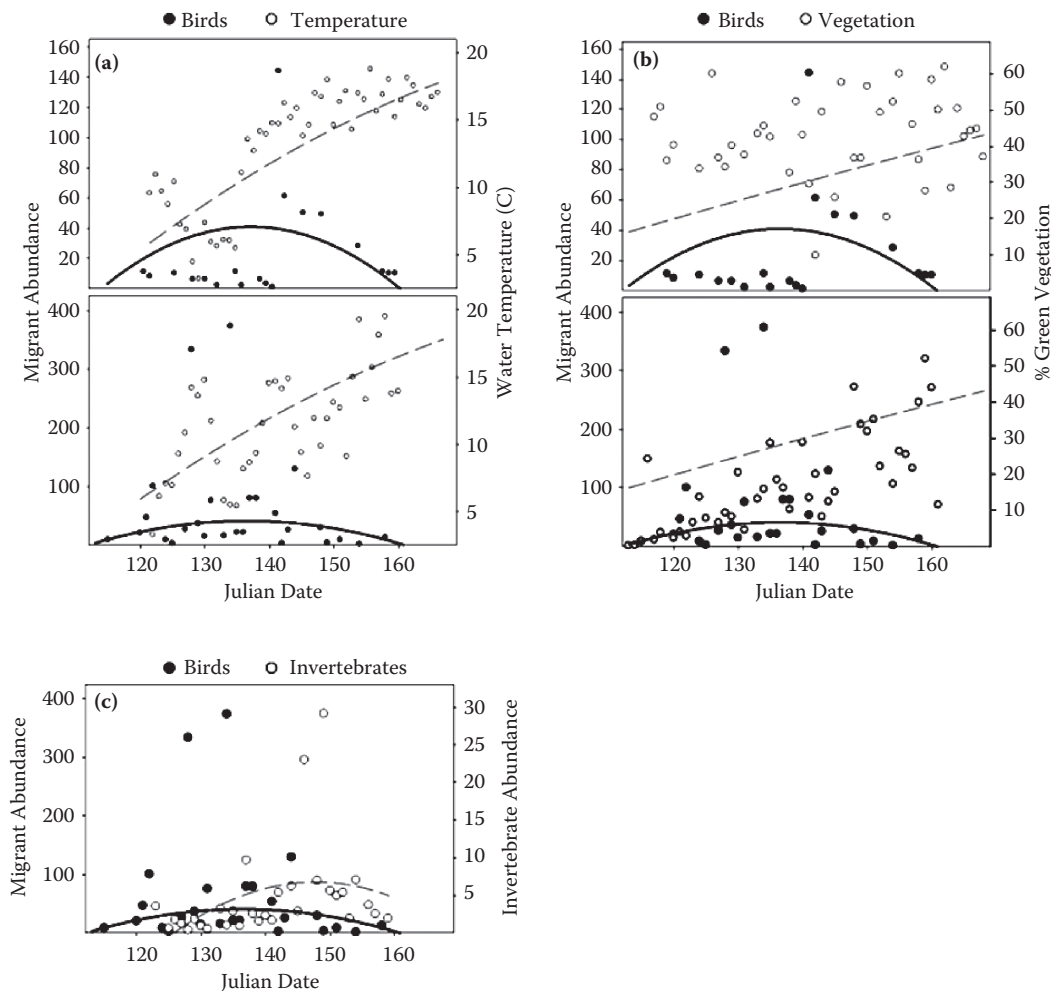


Figure 9.3. (a) In 2010 (top panel) and 2011 (bottom panel), total daily bird abundance increased with water temperature early in the season before declining. (b) Total daily abundance was positively correlated with green vegetation in both 2010 and 2011 until daily abundances peaked. (c) Total daily migrant abundance is correlated with invertebrate abundance (mean number per sample at each wetland) and peaked just prior to invertebrate peak, consistent with our predictions and suggesting a linkage between migration and invertebrate phenology.

food resources available in these habitats through behavioral modifications that optimize trade-offs with predation risk.

We considered the potential risks of changing phenology by examining the relationship between migration phenology and local phenological factors. Predictably, bird abundance increased throughout the early migration period before declining at the end of May. All three local phenological variables we examined were significantly correlated with shorebird abundance, but the relationship between abundance and green vegetation was inconsistent (Figure 9.3b). Bird migration apparently coincides with increasing

water temperature through the migration period and was significantly correlated with invertebrate phenology. In both cases, the pattern follows predictions if migrants are to optimize foraging opportunities, with the peak in migration occurring immediately prior to the peak in food resources (Figure 9.3c). By arriving slightly before the peak in resources (macroinvertebrates) or the abiotic factors driving resource phenology (temperature), migrating shorebirds ensure access to adequate food resources if stopover duration is extended. Early arrival is the most important phenological pattern because it indicates that bird migration is closely linked to timing of limiting

resources such as food (McGrath et al. 2009). We did not find any significant correlation between invertebrate abundance and the local phenological conditions that we measured. The relationship was slightly positive for chlorophyll *a* and slightly negative for temperature, which is inconsistent with what theory would predict, but may be a consequence of our small sample sizes. Given that landscape-level changes driven by agriculture have already caused shorebirds to prefer habitat with lower resource availability (J. J. Fontaine, unpubl. data), any changes to either invertebrate or migration phenology that is not congruent in both magnitude and direction could have severe impacts on migrant populations. Further negative impacts are possible because climate change is heterogeneous and migrants respond at different phenological scales than the resources on which they depend (Both and Visser 2001, Both et al. 2006, but see Marra et al. 2005).

Climate change is expected to be spatially and temporally heterogeneous and has been shown as such in the context of North American migratory bird species (IPCC 2007, Fontaine et al. 2009). Some species have shifted their phenology to match changing climatic conditions, but patterns are inconsistent across taxa (Root et al. 2003). We developed a number of predictions that represent possible scenarios of how invertebrates and migrants might respond to changing climatic conditions. While these are certainly simplified scenarios in the scope of global climate change, they explore a wide range of circumstances under which shorebird migration is likely to occur in the future. Our data show that migrant abundance peaks immediately prior to the peak in food availability (Figure 9.3c), a result that is consistent with the predicted relationship of scenario 1 (Figure 9.1a). We cannot reject the possibility that both migrant and invertebrate phenology has advanced with climate change as predicted under scenario 2 (Figure 9.1b). However, as the effects of climate change increase, it is possible that the phenological relationship between migrants and their food resources will be subject to further changes that could result in patterns shown by our scenarios and ultimately affect populations. Warming is known to lead to earlier migrant arrival in some species, suggesting that migratory species are flexible in their phenology (Crick et al. 1997, Hüppop and Hüppop 2003, Jenni and Kéry 2003, Lehtikoinen et al. 2004, Stervander et al.

2005, Jonzén et al. 2006). It is unclear if migrants will be able to adapt to changes in resource phenology at various locations along their migratory route, especially when that phenology does not change at the same amplitude in all locations.

Successful stopover depends on many environmental and behavioral factors and is driven by a multitude of selection pressures (Petit 2000, Newton 2006). Given that the primary reason for stopover is the acquisition of energy, adequate access to food resources is critical (Hutto 1985, Moore et al. 1995). Due to a collection of human impacts, migratory birds are often required to migrate through highly altered landscapes that may have reduced resource availability (Niemuth et al. 2006), and loss of stopover habitat is predicted to result in declines of migratory species (Skagen 1997, Weber et al. 1999, Harrington et al. 2002). However, some migrants, including arctic-nesting shorebirds, have shown the ability to adapt to alterations to stopover habitats (Krapu et al. 1984, Taft and Haig 2005). One possible reason for the persistence of migratory species despite habitat alteration is a strong phenological link between resources and migration. However, migrants may be less able to buffer against the consequences of using novel habitats if migration and resource phenology are no longer congruent due to climate change (Visser et al. 2004, Both et al. 2006, Both 2010, Jones and Cresswell 2010). Given that spring temperature changes may be more extreme at stopover locations than at breeding sites at the times when birds are using them (Fontaine et al. 2009), migrants may encounter novel trade-offs in resource availability en route. For example, migrants may advance migration to track similarly advancing invertebrate food resources at stopover sites (Figure 9.3b). However, birds may then be more likely to encounter adverse weather events en route or to reach the breeding grounds before adequate food resources are available (Alerstam 1991, Decker and Conway 2009). This scenario would seem unlikely if invertebrates are more sensitive to local conditions and if impacts of climate change are heterogeneous. However, it is the best-case scenario for conservation planners and, in that sense, is worth documenting.

Earlier peaks in migration may also allow individuals to extend stopover beyond the historical norm to take advantage of invertebrate peaks, given no change to food resource phenology (Figure 9.1c). Although the peaks in migration and

food availability become decoupled under this scenario, the fact that migrants still arrive prior to the peak in food resources may allow individuals to counteract the negative effects by changing stopover dynamics. Migratory species are highly adaptable in regard to stopover duration (reviewed by Newton 2006) and are known to stay longer when food resources are lower (Piersma 1987, Ydenberg et al. 2002) or when individuals have inadequate body reserves (Moore and Kerlinger 1987, Kuenzi et al. 1991). However, lean birds are unlikely to stay at stopovers with inadequate food reserves, prompting potentially risky flights that may result in mortality (Newton 2006). Extending stopover duration is not without costs, including increased risk of predation (Ydenberg et al. 2004). Given that stopover initiation is earlier in this scenario, individuals may not incur the potential costs of late arrival to the breeding grounds (Potti 1998, Currie et al. 2000, Weggler 2006). However, if resource phenology shifts to earlier in the year independently of migration phenology (Both et al. 2006; Figure 9.1d of this study), then migrants may not be able to obtain adequate energy reserves and population viability will be threatened. Such a conclusion is supported by the fact that migratory species that advance their arrival date are less likely to decline than those that do not (Møller et al. 2008).

While it is possible that climate change will negatively affect the integration of migration phenology and resource availability, resulting in population declines, the extent of such effects is unknown relative to more long-standing stressors such as habitat loss (Opdam and Wascher 2004). The likely scenario is that the effects of multiple stressors will interact and compound one another (Robinson et al. 2009). For example, climate change is predicted to alter precipitation and evapotranspiration rates and that is expected to alter wetland habitat in the midcontinental region (Johnson et al. 2005, IPCC 2007). However, such a change will also have implications on which crops are planted in the region and how they are cultivated, potentially leading to further land-use changes.

Furthermore, the push for alternative energy sources, such as corn-based ethanol, may motivate land owners to alter farming practices. The additive influence of continued land-use change and changing climatic conditions will obviously alter the wetland habitat upon which migrating

shorebirds rely (Euliss and Musket 1999, Gleason et al. 2003, Johnson et al. 2005) and, in doing so, further to affect shorebird migration in the region. Although migrants in general (Krapu et al. 1984, Stervander et al. 2005, Jonzén et al. 2006) and shorebirds in particular (Taft and Haig 2005) may be particularly adaptable to changing ecological conditions, it is unknown if they will be afforded the evolutionary time needed to adapt to such a suite of negative impacts. Further research is needed to examine the potential for land-use changes and changing climate conditions to act in concert to drive migrant species declines.

ACKNOWLEDGMENTS

We are grateful to field and lab technicians G. Rozhon, J. Gehant, C. Welch, J. Walker, P. Nepp, and V. Simonsen. We thank S. Skagen, D. Riveros-Iregui, J. Brandle, N. Alhadeff, and K. Decker for comments on previous drafts and Wren, Barley, and Caddis for their considerable support. Funding for this project was received from the US Geological Survey National Climate and Wildlife Science Center. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government. The Nebraska Cooperative Fish and Wildlife Research Unit is supported by a cooperative agreement among the US Geological Survey, the Nebraska Game and Parks Commission, the University of Nebraska, the US Fish and Wildlife Service, and the Wildlife Management Institute.

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