CHAPTER ONE

Leaps, Chains, and Climate Change for Western Migratory Songbirds*

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Abstract. Climate change has increased worldwide temperatures, affected seasonal patterns, and altered important sources of natural selection. To manage wildlife populations successfully, we must understand how patterns and processes of climate change alter trade-offs between sources of selection to predict how individuals may respond, populations may evolve, and management actions may ameliorate the costs of changing climates. Here we discuss how the migratory patterns of leapfrog and chain migration facilitate or constrain responses by migratory songbirds to spatial and temporal variation in climate change across western North America. Based on 52 years of climate data, we show that changes in average minimum monthly temperature differ significantly between the spring migration zone in the desert Southwest and breeding locations throughout western North America, and that these differences are most extreme for populations breeding at low latitudes (37°–49°) and exacerbated for species exhibiting leapfrog migration. Given the importance of climate in the evolution of migratory behaviors, such extreme alterations in the geographical patterns of climate may ultimately threaten the long-term population viability of species dependent on low latitudes for breeding or exhibiting leapfrog migration.

Key Words: chain migration, climate change, leapfrog migration, phenology, stopover habitat.

In response to recent changes in global climate, recognizing the degree to which species react to changes in seasonality is an area of increasing conservation concern, as species that are unable to respond are presumed to be at increased risk of extinction (IPCC 2001, Sæther et al. 2004, Rosenzweig et al. 2008). Some species are responding to changes in seasonality by altering phenology to ensure that annual life cycles coincide with optimal ecological conditions (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003). However, while many plant and insect populations have shown shifts in phenology, higher order consumers have responded to a lesser degree, increasing costs to individuals and ultimately impacting populations (Visser et al. 1998, Both and Visser 2001, Both et al. 2006).

In migratory birds, numerous accounts highlight phenological shifts in response to changes in seasonality (Crick et al. 1997, Hüppop and Hüppop 2003, Jenni and Kéry 2003, Lehikoinen et al. 2004, Stervander et al. 2005, Jonzén et al. 2006,

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Tøttrup et al. 2006), but considerable variation remains among species and even populations (Inouye et al. 2000, Both and Visser 2001, Strode 2003, Gordo et al. 2005, Rubolini et al. 2007, Weidinger and Král 2007, Wilson 2007, Møller et al. 2008, Askeyev et al. 2010, Both 2010). Recent research has begun to address the discrepancies, but has largely focused on aspects related to conditions at breeding grounds alone (Gordo 2007, Lehikoinen and Sparks 2010, but see Kanuscak et al. 2004, Both 2010). Due to their implicit dependence on spatially, temporally, and climatically separated habitats, understanding phenological responses of migratory species requires careful consideration of the effects of climate change across multiple temporal and geographic scales (Calvert et al. 2009). Moreover, because conditions during any period of the migratory cycle have implications for subsequent periods (Visser et al. 2004, Bearhop et al. 2005, Lehikoinen et al. 2006), particular attention must be paid to how changing climatic conditions at locations throughout the migratory cycle are interrelated to understanding how individuals and species will respond (Hedenström et al. 2007, Both 2010). For example, warming spring conditions at breeding grounds may favor earlier arrival and reproduction to optimize resource availability for the young (Crick et al. 1997, Both and te Marvelde 2007), but the benefits must be weighed against the cost of advancing migration and the corresponding timing of stopover events (Alerstam 1991, Both 2010). Shifts in the timing or duration of migration must ensure that birds are able to obtain adequate energy resources while avoiding predation and environmental hazards to arrive ultimately at breeding locations at the optimal time (Alerstam and Lindström 1990, Moore et al. 1995, Klaasen 1996, Gannes 2002, Moore et al. 2005). Given the degree of heterogeneity in climate change across landscapes and differences in the responses of local communities (IPCC 2001, Rosenzweig et al. 2008), changes in resource phenology due to climate change may differ greatly at stopover and breeding habitats, leading to differential selection, which may limit the response of individuals and populations to conditions at breeding grounds (Fontaine et al. 2009, Both 2010). However, despite the potential importance of migration in limiting populations (Moore et al. 1995, 2005) and clear evidence that climate change is both spatially and temporally heterogeneous (IPCC 2001, Rosenzweig et al. 2008), we know surprisingly little about how climates are changing across the vast geographical range that migrants occupy (Fontaine et al. 2009, Both 2010), which species and populations are most at risk (Møller et al. 2008), and how migratory patterns and behaviors may influence responses to changing climatic conditions (Petersen 2009).

As an important step in addressing these issues, we examined how the expression of two common migratory patterns, chain and leapfrog migration (Figure 1.1), either constrain or facilitate responses to heterogeneity in climate change for songbirds migrating across western North America. We developed a series of theoretical models that consider variation in the timing and distance of migration to assess how discordance in climate change between migratory regions in the desert Southwest and breeding regions throughout western North America may impact species that express different migratory patterns. Relating spatial and temporal variation in climate change to the timing, distance, and patterns of migration may help to elucidate the overall costs of climate change to individuals and to identify species and populations of particular conservation concern.

METHODS

We gathered unadjusted data from the US Historical Climatology Network (Williams et al. 2007), Alaska Climate Research Center (2009), and Canadian National Climate Data and Information Archive (2009) for 143 weather stations representing 13 states, two provinces and two territories (Figure 1.2). To minimize missing data, we limited our analysis to monthly climate data from 1954 to 2006 for the months of March–June. We were interested in assessing the potential for mismatches between migratory phenology and resource phenology across the spring migratory period, and we limited our analysis to changes in temperature alone. Precipitation clearly plays an important role in the dynamics of the arid systems, particularly as it pertains to productivity and diversity (Sharifi et al. 1988, Bowers 2005, Miranda et al. 2011), but the role of precipitation in phenological events is more ambiguous (Cleland et al. 2007). While precipitation may influence phenology (Llorens and Penuelas 2005,

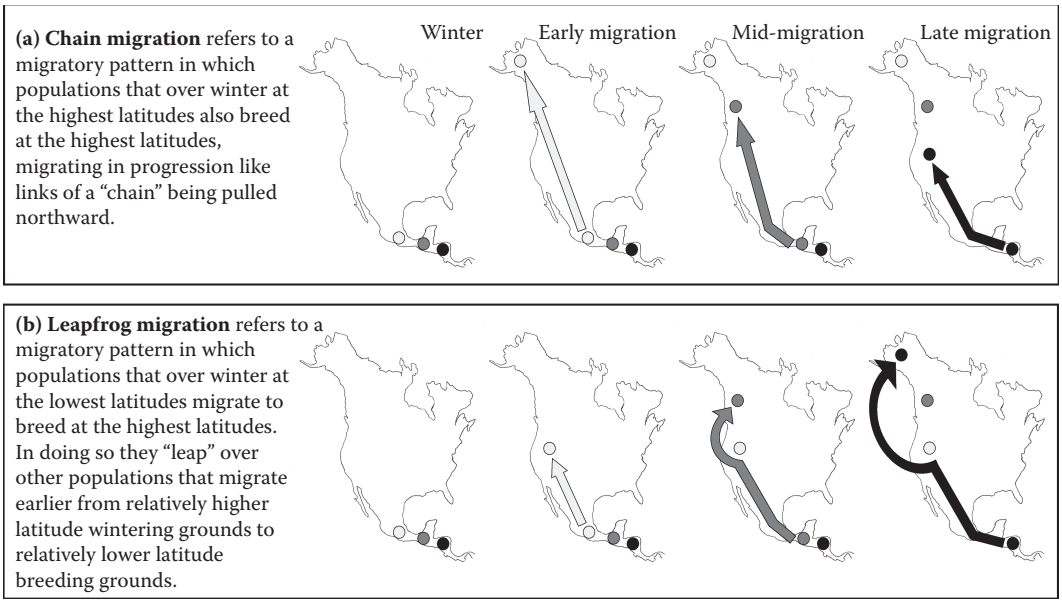

Figure 1.1. Songbird species exhibit a variety of migratory strategies, including (a) chain migration and (b) leapfrog migration. In western North America, species as diverse as Yellow Warblers (*Setophaga petechia*), White-crowned Sparrow (*Zonotrichia leucophrys*), Fox Sparrow (*Passerella iliaca*), and Wilson's Warbler (*Cardellina pusilla*) exhibit leapfrog migration, while American Coot (*Fulica americana*), Sharp-shinned Hawk (*Accipiter striatus*), Hermit Thrush (*Catharus guttatus*), and American Redstart (*Setophaga ruticilla*) are all known to exhibit chain migration. Unfortunately, the migratory strategy of many species remains unknown.

Crimmins et al. 2010), most examples outside of studies of monsoon cycles suggest interactions with temperature (Post and Stenseth 1999, Inouye 2008, Crimmins et al. 2010). Even in highly arid environments, temperature is a more reliable predictor of phenological events (Penuelas et al. 2002, Gordo and Sanz 2005). Moreover, the interannual and geographic variability of precipitation in arid systems is highly dynamic and unpredictable, making precipitation an unreliable climatic condition upon which to evolve a general migratory strategy. Thus, for each station we recorded the latitude, longitude, elevation, and average minimum monthly temperature for each month over the 52 years. We focused on minimum temperature because, across a wide array of ecosystems, changes in minimum temperature are known to influence plant phenology (Crimmins et al. 2008), and thereby the cues some songbirds use to make settlement decisions (McGrath et al. 2009). More importantly, arthropod phenology, and thus the majority of food resources for migratory songbirds, exhibits a threshold response to temperature whereby development and proliferation cease below a given temperature (reviewed by Honěk 1996). Changes in minimum temperature, rather than average temperature, or other climatic conditions such as precipitation are therefore a more relevant estimation of the potential influence of climate change on songbird food resource phenology across the wide range of biomes present in western North America.

Utilizing complete case regression analysis (Haitovsky 1968), we estimated the slope for the change in minimum temperature over the 52-year period for each month, at each climate station (hereafter referred to as the rate of warming). We assigned months as either spring migration (March–May) or breeding arrival (April–June) based on generalities about when western songbirds migrate and arrive at breeding locations. Arrival, which is strongly correlated with the onset of breeding (Moore et al. 2005, but see Ahola et al. 2004), appears sensitive to changing climatic conditions (Jonzén et al. 2006) and has important fitness implications (Moore et al. 2005, Decker and Conway 2009). We also divided the climate stations into latitudinal bands based on generalities about where western songbirds are during migration (desert Southwest: 26°–35°,

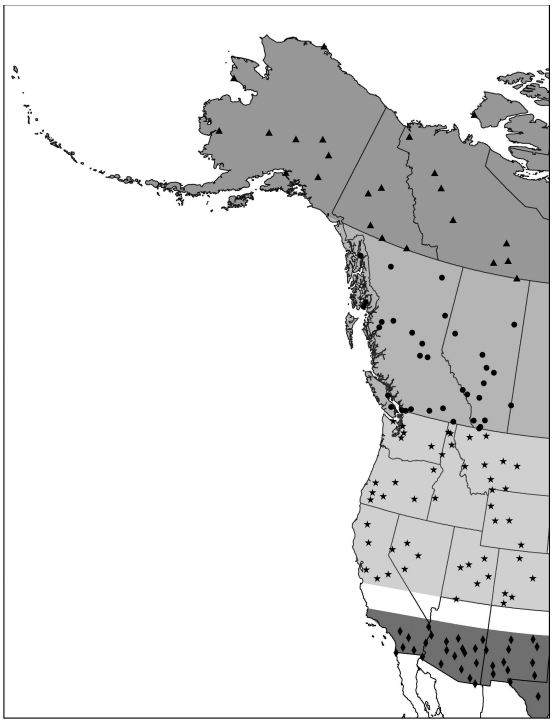

Figure 1.2. The distribution of 143 weather stations representing 13 states, two provinces, and two territories. All analyses were performed on unadjusted data from weather stations managed by the US Historical Climatology Network, Alaska Climate Research Center, and Canadian National Climate Data and Information Archive. Data were divided into four latitudinal bands representing high (▲, n = 23), mid (●, n = 35), and low (★, n = 50) latitude breeding populations as well as the migratory zone (◆, n = 35) used by all populations during the spring migration.

n = 35) versus breeding (western North America: 37°–72°), and further subdivided breeding areas into low (37°–48°, n = 50), mid (49°–59°, n = 35), and high (≥60°, n = 23) latitudinal bands to examine more closely how migration distance may influence the relationship between warming at migratory and breeding locations. Latitudinal bands were selected because they explained significant variation in the rate of warming across latitudes and because they represent important geopolitical zones with the low band representing the continental United States, the mid band the Canadian provinces and the panhandle of Alaska, and the high band the northern territories and the rest of Alaska (Figure 1.2). Choosing latitudinal bands based on climatological and geopolitical importance not only may help elucidate important biological phenomena, but also may facilitate management responses in geographically specific regions. To estimate the importance of spatial autocorrelation, we calculated Moran's I for the 16 possible latitudinal band months.

Utilizing the latitudinal bands to represent potential breeding populations, we developed a series of models to examine the relative rate of warming at migration and breeding locations based on all possible months of migration and arrival across western North America. First, we tested for spatial and temporal patterns using a global GLM (generalized linear model) that included month as a factor; latitude, longitude, and elevation as covariates; and the rate of warming as the dependent variable. We then assigned each station to a latitudinal band and added this categorical variable to the model to ensure that the general patterns continued to be representative.

After testing for the overall effect of month and latitudinal band, we compared the relative rate of warming of migratory habitats in the desert Southwest to breeding habitats throughout western North America by estimating the difference in the rate of warming between latitudinal bands (breeding $-\bar{x}$ migration). This comparison produces eight new values for each of the breeding

location weather stations representing the difference in the rate of warming for each of three possible migration and arrival months, but excluding the difference between May migration and April arrival as an impossible event. For example, to compute the difference in the rate of warming for a bird that migrates through the desert Southwest in April and arrives at a low latitude breeding area in May, we subtract the average rate of warming for the migratory zone of the desert Southwest in April from each of the low latitude climate stations. By repeating this process we were able to estimate the difference in the rate of warming for each breeding habitat weather station for all possible months of migration and arrival. Using the differences as the dependent variable, we developed an additional global GLM model that included migration month, arrival month, and latitudinal band as factors and latitude, longitude, and elevation as covariates to test for the overall effect of each categorical variable and the potential interactions on the relative rate of warming between migration and breeding habitats.

Last, to test the potential for leapfrog or chain migration either to constrain or to facilitate responses to spatial and temporal variation in climate change, we developed a simple model representing each migration type. We made assumptions about how the timing of migration and migration distance interact, such that chain migration is represented by March migrants arriving at high latitude breeding locations in April, April migrants arriving at mid latitudes in May, and May migrants arriving at low latitudes in June (Figure 1.1). In contrast, leapfrog migration is represented by March migrants arriving at low latitude breeding locations in April, April migrants arriving at mid latitudes in May, and May migrants arriving at high latitudes in June. Although the timing of migration and arrival events is theoretical, it is based on the limited information available on migratory patterns of species that stop over in the Southwest (Finch and Yong 2000, Skagen et al. 2005, Paxton et al. 2007, Carlisle et al. 2009, McGrath et al. 2009, Delmore et al. 2012) and general information about the timing of the breeding season at different latitudes throughout North America (Cooper et al. 2005). Using the values from the differences between breeding and migratory locations for each weather station, we tested whether the average difference in the rate of warming was greater for leapfrog or chain migration using a global GLM that included migration type as a factor and longitude, latitude, and elevation as covariates.

RESULTS

After breaking the 143 weather stations into latitudinal bands and considering the rate of warming for each of the months, only 4 of 16 latitudinal band months showed significant ($P < 0.05$) spatial autocorrelation as measured by Moran's index. Given the continuing debate over the benefits of correcting for spatial autocorrelations (Diniz-Filho et al. 2003, Hawkins et al. 2007, Beale et al. 2010) and the relatively weak correlations we found (Moran's I varied from 0.35 to −0.05), all further tests were run on uncorrected data. Over the 52-year period, we found that the rate of warming increased seasonally ($F_{3,428} = 18.72$, $P < 0.001$) and was sensitive to geographic location, but not elevation ($F_{1,428} = 2.18$, $P = 0.141$), with higher latitude ($F_{1,428} = 11.66$, $P = 0.001$) and more westerly locations ($F_{1,428} = 62.95$, $P < 0.001$) warming at a faster rate. When we divided the data into latitudinal bands, the latitudinal effect was lost ($F_{1,428} = 0.67$, $P = 0.415$), and replaced by the significant effect of the bands ($F_{3,428} = 7.95$, $P < 0.001$), indicating that much of the latitudinal variation was represented in the latitudinal bands. Longitude ($F_{1,428} = 66.68$, $P < 0.001$) and month ($F_{3,428} = 17.20$, $P < 0.001$) continued to influence the rate of warming, but there was also a significant interaction between month and latitudinal band ($F_{6,428} = 9.50$, $P < 0.001$).

Based on the estimated marginal means after controlling for elevation, longitude, and latitude, the average increase in minimum temperature for the 35 climate stations located in the desert Southwest was March: 2.35°C ± 0.28°C; April: 1.74°C ± 0.28°C; and May: 2.40°C ± 0.28°C. Using these estimates, we calculated the difference in the rate of warming for all climate stations throughout the three latitudinal bands. Differences in the rate of warming between migration and breeding locations were sensitive to temporal patterns of migration ($F_{2,863} = 33.16$, $P < 0.001$) and arrival ($F_{2,863} = 80.57$, $P < 0.001$). There continued to be a longitudinal pattern ($F_{1,863} = 137.79$, $P < 0.001$), but overall, the model showed limited spatial sensitivity (latitude: $F_{1,863} = 3.17$, $P = 0.075$;

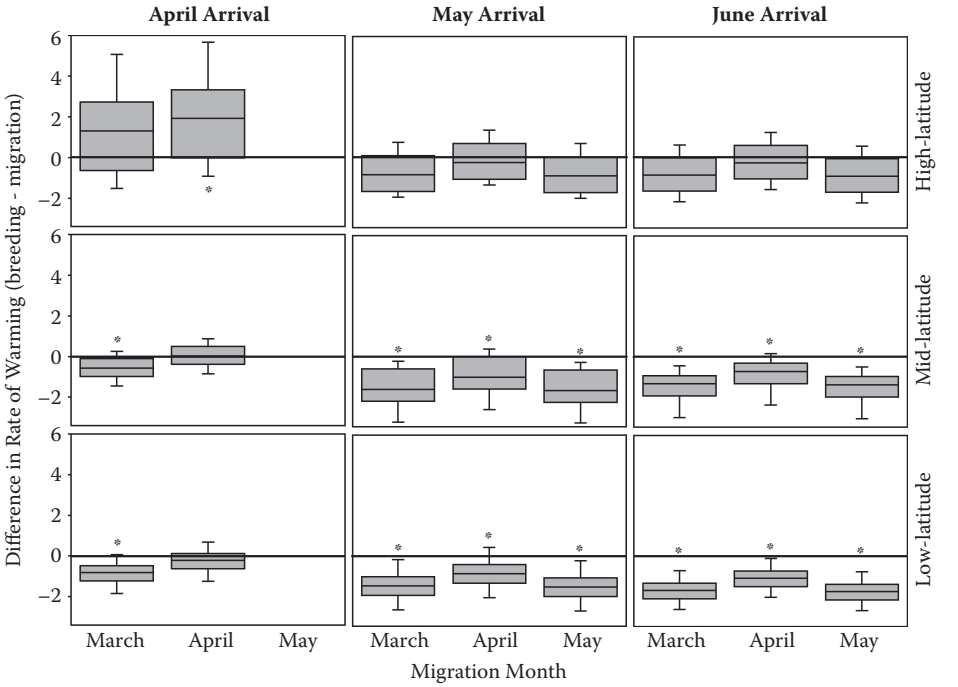

Figure 1.3. Significant differences in the rate of warming between migration and breeding habitats were shown by 15 of 24 hypothetical populations. When compared to the average rate of warming during migration, the rate of warming for breeding habitats was most consistently different for populations breeding at low latitudes and showed the smallest differences for populations breeding at high latitude and migrating in April. Box plots represent 5th, 25th, median, 75th, and 95th percentiles for the relationship between climate change at migration and breeding locations (breeding − $\bar{x}$ migration), where zero indicates breeding and migration locations are changing at the same rate, negative numbers indicate migration locations are warming faster, and positive numbers indicate breeding locations are warming faster. Boxes marked with asterisks are significantly different from zero at $P \leq 0.001$ level according to independent one-sample t-tests.

elevation: $F_{1,863} = 2.02$, $P = 0.155$; latitudinal band: $F_{2,863} = 2.45$, $P = 0.087$). There was, however, a strong interaction between spatial and temporal components resulting in 15 of 24 theoretical populations experiencing discordance in the relative rate of warming between breeding and migratory locations (Figure 1.3; migration month by arrival month by latitudinal band: $F_{17,863} = 2.35$, $P = 0.002$). Moreover, this interaction resulted in a significant difference in the relative rates of warming experienced by the different migration patterns with the theoretical populations expressing leapfrog migration experiencing greater discordance in the rate of warming between migration and breeding locations (Figure 1.4; migration type: $F_{1,215} = 5.21$, $P = 0.024$; longitude: $F_{1,215} = 40.40$, $P < 0.001$; latitude: $F_{1,215} = 0.06$, $P = 0.814$; elevation: $F_{1,215} = 0.47$, $P = 0.492$).

DISCUSSION

Avian migration is among the most well studied of phenological characteristics, yet despite our wealth of knowledge, we still have only a cursory understanding of the mechanisms underlying the ability of migratory birds to respond to changing climatic conditions (Møller et al. 2008). While we might assume that warmer spring temperatures will impose strong selection for earlier arrival at breeding locations, which in turn would lead to changes in the timing or duration of spring migration, such assumptions fail to consider the importance of selection during migration and, ultimately, the trade-offs that occur between advancing breeding phenology and advancing migratory phenology (Ahola et al. 2004, Kanuscak et al. 2004, Both 2010). Given that migratory

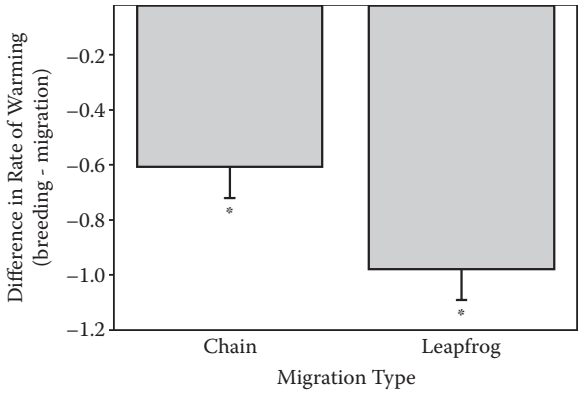

Figure 1.4. The relative discordance in climate change differs between chain and leapfrog migration. Migration type significantly influenced the relative difference in warming between breeding and spring migration habitats, with leapfrog migration seemingly experiencing greater discordance. Columns represent estimated marginal means (± SE) of the difference in warming at migration and breeding locations (breeding – $\bar{x}$ migration) after correcting for longitude, latitude, and elevation, where zero indicates breeding and migration locations are changing at the same rate, negative numbers indicate *migration* locations are warming faster, and positive numbers indicate *breeding* locations are warming faster. Columns marked with asterisks are significantly different from zero at $P \leq 0.001$ level according to independent one-sample *t*-tests.

birds are dependent upon spatially, temporally, and climatically separated habitats, successful management of migratory species requires careful consideration of the effects of climate change across multiple temporal and geographic scales (Calvert et al. 2009).

As an important step in understanding the potential implications of climate change on western migratory songbirds, we considered how spatial and temporal variation in climate change may interact with patterns and processes of migration to constrain or facilitate individual and population responses to changing climatic conditions. Our findings show that despite consistent increases in temperature throughout western North America, the relative rate of warming varied widely among locations and months, leading to significant differences in the rate of warming at migration versus breeding locations for 15 of 24 theoretical populations. While the long-term impact of climate change on migratory bird populations remains unclear, differences in the rate of climate change between migratory and breeding locations are likely to have significant fitness consequences that may constrain responses to climate change per se (Ahola et al. 2004). If we assume that current migratory patterns are adaptive, such that populations have evolved to optimize the timing and duration of migration to coincide with peaks in local phenology (McGrath et al. 2009), then discordance in climate change makes adapting to new conditions more challenging as individuals are forced to balance differential selection pressures among locations. For example, if warming (and thus local phenology) is advancing more rapidly at migratory locations than breeding locations, then individuals must:

1. Migrate earlier to optimize food availability en route (McGrath et al. 2009), but arrive at breeding grounds when food is limited and risk of severe weather is high (Decker and Conway 2009),
2. Time migration to optimize food availability at breeding grounds (Martin 1987, Moore et al. 2005), but after food availability has peaked en route,
3. Extend the migratory period to optimize arrival at all locations, but be exposed to increase risk of predation and severe weather (Moore et al. 2005), or
4. Alter migratory routes to optimize local phenology en route, but be exposed to novel habitats, food resources, and predators.

For each scenario, individuals are exposed to trade-offs that have important implications for migratory bird populations by reducing survival en route, reproductive potential at breeding locations, or potentially both. Moreover, because the trade-offs are in addition to potential costs associated with advancing migratory phenology per se, the potential impacts are likely greater than if climate change were occurring uniformly.

There are important implications for how spatial and temporal variation in climate change may affect the different theoretical populations that we examined. For example, populations breeding at the highest latitudes consistently show the least discordance in the rate of climate change they experience, while low latitude populations show the greatest discordance. This finding may offer an explanation as to why there appears to be a latitudinal gradient in the phenological response of migratory bird populations to changing climates (Sparks et al. 2005, Hüppop and Winkel 2006, Rubolini et al. 2007). While this phenomenon may simply reflect the corresponding latitudinal gradient in warming (IPCC 2001, Rosenzweig et al. 2008), our findings suggest that high latitude populations not only are under the strongest selection from warming at breeding locations, but also are the least constrained by patterns of warming during migration as local phenology is presumably advancing at a similar rate between migratory and breeding habitats. In contrast, populations breeding at low latitudes face the weakest strength of selection due to limited warming at breeding locations, while also experiencing the greatest discordance in the rate of warming between migratory and breeding locations. The apparent latitudinal gradient in the degree of discordance in warming between high and low latitude breeding populations may facilitate responses to climate change at high latitudes while simultaneously constraining responses at low latitudes. The resulting paradox is that even though climate change is less extreme, birds breeding at low latitudes may face more extreme costs relating to the relative timing and duration of migration and breeding, which may ultimately constrain their ability to respond to even minor changes in climate. As for high latitude breeding populations, there appears to be a much tighter correlation between the rate of warming at migratory and breeding habitats, but there may also be greater variation in the degree of discordance among locations within the high latitudinal band. For species that exhibit limited site fidelity or have a high dispersal potential, as may be expected for migratory birds, such variation in discordance may again ultimately constrain adaptive responses to changing climatic conditions.

Although the discordance between climate change at breeding and migratory locations was most extreme for populations breeding at low latitudes, within this region, populations arriving earlier faced less discordance. In contrast, high-latitude populations showed the opposite pattern with populations arriving later showing the least degree of discordance. In concert, the patterns are significant because they highlight the potential for strong directional selection on arrival timing beyond simply considering warming at breeding locations alone. Indeed, in the case of populations breeding at high latitudes, individuals arriving earlier face the greatest discordance in climate, thus, we might expect selection to favor delayed arrival—opposite what is expected from models that consider the effects of warming at breeding locations independently from warming at migratory locations. In contrast, the seasonal increase in the relative degree of discordance for populations breeding at low latitudes favors earlier arrival by migrants and therefore acts additively to what is expected from models that consider climate change at breeding locations alone.

Last, when we considered how patterns of migration might affect the discordance in the rate of warming between migration and breeding locations, we found that migration pattern may play an important role, with the relative rates of warming differing significantly between leapfrog and chain migration. Given the simplicity of our models, any relationship between migratory pattern and the potential costs of spatial and temporal variation in climate change is suggestive that the type of migration pattern a species exhibits has significant implications on the ability of that species to respond to changing climatic conditions. Indeed, our findings suggest that species exhibiting chain migration may be more resilient in the face of changing climates, a hypothesis that to our knowledge has not been previously tested and thus requires further exploration.

Here, we demonstrate that rates of warming vary substantially among locations occupied during the migratory cycle of western songbirds, and in doing so we highlight a nonintuitive source

of selection that may shape the phenology of multiple avian life-history traits. While in some instances spatial and temporal variation in climate change appears to facilitate responses to warming climates, in other instances it clearly constrains both evolutionary and phenotypic adaptation. Such complexity likely underlies the significant variation in the ability of migratory birds to respond to climate change, as has been previously noted by many authors (Crick et al. 1997, Inouye et al. 2000, Both and Visser 2001, Hüppop and Hüppop 2003, Jenni and Kéry 2003, Strode 2003, Lehikoinen et al. 2004, Gordo et al. 2005, Stervander et al. 2005, Jonzén et al. 2006, Tøttrup et al. 2006, Weidinger and Král 2007, Wilson 2007, Møller et al. 2008).

Variation in the response of migratory birds to climatic trends will likely continue to challenge conservation efforts (Parmesan 2007), but by exploring how spatial and temporal variation in climate change impacts migratory birds and how behavioral and life-history strategies both constrain and facilitate responses to climate change, there exists the possibility that research efforts may elucidate the overall costs to individuals and help identify species and populations of particular conservation concern. Although our findings only illustrate theoretical populations, they represent a key first step into developing proactive management strategies to mitigate climate change impacts. For example, in many species there are significant differences in the phenology, duration, and distance of migration among age classes and between sexes (reviewed by Cristol et al. 1999). In the American West, taxa as diverse as songbirds (e.g., Hermit Thrush, *Catharus guttatus*), raptors (e.g., Red-tailed Hawk, *Buteo jamaicensis*), shorebirds (e.g., Western Sandpiper, *Calidris mauri*), and even waterfowl (e.g., Mallard, *Anas platyrhynchos*) exhibit age- and/or sex-specific migratory segregation (Pattenden and Boag 1989, Cristol et al. 1999, Mueller et al. 2000, Stouffer and Dwyer 2003, Bishop et al. 2004). Although such strategies are assumed to be adaptive (Cristol et al. 1999), differential costs of climate change among sexes or age classes due to differences in migration distance or phenology may lead to differential selection within the same population, potentially decoupling evolved adaptive strategies. Unfortunately, excluding Mallards and Northern Pintail (*Anas acuta*), few migratory birds are managed for age- or sex-specific demographic parameters. The resulting outcome could manifest in reduced effective population size or reproductive potential, or altered population or breeding age structure. Similarly, races or populations of the same species also experience different sources of selection due to variation in the rate of climate change, but potential impacts appear particularly high for species that exhibit leapfrog migration.

Differential impacts of climate change represent a unique challenge as populations are rarely managed independently, and while we know the migration patterns for some species, migratory patterns for many species continue to remain an enigma (Blanchard 1941, Phillips 1951, Ryder 1963, Bell 1997, Clegg et al. 2003, Smith et al. 2003, Norris et al. 2006). These problems are further exacerbated because although species are often the target, management actions are carried out locally. Our findings suggest that, without an understanding of the migratory patterns of the species, and more specifically, the local population, it may prove difficult to mitigate against climate change impacts through local management actions alone. Moreover, because most management actions, even species-specific actions, affect the entirety of the community, an understanding of the migratory patterns of various species representing a multitude of populations may be necessary truly to understand and manage climate change impacts on migratory bird communities.

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