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LETTER

Spatial and temporal variation in climate change: a bird's eye view

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Abstract Recent changes in global climate have dramatically altered worldwide temperatures and the corresponding timing of seasonal climate conditions. Recognizing the degree to which species respond to changing climates is therefore an area of increasing conservation concern as species that are unable to respond face increased risk of extinction. Here we examine spatial and temporal heterogeneity in the rate of climate change across western North America and discuss the potential for conditions to arise that may limit the ability of western migratory birds to adapt to changing climates. Based on 52 years of climate data, we show that changes in temperature and precipitation differ significantly between spring migration habitats in the desert southwest and breeding habitats throughout western North America. Such differences may ultimately increase costs to individual birds and thereby threaten the long-term population viability of many species.

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1 Introduction

Global climate change has dramatically altered seasonal climate conditions and led to corresponding advances in phenology (Root et al. 2003). In migratory species, however, advances in phenology are often less than expected (Møller et al. 2008), indicating there may be significant trade-offs with other sources of natural selection. For example, in migratory birds the benefit of advancing breeding must be weighed against the cost of advancing migration (Alerstam 1991). Because many bird species stop en route to refuel, food availability at stopover locations directly influences survival and future reproduction (Alerstam 1991). Given the degree of heterogeneity in climate change across landscapes and differences in the responses of local communities (IPCC 2001), changes in resource phenology at stopover and breeding locations may differ greatly. However, despite the importance of migration in limiting populations (Alerstam 1991), and clear evidence that climate change is both spatially and temporally heterogeneous (IPCC 2001), we know little about the relative rates of climate change at migratory versus breeding locations and thus the potential for selection during migration to limit phenological responses to changing climates (Ahola et al. 2004).

As an important step in addressing this issue, we analyzed the degree of spatial and temporal variation in the rate of climate change between migratory and breeding regions used by > 200 species of migratory birds (Electronic Supplementary Table 1) known to travel through the desert southwest en route to breeding locations throughout western North America. Addressing climate change in the desert southwest may be particularly informative because it's an important wintering area for many short-distance migrants and acts as a migratory funnel for long-distance migrants traveling from the Neotropics.

2 Materials and methods

We gathered unadjusted data from the U.S. Historical Climatology Network (Williams et al. 2007), Alaska Climate Research Center (2009), and Canadian National Climate Data and Information Archive (2009) for 82 weather stations representing 10 states and 4 provinces (Electronic Supplementary Table 2). To minimize missing data we limited our analysis to monthly climate data for March–September of 1954–2006. We focused on minimum temperature and accumulated precipitation because plant and insect phenology, and thus the majority of avian food resources, appear most sensitive to these climate variables (e.g. Crimmins et al. 2008). We also recorded latitude and elevation for each station.

Utilizing complete case regression analysis, we estimated rates of change in temperature and precipitation over the 52-year period for each month, at each climate station. We tested whether rates of climate change were spatially and temporally variable using an ANCOVA that included month as a factor and latitude and elevation as covariates; however, because we were interested in comparing rates of change among regions when each is occupied by migrants, we categorized data by region and time as spring migration, summer breeding, or fall migration 'habitat categories' which we then added to the ANCOVA. Habitat categories were assigned based on generalities about when western birds migrate (Spring: March–May, Fall: July–September) and breed (Summer: May–July) and what regions are predominately used during migration (desert southwest: 31.35°–34.77°) versus breeding (western North America 37.28°–71.28°). The overlap in timing (May and July) and the close proximity of regions (280 km) makes this test highly conservative for detecting differences in the rate of climate change among habitat categories. Analyses were conducted on the complete data set, but for visual simplicity, where appropriate graphs represent mean changes for each station.

3 Results

Over the 52-year period, changes in precipitation varied among the 82 stations from an 18% decline to a 28% increase; however the rate of change was not influenced by latitude (Fig. 1a; $F_{1,574} = 1.361$, $p = 0.244$) elevation (Fig. 1b; $F_{1,574} = 0.29$, $p = 0.590$), or month (Fig. 2a; $F_{1,574} = 1.403$, $p = 0.211$). Changes in minimum temperature also varied among stations from a 5% decline to a 24% increase, but unlike precipitation, temperature changes were influenced by latitude (Fig. 1c;

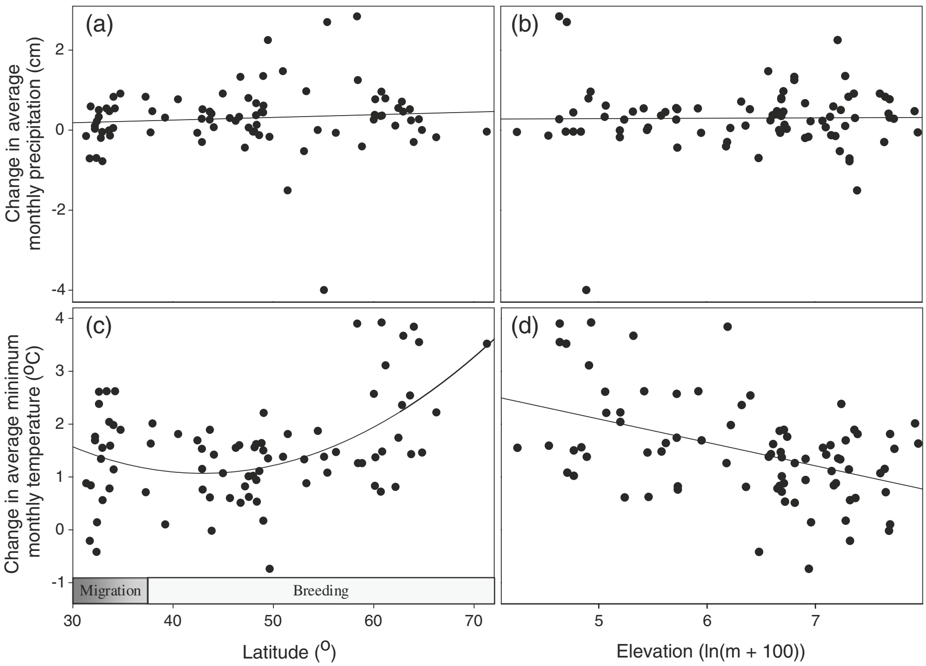

Fig. 1 Changes in temperature, but not precipitation, vary with latitude and elevation. Changes in precipitation are consistent across (**a**) latitudes ($r^2 = 0.008$) and (**b**) elevations ($r^2 < 0.001$); but changes in minimum temperature are more extreme at (**c**) higher latitudes ($r^2 = 0.256$) and (**d**) lower elevations ($r^2 = 0.212$). Elevations were natural-log transformed to correct for higher variance at lower elevations

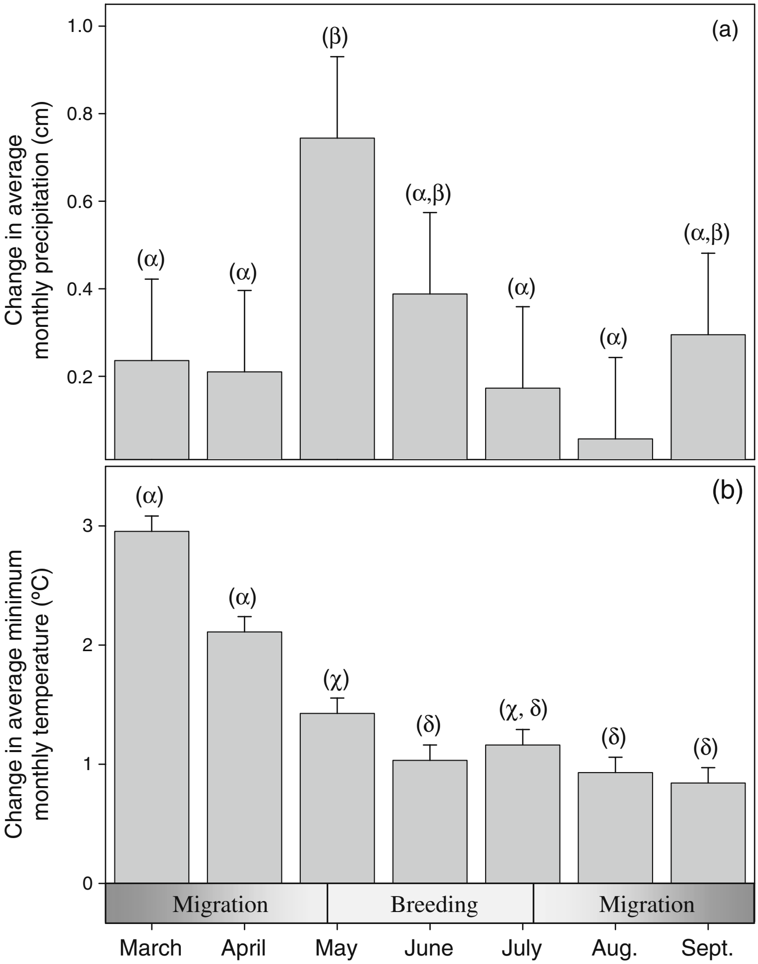

Fig. 2 Changes in temperature, but not precipitation, show a clear seasonal trend. Change in precipitation (**a**) did not differ among months or show any predictable seasonal pattern, but changes in temperature (**b**), differed among months resulting in a clear seasonal decline in the degree of warming. Columns are estimated marginal means (±s.e.m.) uniquely identified when significantly different at the 0.05 level according to an LSD post-hoc test

$F_{2,574} = 17.853$, $p < 0.001$), elevation (Fig. 1d; $F_{1,574} = 48.610$, $p < 0.001$), and month (Fig. 2b; $F_{1,574} = 35.765$, $p < 0.001$), with higher latitudes, lower elevations, and earlier months experiencing more drastic increases in temperature.

When adjusted to consider when birds are present in each region, there was a significant effect of habitat category on precipitation (Fig. 3a; $F_{1,306} = 4.769$, $p = 0.009$), with breeding habitats becoming significantly wetter, driven primarily by increasing May precipitation, as evident by the significant month effect ($F_{1,306} = 2.440$, $p = 0.026$). Habitat category also influenced the rate of temperature change (Fig. 3b; $F_{1,306} = 26.587$, $p < 0.001$), with spring migration habitats warming

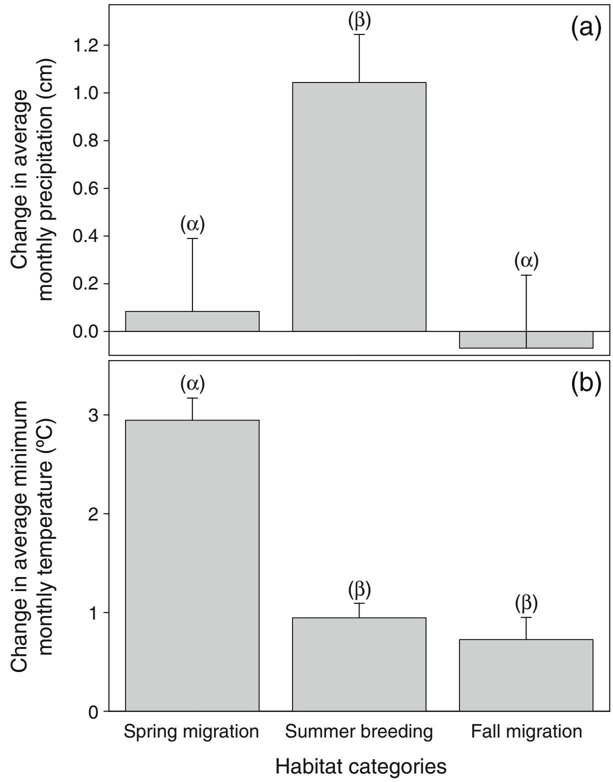

Fig. 3 Migratory birds experience differences in climate change among spring migration, summer breeding, and fall migration habitats. After accounting for when birds are present at breeding versus migratory habitats, climate change differed significantly between habitats, with birds experiencing relatively wetter breeding (**a**) and warmer spring migration habitats (**b**). Columns are estimated marginal means (±s.e.m.) uniquely identified when significantly different at the 0.05 level according to an LSD post-hoc test

significantly more than breeding or fall migration habitats. Moreover the effect of latitude ($F_{1,306} = 12.667$, $p < 0.001$), elevation ($F_{1,306} = 36.274$, $p < 0.001$), and month ($F_{1,306} = 2.067$, $p = 0.038$) continued to be prevalent within each category.

4 Discussion

Our findings show that despite consistent increases in temperature throughout western North America, the relative rate of temperature change varied widely among locations. Although the latitudinal pattern (Fig. 1c) would predict more extreme temperature changes at breeding habitats, we found that spring migration habitats experienced the most extreme increases in temperature (Fig. 3b). This result emphasizes the importance of seasonal declines in temperature change across western North America (Fig. 2b). Moreover, although we failed to find consistent patterns explaining changes in precipitation (Figs. 1a, b; 2a), habitat categories did differ significantly, with breeding locations becoming relatively wetter (Fig. 3a). In combination these findings demonstrate that not only are migratory birds experiencing climate change, but they are experiencing different rates of change throughout their migratory cycle.

To successfully manage future wildlife populations we must understand how climate change alters trade-offs between sources of selection to predict how individuals may respond, populations may evolve, and management actions may ameliorate increasing costs. In a critical first step in addressing this question, we demonstrated that climate change patterns, and thus potential sources of selection, vary significantly among the habitats occupied by birds migrating across western North America. From a bird's perspective, differing rates of climate change may have important fitness consequences. For example, that spring migration habitats are warming faster than breeding habitats likely creates discordance in plant and insect phenology between locations. If phenology is advancing faster at migratory stopover locations than at breeding locations, then individuals are faced with a difficult trade-off: 1) migrate when food availability is optimal en route (McGrath et al. 2009) and arrive at breeding grounds early when food is limited and risk of severe weather is high (e.g. Decker and Conway 2009), or 2) migrate after food availability has peaked en route, but arrive at breeding locations when reproductive potential is optimal. In both scenarios, increased costs to individuals are likely to have important implications for migratory bird populations by reducing survival en route, reproductive potential at breeding locations, or potentially both. Moreover, because costs are additive from one location to another, discordance in the phenology of even two locations may have cascading effects throughout an individual's migratory cycle (Alerstam 1991).

Here, we clearly demonstrate that rates of climate change vary substantially among locations occupied during the migratory cycle of western birds, and in doing so we highlight the importance of considering the potential for climate change per se to impact migratory populations, and perhaps more importantly, how differing rates of climate change throughout the migratory cycle may alter multiple sources of selection acting on individuals. Future research focused on relating spatial and temporal variation in climate change to the timing, duration, and patterns of migration for specific species will elucidate the overall costs of climate change to individuals and help identify species and populations of particular conservation concern.

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