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POPULATION ECOLOGY – ORIGINAL RESEARCH

Climate and weather have differential effects in a high latitude passerine community

Jeremy D. Mizel[1] · **Joshua H. Schmidt**[2] · **Carol L. Mcintyre**[2,3]

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Abstract

Climatic factors act on populations at multiple timescales leading to the separation of long-term climate and shorter-term weather effects. We used passerine counts from 1995 to 2019 in subarctic Alaska (Denali National Park, USA) to assess the impacts of the prior breeding season's weather on breeding season abundance and the impacts of climate measured through shifts in elevational distribution. Weather and climate appear to have had opposing effects on the abundance of some shrub-associated species as evidenced by a positive response to nesting phase temperature over a 1-year lag and a negative response to warming-induced shifts in shrub-dominated habitats over the long term. The latter response was indicated by declines in abundance which occurred in some part through portions of these populations shifting upslope of our fixed sampling frame. Overall, the abundance of species was related to one or more of the lagged effects of weather and the effects of weather alone drove nearly twofold variation in annual abundance in most species. The effect of nesting phase temperature was a strong positive predictor at both community and individual species levels, whereas arrival phase temperature had weak support at both levels. The effects of total precipitation during the nesting phase and snowmelt timing shared mixed support at community and species levels, but generally indicated higher abundance following seasons that were drier and had earlier snowmelt. Together, our findings of opposing effects of climatic variables at different timescales have implications for understanding the mechanisms of population and distributional change in passerines in the subarctic.

Keywords Climate change · Passerines · Phenology · Subarctic · Weather

Introduction

Climate-mediated effects on populations are thought to be greater at high latitudes because these environments represent the geographic limits of species' tolerances (Roots 1989). The spring transition period in these environments is often unpredictable and comprises mortality risk (Brown and Brown 2000). Access to food is starkly delineated by snowmelt and peaks briefly, leaving little margin for producing offspring (Benson and Winker 2001). Extreme weather events may cause mortality or negatively affect individual body condition which in turn may affect reproductive output (Krause et al. 2016; Boelman et al. 2017). The lower temperatures associated with these environments also increase thermoregulatory costs, inducing a tradeoff between self-maintenance and parental investment (Kendeigh 1969; Custer et al. 1986; Pérez et al. 2016). In addition, the seasonality of high latitude environments forces considerable overlap of life history events in migratory species. This implies strong selection but limited flexibility in the timing of these events and, consequently, potential vulnerability to climate change (Wingfield 2008).

Despite the vulnerability of migratory species breeding in seasonal environments, the extent to which climate and weather affect their abundance across the different lifecycle phases is often not well understood, in part, because these

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✉ Jeremy D. Mizel
jeremy_mizel@nps.gov

[1] Arctic Network, U.S. National Park Service, 4175 Geist Road, Fairbanks, AK 99709, USA

[2] Central Alaska Network, U.S. National Park Service, 4175 Geist Road, Fairbanks, AK 99709, USA

[3] Denali National Park and Preserve, U.S. National Park Service, 4175 Geist Road, Fairbanks, AK 99709, USA

processes are often complicated by the presence of effects which carry-over from one phase of the annual cycle to another (e.g., Norris et al. 2004; Saino et al. 2004; Studds and Marra 2011). Studies of migratory birds breeding in temperate North America predominantly find support for weather experienced on wintering grounds affecting abundance in the subsequent breeding season but have found weaker evidence for the effects of weather encountered on breeding grounds (e.g., Wilson et al. 2011; Gorzo et al. 2016). However, weather effects on the abundance of passerines breeding at high latitudes have received relatively little study. Given the time constraints on breeding, the seasonality of the food source, and the presence of tradeoffs between self-maintenance and investment in young, fluctuation in weather and climate may strongly affect population dynamics in these environments. Thus, high latitude passerines are particularly well-suited to addressing hypotheses about the effects of weather and climate on abundance.

While weather may affect population dynamics over short timescales, the accumulated effects of weather over the long-term (i.e., the effects of climate) often involve interactions spanning multiple trophic levels which may induce lags in the response or a pattern of incremental change. Climate effects may take the form of long-term changes in habitat, ecosystem productivity, distribution, and community structure (e.g., Walther et al. 2002; Post et al. 2009). Identifying the respective, and perhaps conflicting, roles of weather and climate on population dynamics is key for understanding how passerine populations may be affected in the future.

Here, we use passerine counts conducted annually from 1995 to 2019 in Denali National Park and Preserve, Alaska, USA (Denali) to assess the impacts of both climate and breeding season weather on the relative abundance of ten migratory species. To do so, we used changes in elevational distribution as a proxy for long-term climate effects based on past work in Denali that found shifts in the distribution of the passerine community due to climate-driven changes in habitat (Mizel et al. 2016). We limited our assessment of weather-abundance relationships to the effects of weather in year $t - 1$ on abundance in year t under the assumption that weather may affect reproductive output which would be realized as variation in abundance in the subsequent year. We expected that climate-induced shrub expansion over the course of the study would result in parallel distributional changes among shrub-associated passerines that would be manifested as net population declines as these gradients shifted upward in elevation relative to our fixed sampling frame (Mizel et al. 2016). We expected that earlier snowmelt, lower precipitation amounts, and warmer temperatures during the arrival and nesting phases would positively affect reproductive output which would be realized as higher abundance in the following year. Support for this set of predictions would imply opposing effects of weather and climate on shrub-associated species in Denali which has implications for understanding the mechanisms of population and distributional change.

Methods

Data collection

We conducted passerine surveys along the easternmost 118 km of the 144 km Denali Park Road in the northeastern portion of Denali (63° 35.8′ N, 149° 38.2′ W). We established three survey routes each comprising 50 point count stations with 0.8 km spacing. These routes coincide with two routes that are used for the North American Breeding Bird Survey, but their respective starting and endpoints are offset. We used the combined data from both sets of routes which yielded 156 total points.

This portion of the road traverses upland coniferous forest, sparsely canopied woodland at treeline, dense riparian and upland shrublands, open shrublands within passes and near shrubline, and alpine habitats including *Dryas*, mixed dwarf shrub tundra, and fellfield. Consequently, the road serves as an elevational transect, capturing an assemblage of passerine species that are distributed according to various vegetation types. Under a broad classification of habitat, we considered six shrub-tundra passerines, one species associated with both forest and open shrublands, and three species associated with forest (Online resource 1).

Trained observers conducted repeated surveys from mid-April to early July and points were surveyed 2–18 times in each year (mean = 5.3 visits/year). Not all points were surveyed in all years. Standard 3-min point count surveys were conducted during favorable weather from 0.5 h before sunrise to approximately 6 h thereafter, and all birds seen or heard within ~ 400 m during the count period were recorded (Bystrack 1981). For the purposes of our analyses, only detections of singing males were used.

Analyses

We used Poisson regression in a Bayesian framework to assess weather and climate effects on the relative abundance (hereafter, abundance) of Denali's passerines (Barker et al. 2018). Under this framework, the model for the log-transform of the mean count includes covariates of abundance in addition to covariates of detectability which are nuisance parameters (Link and Sauer 1997). We restricted our analysis to the ten most abundant species to ensure sufficient data to adequately model covariates of abundance and observation process-related noise. We fit a community-level model in which the observations y_{ijkt} corresponded to the counts made for each species $i = 1, 2, \ldots I$, at each point $j = 1, 2,$

…J, during each repeat survey $k = 1, 2, \ldots K$, in each year $t = 1, 2, \ldots T$.

We specified a model for the log-transform of the mean count λ_{ijkt}:

$$\log\left(\lambda_{ijkt}\right) = X'_{jt}\boldsymbol{\beta}_{1i} + W'_{it}\boldsymbol{\gamma}_{i} + Z'_{jkt}\boldsymbol{\beta}_{2i} + \varepsilon_{ijt},$$

where $\boldsymbol{\beta}_{1i}$ are species-specific vectors of fixed effects coefficients for distribution and trend, $\boldsymbol{\gamma}_i$ are species-specific random slopes for the weather effects, $\boldsymbol{\beta}_{2i}$ are species-specific vectors of fixed effects coefficients for the observation process, the X'_{jt}, W'_{it}, Z'_{jkt} are matrices of covariates, and the ε_{ijt} are normal random variables $N(0, \sigma_i^2)$ used to accommodate repeated sampling of sites within years and extra-Poisson variation.

The $\boldsymbol{\beta}_{2i}$ included coefficients for observation process-related noise and were focused on observer effects and temporal variation in the proportion of the population that was available for detection (i.e., seasonal and diurnal variation in singing intensity; Barker et al. 2018). We included the linear and quadratic effects of Julian date to account for variation in availability over a survey period that typically began prior to the arrival of some individuals and then extended past peak singing. We included the linear and quadratic effects of survey timing relative to sunrise to account for diurnal patterns in singing intensity. We also included an effect for an observer's experience conducting surveys in a prior year.

In addition to these observation process effects, we modeled changes in mean abundance and elevational distribution through the inclusion of trend terms, the linear and quadratic effects of elevation, and the interactions between all of these effects (Mizel et al. 2016). These effects (i.e., the $\boldsymbol{\beta}_{1i}$) were used to assess the indirect effects of climate in the form of distributional change occurring concurrently with the climate-driven migration of trees and erect shrubs into higher elevations in Denali (Stueve et al. 2011; Brodie et al. 2019). Specifically, this structure allowed us to assess changes in the overall shape of species' elevational distributions and to estimate shifts in their optimum elevations over time.

We also included four weather covariates representing the effect of weather in year $t-1$ on abundance in year t (Fig. 1). We acknowledge that weather effects may operate on breeding bird populations on lags of greater than 1 year (e.g., Anders and Post 2006; Pearce-Higgins et al. 2015a), although we did not consider these effects as doing so would have increased the chances of overfitting. In addition, exploratory modeling indicated that the effects of weather were weaker after 1 year (results not shown). We specified the species-specific effects

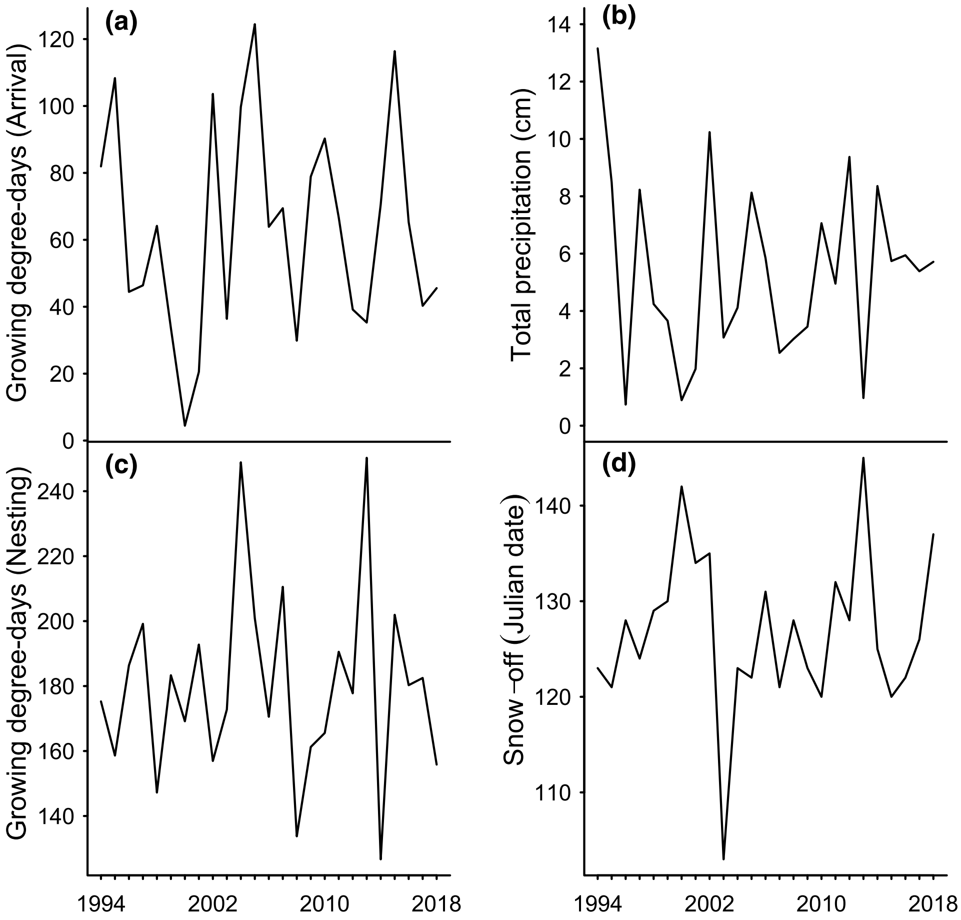

Fig. 1 Weather covariates used in analyses of passerine surveys in Denali National Park, Alaska conducted in 1995–2019. For the purpose of displaying covariates, we used white-crowned sparrow arrival and nesting phases

of four lagged weather covariates as random slopes using an exchangeable prior, $\gamma_{im} \sim N(\mu_m, \sigma_m^2)$ where μ_m is the mean (community-level) response for weather effect m and σ_m is the hierarchical standard deviation for that effect. The covariate data were derived from measurements made at a weather station located at Denali headquarters.

We separated weather effects according to arrival and nesting phases to better understand the mechanisms driving any weather-abundance relationships. Arrival-phase effects included the timing of snowmelt and cumulative growing degree-days (GDD; base 5 °C) during the arrival period for each species in year $t-1$. Nesting-phase effects included total precipitation and GDD observed during the nesting period in year $t-1$. Hereafter, we refer to the effects of GDD accumulated over arrival and nesting phases as arrival and nesting-phase temperature effects, respectively. We did not include the effect of precipitation during the arrival phase because we expected that precipitation would primarily affect reproductive output through variation in food availability and foraging efficiency when adults had the additional demand of feeding young.

We calculated temperature and precipitation variables over species-specific arrival and nesting periods to more accurately reflect the conditions experienced by each species (Online resource 1). The onset of the arrival period was based upon annual estimates of the earliest arriving cohort in our study area from Mizel et al. (2017). The end of the arrival phase marked the start of the nesting period which extended from the date of peak laying to the date of peak fledging for each species. The species-specific nesting periods were based upon observations in interior Alaska from Gibson (2011).

We fit the model in a Bayesian framework using Just Another Gibbs Sampler (JAGS) version 4.3.0 (Plummer 2003) via the runjags package (Denwood 2016) in program R 3.4 (R Core Development Team 2018). We specified vague normal priors for all regression coefficients and half-Cauchy priors for the hierarchal standard deviation parameters (Gelman 2006). We estimated the posterior distributions of the parameters from four Markov chain Monte Carlo chains run for 600,000 iterations. We assessed convergence visually and using the Gelman–Rubin diagnostic (Brooks and Gelman 1998). We scaled continuous covariates (mean = 0, SD = 1) to improve convergence properties. Inferences about the strength of weather effects were based upon whether 95% Bayesian credible intervals (CI) overlapped 0.

Results

All but one species (Fig. 2a) showed evidence of changes in elevational distribution over time, our proxy for climate change effects. With the exception of fox sparrow which showed range expansion (Fig. 3c), all shrub-associated species exhibited upward shifts in their optimum elevation which averaged 93 m (Fig. 3). Among this group, all but one species declined in total abundance across all points (by − 17 to − 55%; Online resource 2). In addition, two of four forest-associated species exhibited upward shifts in their optimum elevations which averaged 168 m (Fig. 2c, d) and a third showed increased abundance near treeline (i.e., in the 800–1000 m elevation zone; Fig. 2b). Total abundance increased by 80–161% in these three species (Online resource 2).

All ten species that we considered exhibited one or more of the lagged effects of weather on breeding season abundance (Table 1). The effect of temperature during the nesting phase was a strong positive predictor of abundance in the following year at both the community and individual species levels (Table 1). Precipitation during the nesting phase was also an important predictor and had a negative impact on abundance in the subsequent year at the community level, although individually, fewer species showed strong evidence of this effect (Table 1). The effect of snowmelt timing on abundance in the following year was not supported at the community level, but individually, five species showed evidence of this effect (Table 1). All of these responses were in the negative direction with the exception of white-crowned sparrow (*Zonotrichia leucophrys*), which by virtue of being the most abundant species likely contributed to the lack of an overall community-level response. Finally, temperatures during the arrival phase were poor predictors of the subsequent year's abundance with only white-crowned sparrow showing evidence of this effect (Table 1; Fig. 4a).

The seven species with relatively early breeding and arrival timing exhibited the positive effects of nesting-phase temperature, while the three latest arriving and breeding species (i.e., those that begin to arrive after April 27; Online resource 1) showed limited evidence of this effect. Variation in abundance of these later-breeding species was better explained by precipitation during the nesting phase and/or snowmelt timing (Table 1).

In general, the effect sizes of nesting-phase temperature, snowmelt timing, and precipitation were similar across species, although snowmelt timing had a particularly large impact on fox sparrow (*Passerella iliaca*) and yellow-rumped (myrtle) warbler (*Setophaga coronata coronata*) abundance in the following year (Fig. 4b). In combination, the effects of the lagged weather covariates alone produced nearly twofold variation in the annual estimates of expected abundance over the course of our study (Fig. 5). Parameter estimates for observation process covariates are presented as means and 95% credible intervals in Online resource 3.

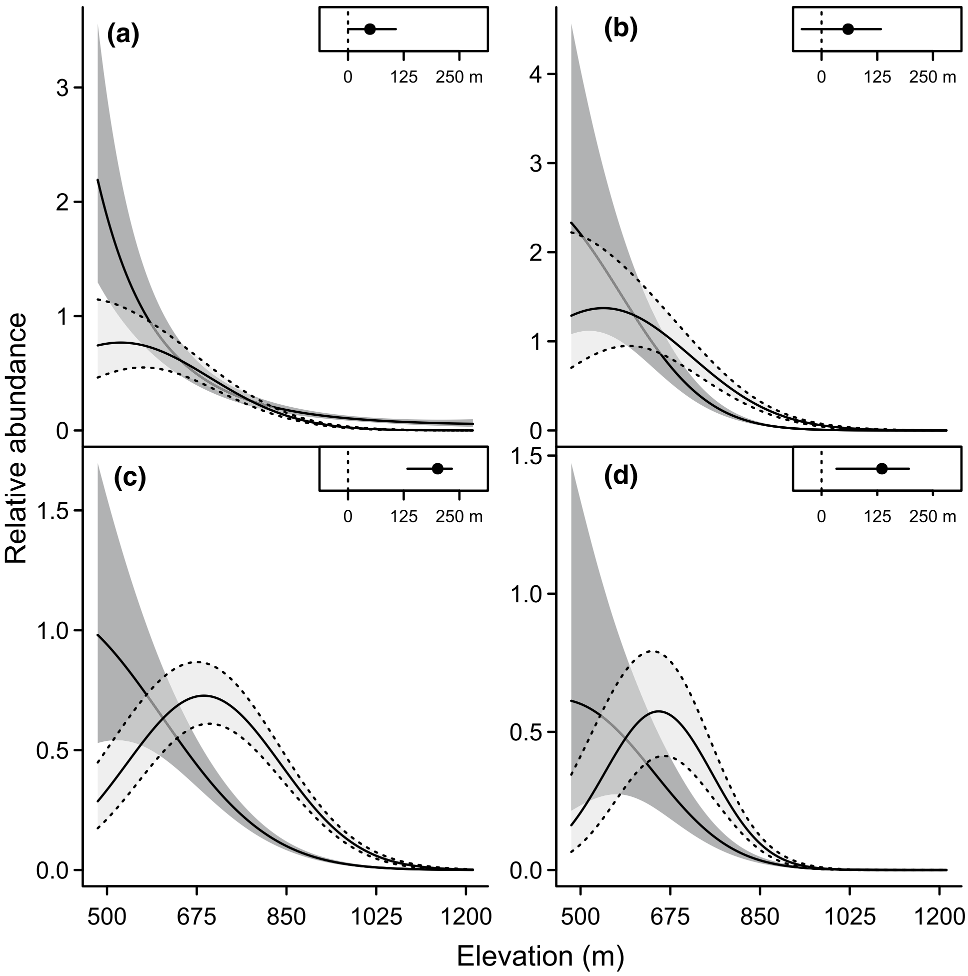

Fig. 2 Predicted abundance-elevation relationships for forest-associated passerines in year 1 (1995) and year 25 (2019) in Denali National Park and Preserve, Alaska. Posterior means for both years are solid lines and 95% credible intervals for 1995 and 2019 have gray and transparent fills, respectively. Insets show the estimated shift in a species' optimum elevation. Means and 95% credible intervals for elevational shifts were derived from the posterior distributions of species' optimum elevations in 1995 and 2019. Species include: **a** American robin, **b** yellow-rumped (myrtle) warbler, **c** dark-eyed junco, and **d** varied thrush

Discussion

We found support for the hypothesis that weather and climate can have opposing effects on passerine abundance due to differences in the temporal scales at which these factors act on populations. Specifically, we observed a positive response to nesting-phase temperature over a 1-year lag and a negative response to warming-induced changes in vegetation structure over the long-term in a subset of shrub-associated species. The latter response was inferred by net declines in abundance which occurred in some part through portions of these populations shifting upslope of our fixed sampling frame. This assemblage-wide shift in elevational distribution paralleled the climate-induced expansion of erect shrubs into higher elevations in the subarctic over time (Myers-Smith and Hik 2017; Brodie et al. 2019). Conversely, we observed upslope shifts and net increases in the abundance of most forest-associated species. These net increases were a partial outcome of upward expansion of their elevational distributions leading to a larger area of overlap with our sampling frame. This pattern of range expansion occurred concurrently with the upslope migration of treeline in Denali (Stueve et al. 2011; Brodie et al. 2019).

The potential for opposing effects of climatic variables at different timescales suggests caution in inferring the process by which climatic variables shape population dynamics and distribution. Many studies investigating the role of climate as a driver of passerine abundance and distribution rely on data from relatively few points in time, such as in resurveys of historical sampling sites (Tingley and Beissinger 2009; Tingley et al. 2012). Our findings suggest it may be difficult to distinguish climate from weather effects with limited temporal replication which is problematic for mechanistic inference when these effects happen to be in the opposite direction. In Denali, warming-induced changes in vegetation structure appear to be driving shifts in the distributions of shrub-associated passerines to areas lying outside of our sampling frame, implying a negative, indirect response to temperature over the long term. Without intensive monitoring revealing that these species are responding positively to temperature over short timescales, one may spuriously infer that the response reflects a negative response to temperature in the form of species tracking their physiological tolerances

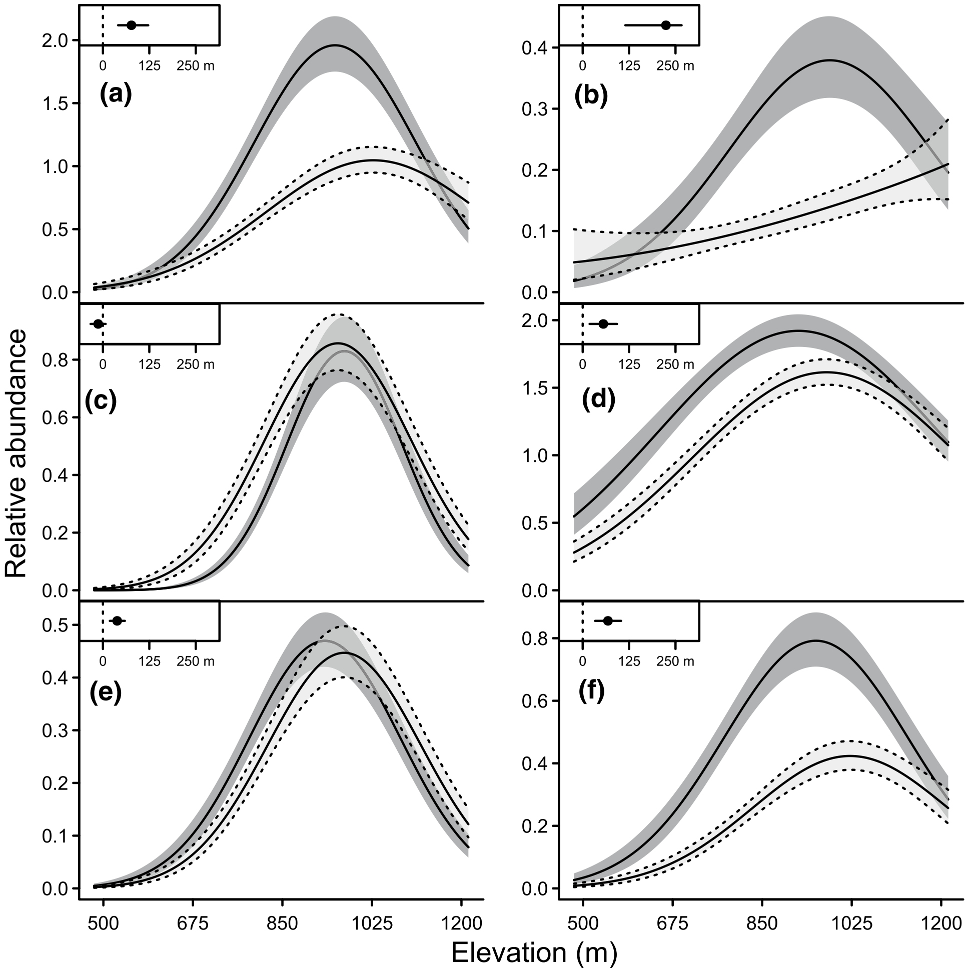

Fig. 3 Predicted abundance-elevation relationships for shrub-associated passerines in year 1 (1995) and year 25 (2019) in Denali National Park and Preserve, Alaska. Posterior means for both years are solid lines and 95% credible intervals for 1995 and 2019 have gray and transparent fills, respectively. Insets show the estimated shift in a species' optimum elevation. Means and 95% credible intervals for elevational shifts were derived from the posterior distributions of species' optimum elevations in 1995 and 2019. Species include: **a** American tree sparrow, **b** savannah sparrow, **c** fox sparrow, **d** white-crowned sparrow, **e** orange-crowned warbler, and **f** Wilson's warbler

or climatic niches through time. Therefore, we encourage practitioners to carefully consider the type and strength of inference possible under a particular sampling design, realizing that any contrasting effects of weather and climate may be inseparable without additional information.

In addition to being pervasive over the community, the effects of weather alone drove nearly twofold variation in annual abundance in most species, suggesting that variation in weather during the short breeding season is a major driver of population dynamics in this passerine community. The majority of species exhibited positive effects of temperatures during the nesting phase, whereas the effects of precipitation were less pronounced. These results are consistent with the observed pattern of latitudinal variation in the response of various taxa to weather; i.e., positive temperature effects are more prevalent among populations at intermediate to high latitudes whereas precipitation effects are more prevalent among populations at lower latitudes, particularly in drought-prone regions (Pearce-Higgins et al. 2015b).

The design of our study did not allow us to resolve the demographic processes underlying the observed relationships between weather and abundance, namely adult survival and the multiple parameters governing reproductive output. However, we suspect that the large effects of breeding season weather on the subsequent year's abundance primarily reflect the sensitivity of reproductive output to variation in weather. Bird species breeding in high latitude and altitude environments have undergone selection for coping with extreme weather and tend to exhibit more variation in fecundity than adult survival in relation to these stochastic events (Martin and Wiebe 2004). While inter-annual variation in the abundance of Denali's passerines certainly integrates fluctuation in adult survival, the latter is more likely to be a function of factors varying over large spatial scales (i.e., spanning the annual cycle; Morrison et al. 2016) and we do not expect that these multiscale factors would be strongly correlated with inter-annual variation in breeding season weather, particularly across a community of species that have widely dispersed passage and wintering areas.

In addition to affecting reproductive output and adult survival, weather may drive variation in breeding dispersal through its effects on spring phenology and resource availability during the territory settlement period, which could be realized as changes in abundance (Rushing et al. 2015;

Table 1 Posterior means and 95% credible intervals for weather effects on the abundance of passerines in Denali, 1995–2019

Species	β_0	$\beta_1\mathrm{GDD}^{\mathrm{Arrival}}_{t-1}$	$\beta_2\mathrm{GDD}^{\mathrm{Nesting}}_{t-1}$	$\beta_3\mathrm{precip}_{t-1}$	$\beta_4\mathrm{snowoff}_{t-1}$
Community mean	–	0.02 (−0.00, 0.05)	**0.06** **(0.03, 0.11)**	**−0.05** **(−0.09, −0.01)**	−0.04 (−0.10, 0.02)
Community SD	–	0.02 (0.00, 0.05)	0.05 (0.02, 0.10)	0.06 (0.02, 0.10)	0.08 (0.04, 0.14)
White-crowned sparrow	0.56 (0.51, 0.61)	**0.03** **(0.01, 0.06)**	**0.05** **(0.03, 0.07)**	−0.01 (−0.04, 0.01)	**0.06** **(0.04, 0.09)**
American tree sparrow	0.31 (0.24, 0.38)	0.03 (−0.00, 0.07)	**0.06** **(0.02, 0.10)**	−0.02 (−0.07, 0.02)	0.02 (−0.02, 0.07)
Fox sparrow	−0.20 (−0.29, −0.12)	0.00 (−0.05, 0.04)	**0.08** **(0.04, 0.12)**	**−0.13** **(−0.19, −0.08)**	**−0.12** **(−0.17, −0.07)**
Wilson’s warbler	−0.60 (−0.69, −0.51)	0.03 (−0.00, 0.07)	0.00 (−0.04, 0.04)	**−0.08** **(−0.12, −0.04)**	**−0.05** **(−0.09, −0.00)**
Orange-crowned warbler	−0.80 (−0.88, −0.71)	0.02 (−0.01, 0.05)	0.02 (−0.02, 0.06)	−0.01 (−0.05, 0.02)	**−0.07** **(−0.11, −0.03)**
Savannah sparrow	−1.53 (−1.66, −1.4)	0.01 (−0.04, 0.05)	0.05 (−0.01, 0.10)	**−0.10** **(−0.16, −0.04)**	0.00 (−0.07, 0.06)
American Robin	−2.63 (−2.79, −2.47)	0.03 (−0.01, 0.07)	**0.12** **(0.06, 0.19)**	−0.02 (−0.08, 0.04)	−0.02 (−0.10, 0.06)
Dark-eyed junco	−2.50 (−2.64, −2.36)	0.04 (−0.00, 0.09)	**0.07** **(0.01, 0.12)**	−0.01 (−0.06, 0.05)	0.02 (−0.05, 0.09)
Yellow-rumped warbler	−3.29 (−3.51, −3.09)	0.02 (−0.04, 0.06)	**0.09** **(0.03, 0.16)**	−0.04 (−0.12, 0.03)	**−0.12** **(−0.21, −0.03)**
Varied thrush	−4.59 (−4.93, −4.24)	0.03 (−0.02, 0.08)	**0.10** **(0.02, 0.19)**	−0.06 (−0.14, 0.03)	−0.09 (−0.20, 0.02)

Bold numbers indicate weather effect estimates with 95% credible intervals that do not include 0

Gorzo et al. 2016). However, this situation would more likely reflect weather effects on the current year’s abundance rather than its lagged effects. In addition, where breeding dispersal and/or propensity show large inter-annual variation, the lagged effects of weather may be more difficult to detect from count data alone, which was the not the case in our study. That is, when both processes are operating, they may have opposing or similar effects on abundance in any given year, limiting sensitivity to both effects. Such a pattern is evidenced in North American grassland birds which show relatively weak effects of breeding ground weather on the subsequent year’s abundance, but are also known to exhibit large inter-annual variation in breeding dispersal, responding in part to the presence or absence of drought conditions during the settlement period (Gorzo et al. 2016). These types of responses are illustrative of the potential for weather to affect populations on multiple timescales concurrently (i.e., on a 1-year lag and in the current year). Extending this concept further, variation in the abundance of invertebrate prey itself may be lagged relative to growing season weather which in turn may result in weather effects on bird abundance operating on multi-year lags (Anders and Post 2006; Pearce-Higgins et al. 2015a). Although we did not consider weather effects lagged over multiple years, seed crops of conifers (i.e., *Picea glauca*) in Denali appear to show a multi-year lag in their response to growing season weather (Roland et al. 2014), suggesting that other forms of plant reproduction and perhaps the abundance of higher trophic-level organisms (e.g., invertebrate larvae) could show similar patterns.

While inter-annual variation in breeding dispersal has important implications for abundance, we expect that the observed lagged effects of weather in Denali’s passerines reflect to a larger extent the role of weather-mediated access to food in regulating reproductive output. Although we found weak effects of temperatures during the arrival phase, delayed snowmelt had a strong negative effect on the subsequent year’s abundance for four of the ten species that we considered. In arctic tundra, invertebrate abundance shows a strong positive relationship with temperature (Tulp and Schekkerman 2008; Bolduc et al. 2013) and their emergence is closely linked with the timing of snowmelt (Høye and Forchammer 2008). Thus, early snowmelt, which is linked to earlier spring warming, may correspond to the increased availability of invertebrate prey during a period in which these resources are critical for renewing fat stores and producing eggs (Klaassen et al. 2001; Visser et al. 2004;

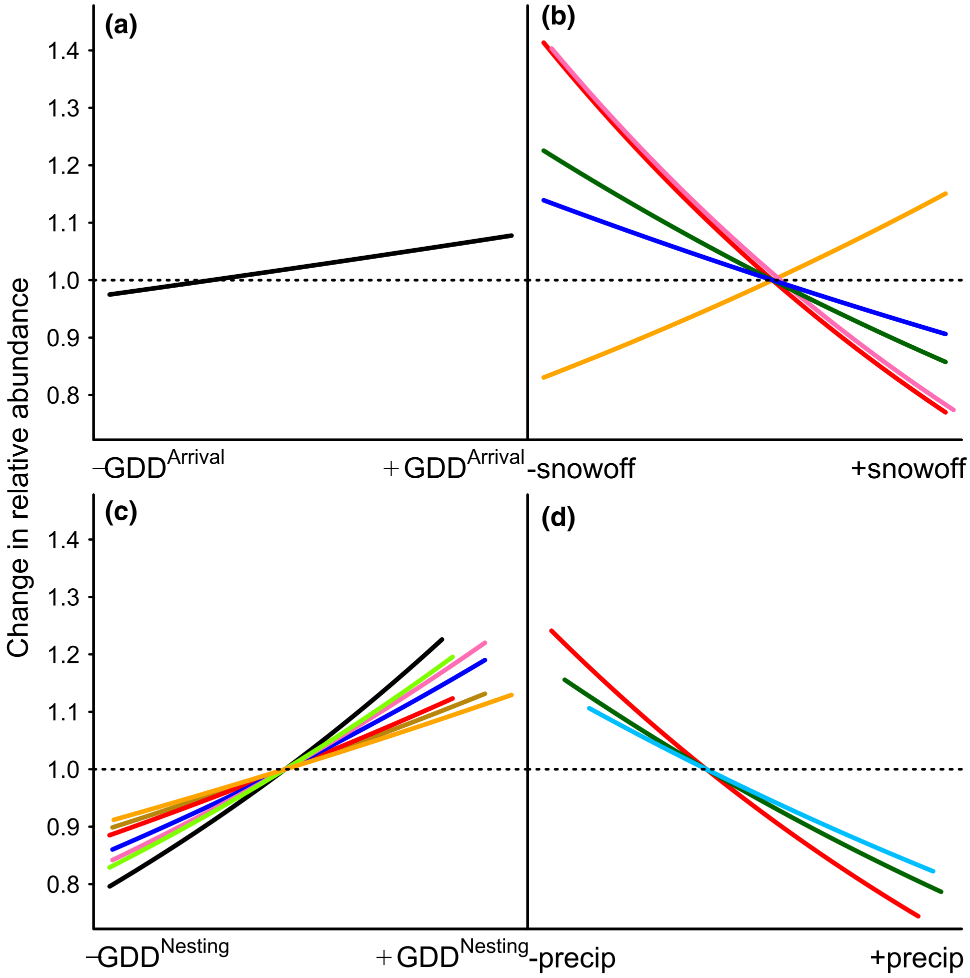

Fig. 4 Species-specific effect sizes for weather covariates. These represent the expected change in relative abundance per unit of the scaled covariate while holding the intercept and all other covariates at 0. That is, they are predictions of the exponentiated coefficients over the observed range of the covariate. The intercept has been removed to allow plotting the effects from all species on the same scale. Relationships are only displayed for those effects with 95% credible intervals that did not overlap 0. The line colors corresponding to each species are: white-crowned sparrow (orange); American tree sparrow (brown); fox sparrow (red); Wilson's warbler (light blue); orange-crowned warbler (pink); savannah sparrow (dark green); American robin (black); dark-eyed junco (purple); yellow-rumped warbler (dark blue); and varied thrush (light green)

Meltofte et al. 2008). However, the effects of snowmelt timing were heterogenous across the community. White-crowned sparrow showed a positive response to snowmelt timing, indicating higher abundance in years following delayed snowmelt. This species is apparently well-adapted to persistent snowcover and their response may reflect a different mechanism underlying variation in reproductive output than prey availability during spring, i.e., a linkage between deeper snowpack and a prolonged period before food availability is diminished (Morton et al. 1972).

Weather conditions during the nestling phase also directly affect food availability and nestling survival (Visser et al. 2004; Meltofte et al. 2007). It is this set of mechanisms that appear to be emphasized by our findings that the effects of temperature were largely restricted to the nesting phase and had greater support than the effects of snowmelt timing at both the community and species levels. Increased nest success has been linked to warm temperature anomalies (Skagen and Adams 2012), particularly in northern regions (Bolduc et al. 2013; Socolar et al. 2017) and may reflect weather-mediated variation in prey availability (Tulp and Schekkerman 2008). At lower temperatures, insect activity is reduced in tundra habitats, suggesting that foraging efficiency is lower (Bolduc et al. 2013). Lower temperatures also increase thermoregulatory costs, inducing a tradeoff between self-maintenance and parental investment (Kendeigh 1969; Custer et al. 1986; Pérez et al. 2016). Simultaneously, lower temperatures force females to brood young that are not yet endothermic, at the expense of feeding them (Lanctot and Laredo 1994; Hussell and Montgomerie 2002; Meltofte et al. 2007). Exposure of nestlings to periods of adverse weather may cause mortality (Low and Pärt 2009; Socolar et al. 2017) and snowstorms during the breeding season have a substantial effect on reproductive success in Arctic-breeding passerines (Chmura et al. 2018), although these events are less common in our study area. In addition, conditions experienced by nestlings may have carry-over effects on first-year survival (Mitchell et al. 2011).

Although the effect of nesting phase temperature had the most support across the community, the three latest arriving and breeding species showed weak evidence of this effect. Instead, two of these species exhibited the negative effects of total precipitation over the nesting phase which is consistent with extended periods of rain suppressing invertebrate

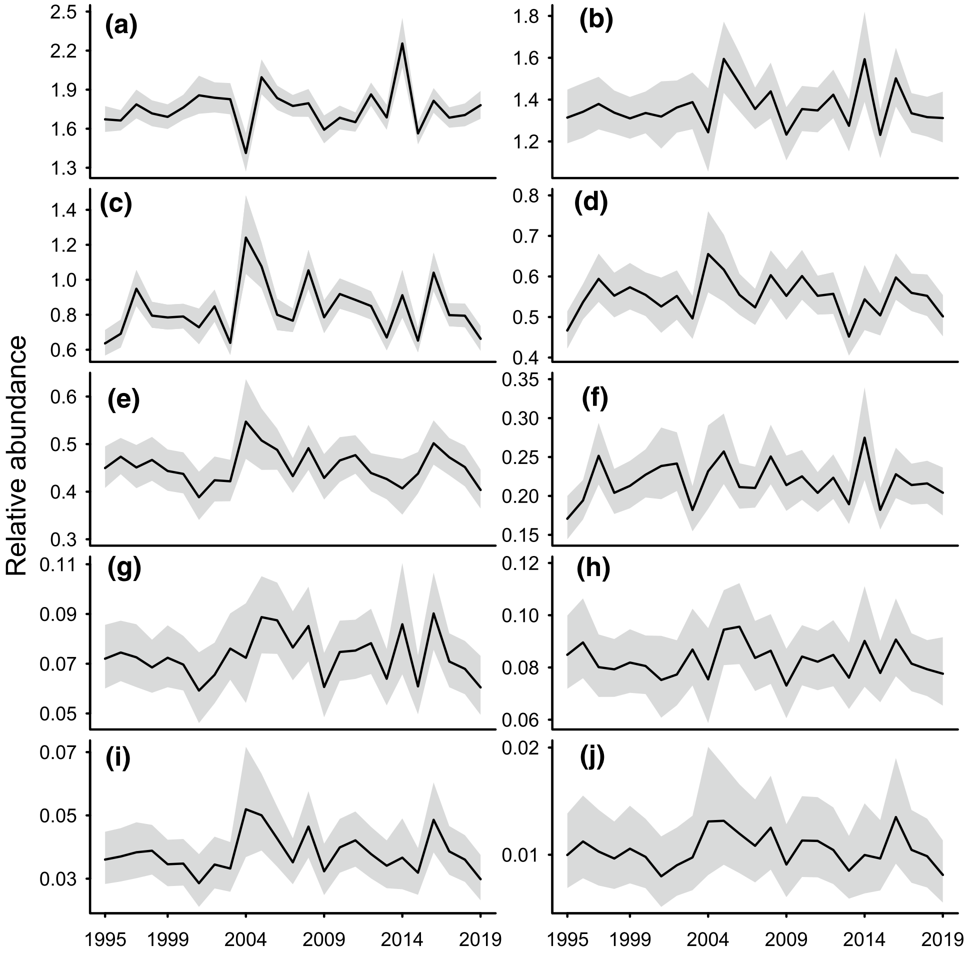

Fig. 5 Variation in relative abundance for ten passerine species breeding in Denali National Park, Alaska (1995–2019), as a function of weather alone. Predictions are a function of the intercept and the four weather covariates with all other covariates set to 0 (i.e., their mean values). Making predictions at the mean elevation has resulted in some forest-associated species displaying low abundance. Species include: **a** white-crowned sparrow, **b** American tree sparrow, **c** fox sparrow, **d** Wilson's warbler, **e** orange-crowned warbler, **f** savannah sparrow, **g** American robin, **h** dark-eyed junco, **i** yellow-rumped warbler, and **j** varied thrush. Shaded regions denote 95% credible intervals

activity and feeding of young (Skagen and Adams 2012; Öberg et al. 2015). While late-breeders were poorly represented in our study, the weak temperature effects exhibited by these species may be partially explained by their young typically hatching after a mid-summer shift towards a wetter weather pattern in Denali, as is evidenced by considerably higher precipitation amounts after the third week of June. Thus, access to food (i.e., food availability and foraging efficiency) may be more strongly correlated with precipitation in these species due to their nesting phase coinciding with a wetter weather pattern and a period in which there is lower incidence of relatively cold temperatures.

Warming at high latitudes is amplified (Clegg and Hu 2010; Stewart et al. 2013), suggesting that these systems will be disproportionately affected by climate change (Post et al. 2009). Under a warming climate, Denali's passerines are undergoing profound changes in population size and distribution. Warmer temperatures may be associated with higher reproductive output and/or adult survival in a given year, but in some cases, these effects may be partially overridden by vegetation change which is inducing shifts in the distribution of shrub-associated species to areas lying outside of our sampling frame. Thus, weather and climate effects may not be compensatory at the scale of our study area for some shrub-associated species. The complex roles of climatic variables in shaping population dynamics and distribution, and, in particular, their relatively large effects over short timescales may trigger potentially transitory changes in species abundance, and thus present challenges for accurate prediction of the community trajectory into the future.

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Author contribution statement JDM, JHS, and CLM conceived and designed the experiments. CLM and JDM performed the experiments. JDM analyzed the data. JDM and JHS wrote the manuscript.

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