10-2023

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ENVIRONMENTAL RESEARCH
LETTERS

LETTER

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Abstract

Assessments of the potential responses of animal species to climate change often rely on correlations between long-term average temperature or precipitation and species' occurrence or abundance. Such assessments do not account for the potential predictive capacity of either climate extremes and variability or the indirect effects of climate as mediated by plant phenology. By contrast, we projected responses of wildlife in desert grasslands of the southwestern United States to future climate means, extremes, and variability and changes in the timing and magnitude of primary productivity. We used historical climate data and remotely sensed phenology metrics to develop predictive models of climate-phenology relations and to project phenology given anticipated future climate. We used wildlife survey data to develop models of wildlife-climate and wildlife-phenology relations. Then, on the basis of the modeled relations between climate and phenology variables, and expectations of future climate change, we projected the occurrence or density of four species of management interest associated with these grasslands: Gambel's Quail (*Callipepla gambelii*), Scaled Quail (*Callipepla squamat*), Gunnison's prairie dog (*Cynomys gunnisoni*), and American pronghorn (*Antilocapra americana*). Our results illustrated that climate extremes and plant phenology may contribute more to projecting wildlife responses to climate change than climate means. Monthly climate extremes and phenology variables were influential predictors of population measures of all four species. For three species, models that included climate extremes as predictors outperformed models that did not include extremes. The most important predictors, and months in which the predictors were most relevant to wildlife occurrence or density, varied among species. Our results highlighted that spatial and temporal variability in climate, phenology, and population measures may limit the utility of climate averages-based bioclimatic niche models for informing wildlife management actions, and may suggest priorities for sustained data collection and continued analysis.

1. Introduction

Assessments of species' vulnerability to climate change (e.g. Glick *et al* 2011, Pacifici *et al* 2015, Staudinger *et al* 2015, Foden *et al* 2019) typically correlate wildlife occurrence or abundance with long-term mean temperature or precipitation (Pearson and Dawson 2003, Elith and Leathwick

2009, Garcia *et al* 2014). Average climate is associated with the long-term geographic distributions of many species, but climate extremes (e.g. droughts, floods, heat waves), which are becoming more frequent and intense (Meehl and Tebaldi 2004, IPCC 2012), may be equally relevant to organisms' body condition and population dynamics (Zimmerman *et al* 2009, Germain and Lutz 2020, Rangwala *et al* 2021, Stewart *et al* 2021). Extremes can affect wildlife physiologically or via changes in the amount and quality of habitat or components of habitat (Parmesan *et al* 2000, Maxwell *et al* 2019, Román-Palacios and Wiens 2020, Turner *et al* 2020).

Climate-induced local extinctions and population declines more often are attributable to changing interspecific interactions, particularly those that reduce food availability, than to exceedance of physiological tolerances (Cahill *et al* 2013, Ockendon *et al* 2013, Gunderson *et al* 2017). For example, effects of climate change on wildlife that are mediated by plant phenology (the timing, duration, and magnitude of primary productivity and other aspects of plants' annual life cycles), such as changes in the quantity and quality of food and shelter, may be particularly strong (Asch *et al* 2007, McKinney *et al* 2012). Phenology variables can often explain or predict the density or occurrence of herbivores, omnivores, and insectivores (Osborne and Suárez-Seoane 2007, Mueller *et al* 2008, Tuanmu *et al* 2011, Bischof *et al* 2012, Butler *et al* 2017).

Plant phenology can be sensitive to extreme and fluctuating climate, such as individual storms and precipitation variability (Knapp *et al* 2008, Thomey *et al* 2011). Identifying the climate variables to which phenology responds is necessary to project how wildlife may respond to the phenology-mediated effects of climate change. However, the outputs of many downscaled climate models do not effectively represent spatial structure or extreme temporal variation in precipitation and temperature. By contrast, the localized constructed analogs (LOCAs) statistical downscaling method (Pierce *et al* 2014) was designed to simulate spatial structure and temporal extremes with good fidelity to observed historical extremes. Therefore, LOCA outputs may be reasonable projections of future extremes, and well-suited to generate variables needed to predict phenology.

Modeling relations between climate and phenology also requires spatially extensive vegetation data with relatively high temporal resolution, which seldom are available from field studies. Vegetation indices derived from remotely sensed surface-reflectance data can serve as a proxy for some types of field measurements and for the location and quality of habitat for multiple taxonomic groups (Marshal *et al* 2006, Kostelnick *et al* 2007, Osborne and Suárez-Seoane 2007, Viña *et al* 2008, Stoner *et al* 2016, Butler *et al* 2017). Vegetation indices are related

mechanistically to diet quality, body mass, and breeding phenology of herbivores (Pettorelli *et al* 2011).

In this study, we explored the relations between vegetation phenology, climate, and wildlife population responses in the grasslands of the southwestern United States ('Southwest'). We focused on four species that are associated closely with Southwest grasslands and are considered management priorities: Gambel's Quail (*Callipepla gambelii*), Scaled Quail (*Callipepla squamat*), Gunnison's prairie dog (*Cynomys gunnisoni*), and American pronghorn (*Antilocapra americana*). Our primary objectives were to infer how these species may respond directly and indirectly to climate change and to determine how projected responses are influenced by including climate extremes as predictors. We first developed predictive models of vegetation phenology as a function of climate averages, extremes, and variability. We then developed predictive models of occurrence and density of wildlife populations as a function of climate and phenology variables, explicitly testing whether models that included both climate averages and extremes explained more variance in occurrence or density of each species than models that included only averages. We used these models to project future phenology and population measures, and we compared projections of population measures from models with and without climate extremes.
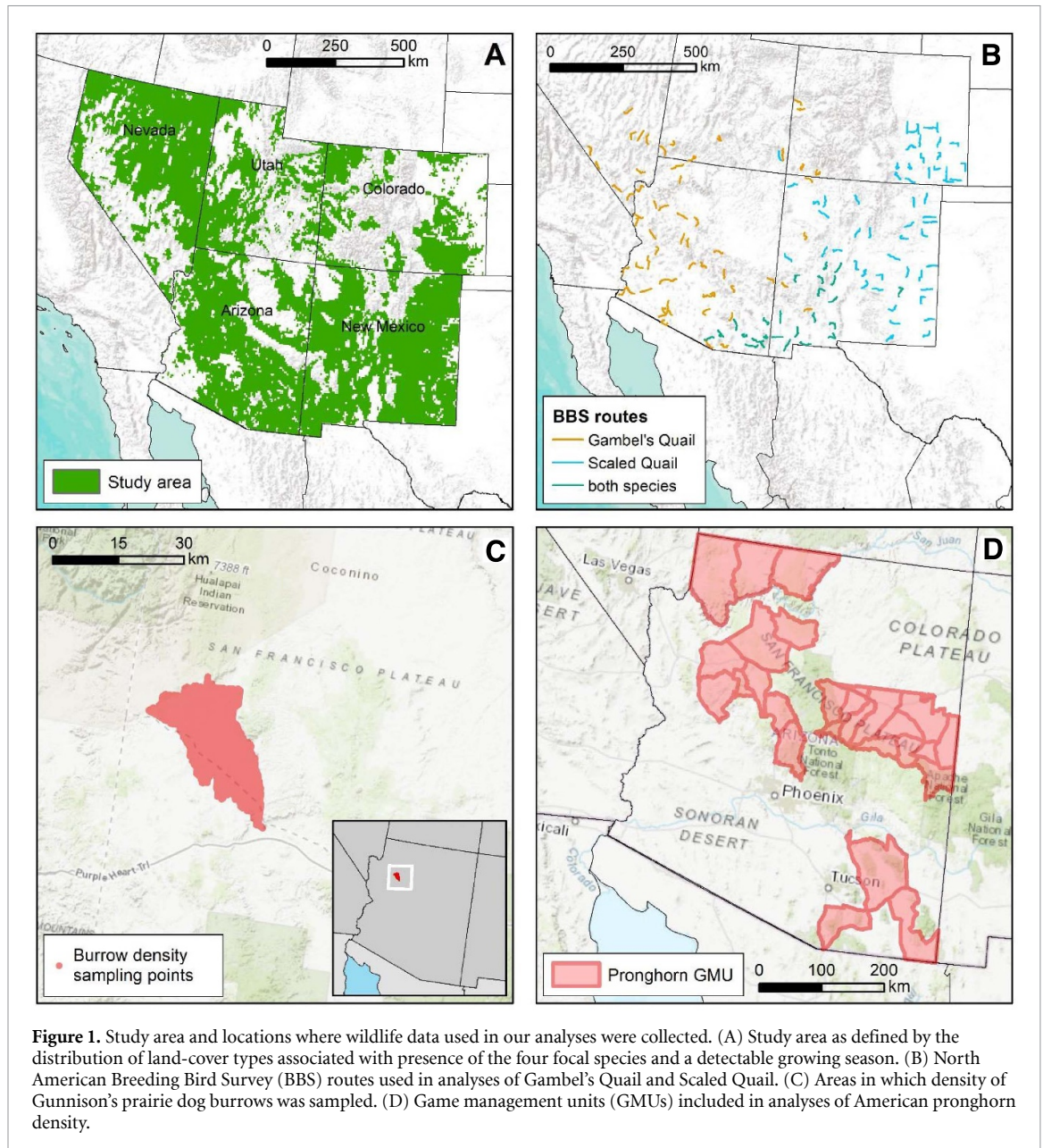
2. Methods

2.1. Study area
Our study area encompassed portions of Arizona, Colorado, New Mexico, Nevada, and Utah that overlap the Great Basin, Mojave, Sonoran, and Chihuahuan deserts (figure 1(A)). We limited the study area to include only land-cover types used by one or more of our focal species, which we identified from three data sources: maps of predicted habitat (30 m rasters) for each species from the U.S. Geological Survey's Gap Analysis Project (USGS 2018); maps of Gunnison's prairie dog colonies provided by the Arizona Game and Fish Department (AZGFD); and global positioning system locations of collared American pronghorn from eight telemetry studies conducted by AZGFD. Details are in supplementary material, appendix A.

2.2. Data sources
2.2.1. Climate data
We obtained gridded daily, 6 km resolution data for the period 1950–2015 on maximum temperature, minimum temperature, precipitation, soil moisture, and potential evapotranspiration (Livneh *et al* 2015). We obtained LOCA projections of historical (1950–2005) and future (2006–2100) values of maximum and minimum temperature and precipitation

Figure 1. Study area and locations where wildlife data used in our analyses were collected. (A) Study area as defined by the distribution of land-cover types associated with presence of the four focal species and a detectable growing season. (B) North American Breeding Bird Survey (BBS) routes used in analyses of Gambel's Quail and Scaled Quail. (C) Areas in which density of Gunnison's prairie dog burrows was sampled. (D) Game management units (GMUs) included in analyses of American pronghorn density.

and associated Variable Infiltration Capacity hydrological model-derived soil moisture and potential evaporation (Vano *et al* 2020) under two emissions scenarios (representative concentration pathways [RCPs] 4.5 and 8.5) from ten global climate models (GCMs; supplementary material, table A2), also at daily, 6 km resolution. We selected GCMs that best represent the climate, including extremes, of the Southwest (Rupp *et al* 2013). Because the historical precipitation and temperature data served as the training data for LOCA projections (Pierce *et al* 2014), the historical and projected future data were fully compatible and comparable.

2.2.2. Vegetation phenology data

We focused on seven phenology variables that are based on two-band enhanced vegetation index (EVI) (Jiang *et al* 2008) values from Moderate Resolution Imaging Spectroradiometer or Advanced Very High Resolution Radiometer imagery. Our phenology variables collectively summarized the magnitude, timing, and duration of primary productivity: amplitude; peak EVI; day of peak EVI; start, end, and length of growing season; and cumulative EVI. Definitions are in supplementary material, appendix A. We acquired annual, 0.05° (∼5 km) resolution data on land-surface phenology from 1981 to 2016 from the Vegetation Index and Phenology Lab, University of Arizona (vip.arizona.edu). Phenology variables were available for up to three distinct growing seasons per year for each grid cell, with growing seasons identified using a phenology algorithm that applied thresholds for minimum magnitude and duration of EVI increase above baseline level (Didan *et al* 2018). If the algorithm identified multiple growing seasons in a particular grid cell and year, we used

phenology metric data for the growing season with the highest peak EVI; such instances were uncommon, and occurred primarily for grid cells in the hot, North American Monsoon-influenced Mojave, Sonoran, and Chihuahuan deserts.

2.2.3. Wildlife data

We obtained information on occurrence of Gambel's Quail and Scaled Quail from the North American Breeding Bird Survey (BBS; Pardieck *et al* 2017), which records bird species detected at 0.8 km (0.5 mi) intervals along a 39.4 km (24.5 mi) route. We only considered BBS data from 1997 to 2015 because this was the period for which BBS, phenology, and climate data were all available. We analyzed data from routes along which either species had been detected during this period (figure 1(B)), which included 45 routes and 610 route-years for Scaled Quail, and 35 routes and 534 route-years for Gambel's Quail. Surveys were conducted from late April through early July, with most in May. We condensed the data for samples along routes into a binary variable indicating whether each quail species was detected anywhere along the route in each sampling year.

We obtained information on the density of Gunnison's prairie dogs from annual surveys of the Aubrey Valley population (northwestern Arizona) by AZGFD from 2007 to 2015 (figure 1(C)). Burrow densities, which are correlated with prairie dog densities, were estimated by counting the number of active prairie dog burrows along 250 m transects (Biggins *et al* 1993). Sampling occurred from late May through late August, and survey dates varied among years. The data included 20 556 observations, each representing one 250 m sampling unit in one year.

We obtained annual estimates of American pronghorn abundance for 32 game management units (GMUs) in Arizona from 2008 to 2015. Abundance estimates were based on double-observer aerial surveys in the same general areas each year (Magnusson *et al* 1978, Cook and Jacobson 1979, Graham and Bell 1989). Surveys were conducted during 1 June–15 September, with most surveys conducted in August. We removed GMUs for which abundance estimates were missing for more than half of the survey years. Our analysis included 25 GMUs (figure 1(D)) and abundance estimates for 200 GMU years. We modeled the response variable as estimated abundance per sampled area (i.e. density).

2.3. Modeling climate-phenology relations

We modeled relations between phenology variables (response variables) and climate variables (predictor variables) to estimate the extent to which climate reliably predicted phenology. We used daily historical climate data (section 2.2.1) to derive variables describing averages, extremes, and variability of temperature, precipitation, soil moisture, and potential evapotranspiration at a monthly and water-year
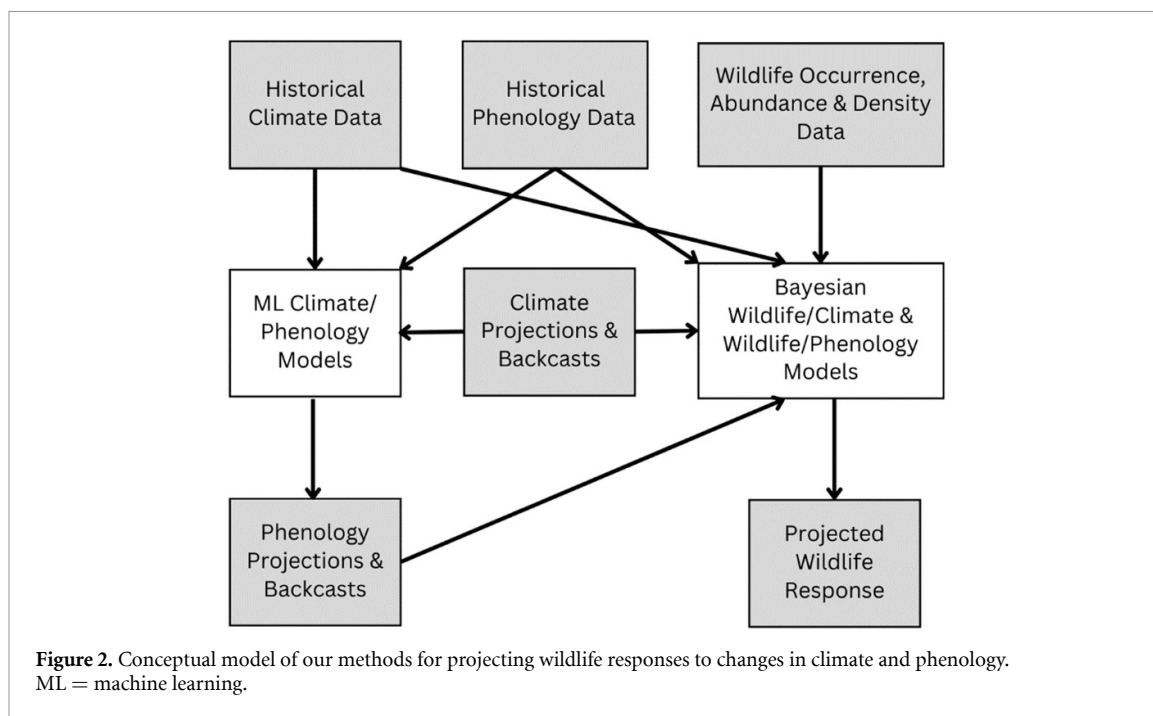
(1 October–30 September) resolution. Our climate extremes variables loosely were based on those developed by the Expert Team on Climate Change Detection and Indices (Klein Tank *et al* 2009). Coauthors of our study independently selected climate variables that they believed to be associated with each phenology variable. We retained climate variables selected by two or more coauthors as predictors in climate-phenology models. Each phenology variable ultimately was associated with 12–32 climate predictor variables (table A5). We also included as predictors three non-climate variables that may influence vegetation phenology (or remotely sensed estimates of phenology): land-cover type (from the Southwest Regional Gap Analysis Project; Lowry *et al* 2007), soil type, and Level II terrestrial ecoregion (Commission for Environmental Cooperation 1997), each calculated as the modal value within each climate grid cell.

We used the random forest machine learning algorithm (Breiman 2001), a tree-based ensemble learning method, to model relations between phenology and climate. We selected this method because it automatically handles nonlinear relations and captures interactions between predictors (Elith *et al* 2008), both of which are common in complex ecological data such as ours. Preliminary analyses also suggested that random forests outperformed other machine learning algorithms (appendix A). One disadvantage of machine learning models is that their outputs may be less interpretable than those of traditional regression models. However, we focused on maximizing predictive performance rather than explaining mechanistic links between climate and phenology or identifying the individual climate variables most strongly associated with phenology. We used data from 1981 to 2008 as the training data to fit random forest models, and withheld data from 2009 to 2015 for assessing model performance. Additional detail on model tuning, training, and testing is in supplementary material, appendix A.

2.4. Modeling climate-wildlife and phenology-wildlife relations

2.4.1. Predictor variables

We consulted the literature and subject-matter experts within AZGFD to identify climate and biological and physical variables known or hypothesized to be associated with the spatial distribution or population measures of each focal species (supplementary material, table A3). We also developed a set of variables to capture the potential stresses of climate extremes on wildlife (supplementary material, table A4), and we included the seven annual phenology variables described above as predictor variables for each focal species. We included time-lagged versions of each climate and phenology variable, with lags of 1 and 2 years for Gambel's Quail, Scaled Quail, and Gunnison's prairie dog; and lags of 1, 2, and 3 years for American pronghorn, which has a longer

Figure 2. Conceptual model of our methods for projecting wildlife responses to changes in climate and phenology. ML = machine learning.

generation time than the other species (Hoogland 1995, Cooke *et al* 2018, Bird *et al* 2020). Full methods are in supplementary material, appendix A.

2.4.2. Bayesian wildlife models

We used hierarchical Bayesian models to assess the relations between climate, phenology, and population measures (figure 2). Each model contained predictors that are relatively time-invariant (e.g. elevation, topography) and predictors that reflected climate and phenology during each observation year. We aimed to identify the predictors that explained annual changes in species occurrence or density rather than those that explained decadal or longer-term trends. Such trends likely respond in part to deterministic changes in habitat amount as a result of land use. We made the simplifying assumption that land use did not appreciably change habitat amount over the period of analysis. For quail and Gunnison's prairie dogs, we used a varying intercept with hierarchical priors to account for interannual variability and potential correlations between annual estimates of occurrence or density. For American pronghorn, we modeled the relations between predictors and the finite rate of population change (λ) explicitly (see supplementary material, appendix A for all model specifications and priors) to better reflect annual abundance estimates that are linked to the abundances of *Antilocapra* spp. in the Southwest in the previous year (Whittaker *et al* 2003, Woodruff *et al* 2016). Details are in supplementary material, appendix A.

We examined the effect of climate extremes on wildlife responses by comparing the performance of two models for each species. The first model included variables representing climate means,

annual phenological metrics, or time-invariant biophysical variables (means model). The second model included all variables in the means model and variables representing climate extremes (extremes model). We assessed model performance with the leave-one-out information criterion (LOOIC) (Vehtari *et al* 2017). Models with lower LOOIC values are judged to have better predictive performance, and differences in the expected log predictive density >4 indicate strong evidence, or low uncertainty, that the model with the lower LOOIC value strongly outperforms the others. We considered predictors to be strongly associated with occurrence or density if more than 95% of the posterior predictive mass lay to one or the other side of 0. Given the number of variables included in each model, we used regularizing priors to reduce the risk of overfitting. These regularizing priors 'shrink' regression coefficient estimates towards 0 for uncertain or uninformative parameters while allowing informative parameters to be estimated in the context of the other variables in the model. As a result, our estimates of posterior predictive density are likely conservative; however, we did not attempt to interpret effects of individual variables (e.g. via marginal effects or odds ratios) because our main interest was identifying predictors that should be included in future projections rather than interpreting any single variable.

2.5. Assessing model performance

We assessed performance of climate-phenology models with two measures of prediction accuracy: coefficient of determination (R^2), the proportion of variation in the observed phenology values that is explained by the climate predictor variables; and mean absolute error (MAE), the absolute average

distance between the observed phenology values and predicted phenology values. R^2 of models with different phenology response variables can be directly compared because R^2 is a unitless proportion, but MAE cannot because phenology variables have different units and ranges of values. We mapped prediction errors to determine whether and how model performance varied across the study area.

We assessed performance of wildlife models with graphical posterior predictive checks and Freeman-Tukey's measure of discrepancy. Posterior predictive checking is a qualitative approach for evaluating model fit. We determined whether our models were plausible by drawing 1000 random draws from the posterior predictive distribution of each model and compared the distribution of those values to those in the original data with respect to measures of central tendency, variation, and skewness (Gabry *et al* 2019). We calculated Freeman-Tukey's measure of discrepancy according to:

$$D_{\text{observed}} = \sum_i \sqrt{\left(y_i^{\text{observed}} - \mu_i\right)^2};$$

$$D_{\text{predicted}} = \sum_i \sqrt{\left(y_i^{\text{predicted}} - \mu_i\right)^2}.$$

where the observed discrepancy (D_{observed}) reflects the difference between the observed value (y_i^{observed}) and the model-based prediction (μ_i), and the predicted discrepancy ($D_{\text{predicted}}$) reflects the difference between samples drawn from the posterior predictive distribution ($y_i^{\text{predicted}}$) and the model-based prediction. The posterior predictive fit is the proportion of sampled discrepancies that exceed the observed discrepancy, and values near 0.5 indicate excellent model fits (Gelman *et al* 2013).

2.6. Projecting future changes in phenology

We used the machine learning models of climate-phenology relations, trained on historical climate data, and the LOCA projections to project future phenology. We generated annual projections of each phenology variable for each combination of GCM and RCP, and summarized results for three future periods: 2021–2050 (*2030s*), 2041–2070 (*2050s*), and 2061–2090 (*2070s*). We calculated the median predicted annual phenology values for each grid cell within each future period for each GCM and RCP. We used climate model backcasts to make retrospective median predictions of phenology for a reference period (1981–2010), then calculated the differences between projected and retrospective medians (*deltas*) to illustrate the range of potential changes in phenology. Comparing model projections to model backcasts rather than historical observations avoids conflation of biases in GCM output with potential effects of climate change (Sofaer *et al* 2017).

2.7. Characterizing species responses to future climate and phenology

We used modeled past and future values of climate and phenology variables to project the responses of wildlife species to future conditions. For each species and grid cell (or GMU for American pronghorn), we generated yearly projections of each combination of GCM and RCP in four steps. First, we multiplied projected values of influential climate and phenology variables by the coefficients of these variables from the Bayesian wildlife models. Second, we summed the resulting values across variables. Third, we back-transformed to the original units of analysis (occurrence or density). Fourth, we calculated the proportional change in the medians of the back-transformed values (across years, RCPs, and GCMs) between the reference period and each future period (2030s, 2050s, and 2070s) as an index of species' responses to changes in climate and phenology. These indices assume that values of all biological and physical predictors, and any climate or phenology predictors that we did not identify as influential, remain at their means in the data we used to fit the models. Therefore, the indices are not predictions of the absolute change in occurrence or density.

We projected each species' responses to future climate and phenology with the means model and the extremes model. We focused on the projections from the model with the lower LOOIC when interpreting projected responses.

3. Results

3.1. Relations between climate and phenology

Predictive performance (R^2) of climate-phenology models ranged from 0.25 for amplitude to 0.65 for cumulative EVI. In ecological research, these effects often are considered moderate to large (Cohen 1988, Møller and Jennions 2002). Predictive performance of some phenology metrics varied considerably across the study area (supplementary material, figures B1–B7), which may reflect differences in land cover and the seasonality of precipitation and other climate variables among ecosystems. Prediction error for most of the phenology variables tended to be highest along the margins of the study area, where grassland cover types transitioned to non-grasslands. The smallest prediction error for most phenology variables was in grasslands in eastern New Mexico and eastern Colorado.

Models of cumulative EVI ($R^2 = 0.653$, MAE = 5.34), amplitude ($R^2 = 0.247$, MAE = 0.02), and peak EVI ($R^2 = 0.453$, MAE = 0.03) had relatively uniform and low prediction error across the Southwest, although these models showed scattered small pockets of high-error grid cells throughout the study area (figures B1, B2 and B6). Models for the remaining phenology variables had more discernable spatial patterns of prediction error. Prediction error

for day of peak EVI ($R^2 = 0.565$, MAE $= 25.9$ d) was relatively high in Arizona and southern Nevada and low in the northernmost portion of the study area (figure B3). Prediction error for length of growing season ($R^2 = 0.510$, MAE $= 37.5$ d) and end of growing season ($R^2 = 0.443$, MAE $= 39.1$ d) was relatively high in northwestern Arizona and southern Nevada and low in the eastern and northern portions of the study area (figures B4 and B5). Prediction error for start of season ($R^2 = 0.416$, MAE $= 28.2$ d) was high in southwestern Arizona but low elsewhere (figure B7).

3.2. Relations between climate and wildlife and phenology and wildlife

Graphical posterior predictive checks of climate-wildlife and phenology-wildlife models (supplementary material, figures A1–A8) indicated that all models plausibly fit the data. The Freeman-Tukey discrepancy values for the means models were 0.498, 0.511, 0.560, and 0.761 for Gambel's Quail, Scaled Quail, Gunnison's prairie dog, and American pronghorn, respectively. Similarly, discrepancy values for the extremes models were 0.522, 0.513, 0.559, and 0.760 for Gambel's Quail, Scaled Quail, Gunnison's prairie dog, and American pronghorn, respectively.

The extremes model clearly outperformed the means models for Scaled Quail, American pronghorn, and Gunnison's prairie dog (table 1). The means model marginally (difference in expected log predictive density <4) outperformed the extremes model for Gambel's Quail.

Climate and phenology variables were influential predictors of population measures of all focal species (table 1). The majority of the influential climate predictors were monthly extremes (minimum or maximum climate variables). For instance, monthly maxima of daily precipitation and potential evapotranspiration, and monthly minima of daily minimum temperature, were strongly related to occurrence or density of Scaled Quail, Gunnison's prairie dog, and American pronghorn. Consistent with differences in life history, the most relevant months varied among species.

Predictors related to the amount of greenness, particularly cumulative EVI and amplitude, were influential for all species. Predictors related to the timing of greenness, especially start of growing season, were also influential in models of all species. These phenology variables may indicate overall productivity of grasses and how quickly food or shelter becomes available after winter.

Of the 65 climate and phenology variables identified as influential in the best models across all focal species, 38 lagged by 1–3 years (table A6). Although relations between each species and variable are difficult to interpret, population measures generally were most strongly associated with conditions in years prior to the year of measurement.

Models of the density of American pronghorn, which were evaluated at the extent of GMUs that encompassed many grid cells, suggested that averages of climate or phenology variables over large areas may not reflect the conditions experienced by wildlife. Most of the influential predictors of American pronghorn were minima, maxima, or standard deviations rather than means or medians (table A6).

3.3. Projected changes in phenology

Projected changes of the seven phenology variables differed in magnitude and direction across the Southwest (figure 3). Patterns were qualitatively similar among RCPs and among future periods, but we projected larger changes under the higher emissions scenario and for later periods (figure 3; supplementary material, figures C1–C5).

Our results suggested that the magnitude of greenness generally will decrease or change little over time (figure 3; supplementary material, figures C1–C5). Amplitude was projected to decrease across the northern half of the study area, where precipitation is dominated by winter snow, and to remain relatively constant in the southern half, where precipitation is dominated by the North American Monsoon. Peak EVI was projected to decrease slightly across most of the Southwest, especially southwest Arizona and near the borders of northern Utah and northern Colorado.

Projections related to the timing of greenness were less consistent (figure 3; supplementary material, figures C1–C5). The day of peak EVI was projected to occur earlier in the southern half of the study area and remain constant or occur slightly later in the northern half, where green-up still may be prolonged despite increases in winter temperatures. The start of the growing season was projected to occur later in the Four Corners region, earlier in the northern portion of the study area, and at approximately the same time in the eastern portion of the study area. The end of the growing season was projected to occur earlier across most of the Southwest, possibly indicating a trend toward development of drought conditions earlier in the year. The length of the growing season may decrease in the Four Corners region.

Cumulative EVI, which is influenced by both the magnitude and timing of greenness, was projected to increase across much of Nevada and northern Utah, decrease slightly across much of Arizona, and remain relatively constant elsewhere.

3.4. Projected wildlife responses to future climate and phenology

Projected responses of each focal species were qualitatively similar for different future periods and emissions scenarios. Larger responses were projected for later periods and the higher emissions scenario (supplementary material, figures E1–E4).

Table 1. Climate and phenology variables strongly associated (more than 95% of the posterior predictive mass greater or less than 0) with wildlife population measures in models including and excluding climate extremes for each focal species. T_{min}, minimum temperature; P, precipitation; PET, potential evapotranspiration; EVI, enhanced vegetation index; N/A, not applicable.

Species	Model[a]	ΔLOOIC[b]	ΔELPD[c]	Important predictor variables		
				Phenology	Climate averages	Climate extremes
Gambel's Quail	Extremes	6.3	3.2	Cumulative EVI Day of peak EVI	None	Monthly maximum P (March, August, October, December) Monthly maximum PET (September) Monthly maximum T_{min} (February)
	Means	0	0	Cumulative EVI Day of peak EVI	Dec–Jan P	N/A
Scaled Quail	Extremes	0	0	Amplitude Cumulative EVI Peak EVI Start of season	None	Monthly maximum P (February, July, August, September) Monthly maximum PET (June, August, September) Monthly maximum T_{max} (May, June) Monthly minimum T_{min} (January, November)
	Means	86.4	43.2	Amplitude Cumulative EVI End of season Peak EVI Start of season	Water year P	N/A
Gunnison's prairie dog	Extremes	0	0	Amplitude Cumulative EVI Day of peak EVI End of season Peak EVI Start of season	None	Monthly maximum P (January, March, May, July, September) Monthly maximum PET (June, July) Monthly maximum T_{max} (June, August) Monthly minimum T_{min} (January, February, November, December)
	Means	467.3	233.6	Amplitude Cumulative EVI Day of peak EVI End of season Length of season Peak EVI	April–May P June–September P October–March P	N/A

(Continued.)
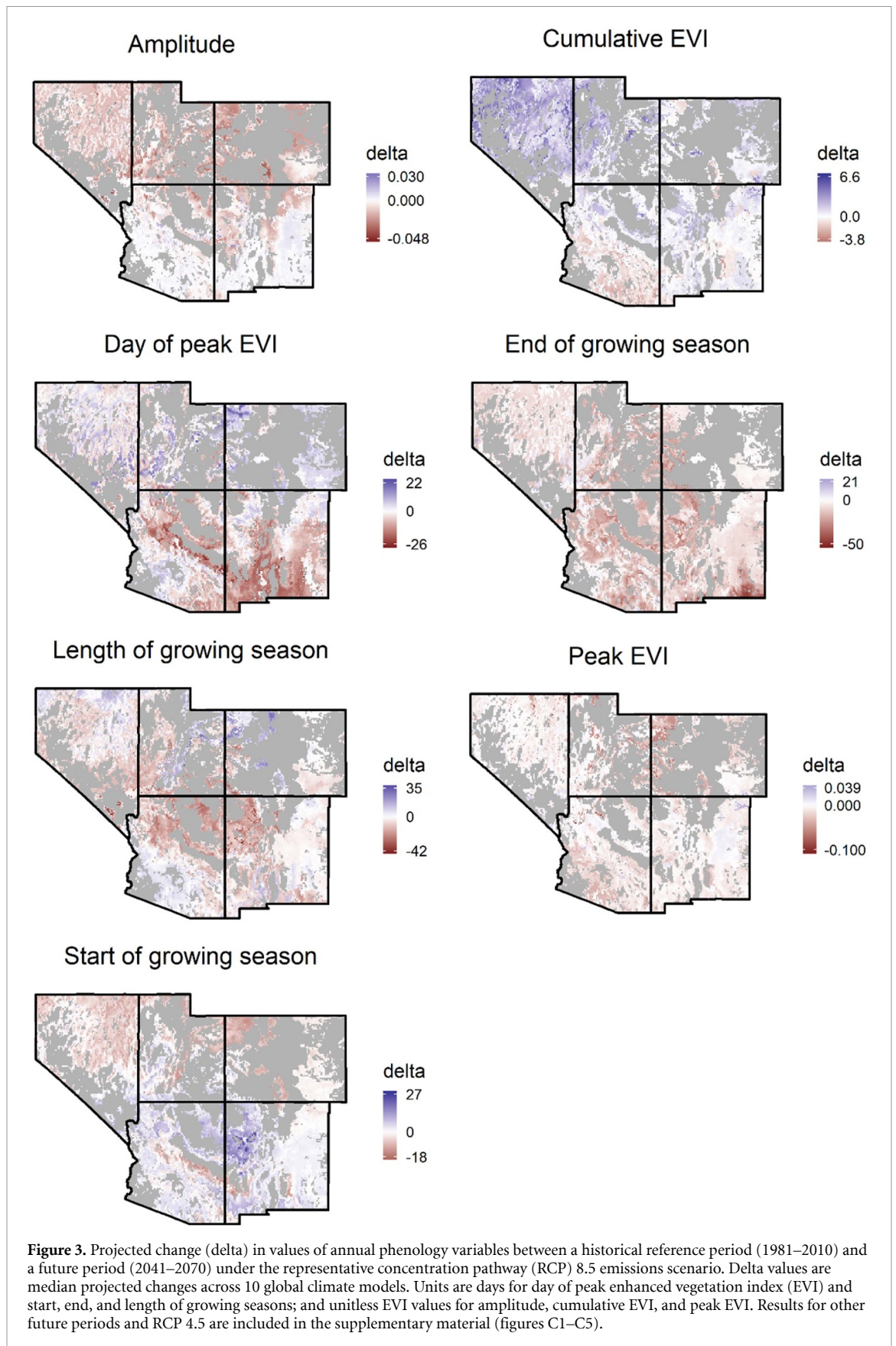
Table 1. (Continued.)

Extremes	0	0	Amplitude Length of season Start of season	April–August P Apr–Jun P	Monthly maximum P (January, February, May, August, October, November) Monthly maximum PET (May, June, July, August) Monthly minimum T_{min} (December)
American pronghorn					
Means	4214.9	2107.5	Amplitude Cumulative EVI Day of peak EVI End of season Length of season Start of season	April–August P April–June P October–April P Water year P	N/A

[a] The means models included predictors representing climate means, annual phenology metrics, or biophysical variables that did not change through time. The extremes models included all of the predictors in the means model plus predictors representing climate extremes.
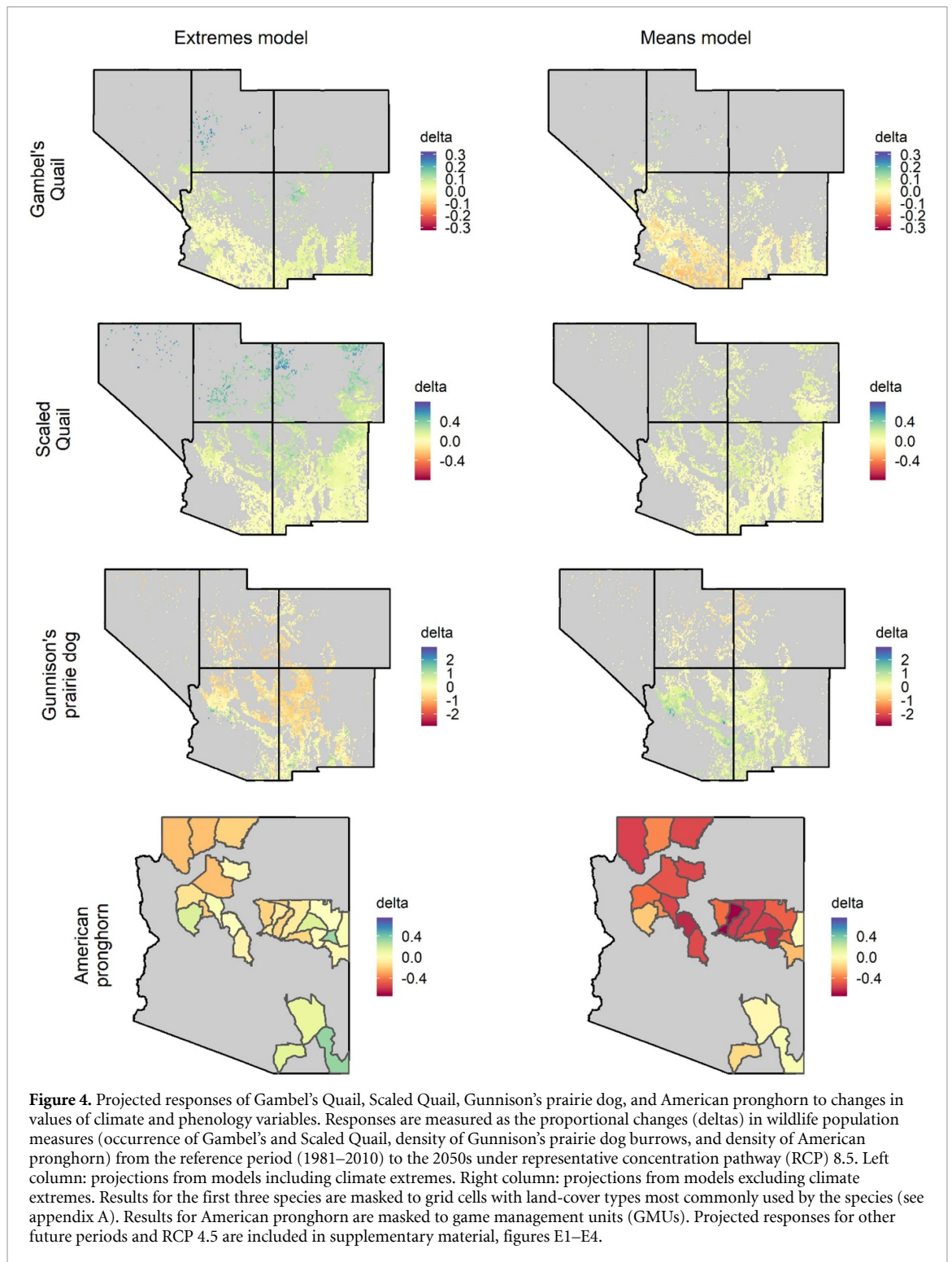
[b] Difference in leave-one-out information criterion; lower LOOIC values indicate models with better predictive performance.

[c] Difference in expected log predictive density; ΔELPD > 4 indicates strong evidence that the model with the lower LOOIC value strongly outperforms the other model.

Figure 3. Projected change (delta) in values of annual phenology variables between a historical reference period (1981–2010) and a future period (2041–2070) under the representative concentration pathway (RCP) 8.5 emissions scenario. Delta values are median projected changes across 10 global climate models. Units are days for day of peak enhanced vegetation index (EVI) and start, end, and length of growing seasons; and unitless EVI values for amplitude, cumulative EVI, and peak EVI. Results for other future periods and RCP 4.5 are included in the supplementary material (figures C1–C5).

The best model of Gambel's Quail occurrence (the means model) predicted negative responses to future climate and phenology in the species' southwestern range and neutral or slightly positive responses elsewhere. However, the extremes model, which performed almost as well as the means model, predicted

Figure 4. Projected responses of Gambel's Quail, Scaled Quail, Gunnison's prairie dog, and American pronghorn to changes in values of climate and phenology variables. Responses are measured as the proportional changes (deltas) in wildlife population measures (occurrence of Gambel's and Scaled Quail, density of Gunnison's prairie dog burrows, and density of American pronghorn) from the reference period (1981–2010) to the 2050s under representative concentration pathway (RCP) 8.5. Left column: projections from models including climate extremes. Right column: projections from models excluding climate extremes. Results for the first three species are masked to grid cells with land-cover types most commonly used by the species (see appendix A). Results for American pronghorn are masked to game management units (GMUs). Projected responses for other future periods and RCP 4.5 are included in supplementary material, figures E1–E4.

positive changes across nearly all of the species' range. Responses of Gambel's Quail were projected by both models to be most favorable in the species' northern and southeastern range, and least favorable in the southwestern range (figure 4; supplementary material, figure E1).

The best model of Scaled Quail occurrence (the extremes model) projected almost uniformly positive responses to future climate and phenology across the land-cover types with which the species commonly

is associated. Responses of Scaled Quail were most favorable in the northern range, least favorable in the southern range, and moderately favorable in the center (figure 4; supplementary material, figure E2).

The best model of Gunnison's prairie dog burrow density (the extremes model) projected larger areas of negative response than of positive response to future climate and phenology within the land-cover types with which the species is associated (figure 4; supplementary material, figure E3). Areas with positive

responses were mostly in the species' southern range, and most areas with negative responses were in the center of its range.

The best model of American pronghorn density (the extremes model) projected a positive effect of changes in climate and phenology in GMUs in southeastern Arizona, a negative effect in northwestern Arizona, and both positive and negative effects in central Arizona (figure 4; supplementary material, figure E4).

For Gambel's Quail and Gunnison's prairie dog, the means and extremes models projected different directions (positive or negative) of response across large portions of the study area (figure 4). The extremes model predicted generally more favorable responses across the species' range than did the means model for all species except Gunnison's prairie dog.

4. Discussion

Species' geographic distributions and abundances are determined by myriad biotic and abiotic factors (e.g. Hutchinson's 1957 *n*-dimensional hypervolume concept). Addressing wildlife responses to climate extremes and vegetation phenology has been challenging because climate models have not accurately captured extremes and phenology projections have not been available. By contrast, our work not only examines relations between climate and phenology but capitalizes on improved climate projections and remotely sensed phenology data to infer wildlife responses to climate change.

We found strong evidence that climate extremes affect wildlife species associated with Southwest grasslands. For three of our four focal species, the wildlife model including climate extremes variables explained considerably more observed variation in population responses than the model without climate extremes, and the two models were comparable for the fourth species. Monthly extremes of precipitation were associated with population responses of all species, although the most relevant months varied among species. The infrequent, unpredictable precipitation in Southwest deserts can trigger pulses of primary productivity (Noy-Meir 1973), and a single major precipitation event may influence vegetation growth more than a series of smaller events (Reynolds *et al* 2004). Therefore, extreme precipitation during particular life stages (e.g. during lactation for American pronghorn) can have a strong influence on population dynamics (Gedir *et al* 2015).

Minimum daily temperatures during late autumn or early winter, which were associated with population measures of three species, could be related to metabolic requirements, other physiological stresses, or predation (Kendeigh 1945, Briga and Verhulst 2015, Brodin *et al* 2017). Population measures of all

species were related to extremes of potential evapotranspiration during summer. Potential evapotranspiration reflects not only temperature but solar radiation, wind speed, soil moisture, and vegetation cover (Allen *et al* 1998).

Our results also demonstrate that phenology-mediated effects of climate on wildlife may be substantial. Measures of the timing of greenness were influential predictors of population responses of all species, and sometimes more influential than the magnitude of greenness. Again, however, remotely sensed phenology variables do not necessarily identify the habitat characteristics represented by these variables.

The modest predictive performance of our climate-phenology models likely reflected several limitations. For example, reflectance from bare ground in sparsely vegetated grasslands can make it difficult to detect a phenology signal via remote sensing (Huete 1988). The spatial resolution of our phenology data (6 km) may have masked finer-resolution variation in phenology. Multiple growing seasons per year, or growth pulses in response to precipitation events, may not be well captured by our phenology variables. Moreover, regional variation in land-cover types, phenology, and climate-phenology relations is difficult to represent in a single model.

The positive predicted responses of our focal species to future climate and phenology across substantial portions of their ranges (figure 4) were unexpected given that these species occupy some of the hottest and driest environments in the United States (Gonzales *et al* 2018). Additionally, personal observations of AZGFD biologists suggest that Gambel's Quail and Scaled Quail do not respond positively to unusually hot or dry conditions. However, previous assessments also suggested neutral or positive responses to climate change by American pronghorn and quail in the Southwest (Gedir *et al* 2015, Tanner *et al* 2017).

We recognize that our projections do not account for numerous other factors that affect the status of wildlife populations, such as disturbance processes (Singelton *et al* 2019), including the spread of non-native invasive species (Steidl *et al* 2013), and urban and exurban development (Theobald *et al* 2013). Climate change may alter biotic interactions between animal species and their competitors, pathogens, or predators (Blois *et al* 2013, Bastille-Rousseau *et al* 2018). Furthermore, climate change eventually may lead to transitions among grasslands, woodlands, and shrublands (Notaro *et al* 2012). We believe that management actions that address well-known threats to native species, including changes in land use, habitat fragmentation, fire regimes, and water management, may continue to provide substantive benefits despite rapid changes in climate.

5. Conclusions

Bioclimatic niche models based on long-term climate averages are now commonly used to predict wildlife responses to climate change. Our study indicates that this approach can be improved by incorporating climate extremes and phenology-mediated effects of climate, and that doing so can lead to substantially different predictions. Our findings further suggest that spatial variation in response to climate change across a species' regional range may be considerable, especially among areas with different seasonality and dominant forms of precipitation (e.g. snowfall versus summer rainfall or a near-equal distribution). We encourage consideration of these issues when anticipating the effects of climate change on wildlife species and populations.

Future research could implement the approach demonstrated here in other ecosystems, for other wildlife taxa, and for smaller spatial extents with less heterogeneous climate-phenology relations that could allow for more accurate model predictions. Research with experimental methods better suited to clarifying the mechanisms underlying observed associations among climate extremes, vegetation phenology, and wildlife responses is also needed. Development of annual phenology metrics that better capture multiple growing seasons and other complex phenological patterns could lead to better projection of wildlife responses to climate change in the Southwest and other regions with similar environments.

Data availability statement

The data cannot be made publicly available upon publication due to legal restrictions preventing unrestricted public distribution. The data that support the findings of this study are available upon reasonable request from the authors.

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