Sensitivity to climate change for two reptiles at the Mojave–Sonoran Desert interface

C.W. Barrows*

Center for Conservation Biology, University of California, Riverside, CA 92521, USA

A B S T R A C T

The high temperatures and extended droughts that characterize habitat for desert-living reptiles may already approach their physiological tolerances and so could put them at risk due to climate change. Here I examined climate change sensitivity for desert tortoises, *Gopherus agassizii*, and common chuckwallas, *Sauromalus ater*, two large-bodied reptiles that occur across the Mojave–Sonoran Desert interface. I employed the Mahalanobis D^2 statistic to model their niche spaces and then assessed climate-change sensitivity by altering climate variables along a gradient of increasing temperature and decreasing precipitation. While shifting climate variables, I held terrain and soils variables that otherwise define these species' preferred habitat constant, providing a more realistic prediction of available niche space. Both reptiles' modeled niches responded to climate change by shifting to higher elevations and increasingly away from their Sonoran Desert distribution. At moderate predictions of climate change (+2 °C, −50 mm precipitation) desert tortoises' suitable habitat was reduced by nearly 88% in the Sonoran Desert portions my study area, and nearly 66% in the Mojave Desert regions. Under the same scenario chuckwallas lost nearly 92%, but increased 120% respectively. Within the context of climate change potential increases in drought frequency appear to present the greater challenge for these species.

1. Introduction

Among vertebrates, diurnal reptiles occurring in arid regions may be particularly sensitive to climate change to due to their ectothermia, relative sedentary behavior and occurrence where high temperatures and drought may already approach physiological limits (Root and Schneider, 2002; Hannah et al., 2005; Barrows et al., 2010). Empirical data for local extinctions support that prediction for arid-montane lizards (Sinervo et al., 2010). Predicting how additional shifts in climate will impact biodiversity is challenging; scaling global circulation models to more local-scale predictions of climate change where impacts to biodiversity become relevant has proved elusive (Root and Schneider, 2002). In lieu of local-scale predictions, modeling the sensitivity of species to a range of climate change scenarios can provide insights into potential effects of local-scale changes in temperature and precipitation (e.g. Midgley et al., 2002; Araújo et al., 2006).

A useful tool in assessing species sensitivity to changing conditions is niche modeling which attempts to assess the complex interaction of climate with other key habitat variables that constrain a species' distribution (Rotenberry et al., 2002, 2006; Browning et al., 2005). Recent studies using niche modeling have provided important insights into the biotic interactions as well anthropogenic constraints that may impact a species' sensitivity to climate change (Barrows et al., 2008, 2010; Preston et al., 2008). Spatially explicit niche models can predict shifts in habitat envelopes across a gradient of climate simulations, shifts that can identify future climate-change refugia as well as identify important linkages where populations will likely move in response to climate change.

Here I present results using niche models to assess climate-change sensitivity for the desert tortoise (*Gopherus agassizii*) and a lizard, the common chuckwalla (*Sauromalus ater*) occurring at the Mojave–Sonoran desert interface. Due to the large temperature-precipitation gradients, the interface between ecoregions, defined by changes in climatic regimes, provides opportunities to examine climate-change sensitivity for species, especially reptiles whose distributions span those regions. This is a region expected to experience some of the greatest departures from current climate conditions (Seager et al., 2007; Kerr, 2008). Desert tortoises in this region are found at elevations of 0–1220 m (Stebbins, 1985) although in this area are more typically found above 500 m, and have a diet largely comprised of annual plants (Jennings, 2002).

* Tel.: +1 760 834 0594; fax: +1 760 834 0934.
E-mail address: cbarrows@ucr.edu.

Chuckwallas are common from 0 to 1370 m (Kwiatkowski et al., 2009) but can occur up to 1830 m (Stebbins, 1985), and have a diet that includes annual plants as well as a variety of perennial plants (Johnson, 1965; Nagy, 1973; Berry, 1974; Kwiatkowski and Sullivan, 2002). Their overall similarities (ectothermia, large size, long lifespan, vegetarian diet) along with differences (elevation tolerances, specific diet composition) create a comparison that can provide insights into causal explanations for differences between these two species' modeled sensitivity to climate change. Research to date indicates the tortoises may be sensitive to climate change, especially with regard to increased aridity and the incidence of drought (Henen et al., 1998; Duda et al., 1999; Curtin et al., 2009). No similar analyses have been conducted for chuckwallas.

The predicted magnitude of climate shifts for this region (Seager et al., 2007; Kerr, 2008) could indicate a poor prognosis for the sustainability of populations restricted to this desert environment. However, an alternative hypothesis considers the broad range of climatic conditions desert reptiles have evolved with (Huey et al., 2009). In extremely arid environments variation in annual precipitation is high; long periods of drought are often broken with rare pulses of wet conditions (Noy-Meir, 1973; Bell, 1979; MacMahon, 1979). Having evolved in such a highly variable environment may afford some resilience to a changing climate. The relative influence of these forces (shifting climatic envelopes versus adaptation to a harsh and variable climate) may depend on the adaptive strategy employed by a species. My objective was to examine shifts in suitable habitat for both desert tortoises and common chuckwallas to identify potential habitat refugia, and within a context of their physiological and behavioral responses to climate stress, identify mechanisms that may facilitate their differential survival within those refugia.

2. Methods and materials

2.1. Study area

My study area was confined to a 679,585 ha area including Joshua Tree National Park and a 10 km buffer surrounding the Park's boundary, hereafter referred to as the Park, including portions of San Bernardino and Riverside Counties, California, USA (Fig. 1). The Park ranges in elevation from 335 m in the Pinto Basin at its eastern border to 1682 m at Eureka Peak near its western margin, and includes broad valleys as well as rugged mountain slopes. The roughly eastern half of the Park is considered within the Colorado subdivision of the Sonoran Desert, while the western half is within the Mojave Desert (Fig. 1). Mean precipitation is near 100 mm in the Sonoran Desert portions of the Park whereas in the Mojave Desert portions it is twice that amount; winter minimum temperatures in the Mojave are typically sub-freezing while freezing temperatures in the Sonoran areas of the Park are rare (Western Region Climate Center, http://www.wrcc.dri.edu/index.html).

2.2. Niche modeling

I used the Mahalanobis distance statistic (D^2) (Clark et al., 1993; Rotenberry et al., 2002, 2006; Browning et al., 2005) to model the distribution of suitable habitat for each of the reptile species. The Mahalanobis statistic yields for any location an index of its habitat similarity (HSI) to the multivariate mean of the habitat characteristics for locations where the target species have been observed (the calibration data set). This statistic has several advantages over many other geographic information system (GIS) modeling approaches, the foremost being that only species-presence data are required for the dependent variable.

Data for locations for each reptile species were collected from a variety of sources including local biologists, wildlife observation
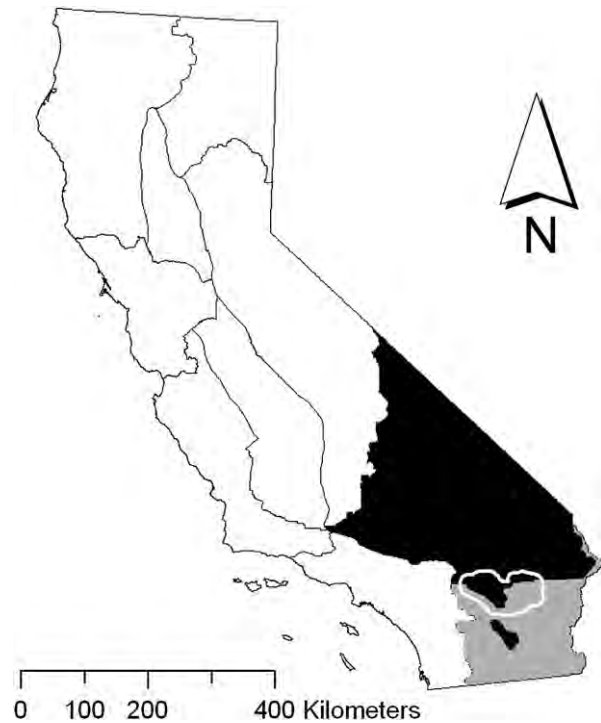

Fig. 1. Location map for the study area within California. Dark shaded area represents the Mojave Desert ecoregion; lightly shaded area represents the Sonoran Desert ecoregion. White border indicates the study area, a 10 km buffer of the Joshua Tree National Park boundary within which all modeling occurred.

cards provided by Park visitors, data bases developed through previous research within the Park, along with collections at the University of California Museum of Vertebrate Zoology, California Academy of Sciences, and California Natural Diversity Data Base of the California Department of Fish and Game. Only records that could be georeferenced to <200 m resolution were accepted. Because only positive occurrence data are required, historic location records from museums and field notes can be used, regardless of survey methodology, as long as there is sufficient precision in the site location. This also avoids the uncertain assumption of correct identification of unoccupied habitats (Knick and Rotenberry, 1998; Rotenberry et al., 2002; Browning et al., 2005).

For the niche-modeling process, a GIS map of the greater Joshua Tree National Park region was divided into 169,916 200 × 200 m diameter cells. Each cell was scored for the underlying abiotic environmental variables, hereafter referred to as the map-points data. Environmental variables were calculated for each cell containing a species' observation and used to create the calibration data set from which a species' niche model was created (Table 1). Once a model was created, it was used to calculate HSIs for the selected Mahalanobis distance partition for every cell on the map. Following Rotenberry et al. (2006), HSI was rescaled to range from 0 to 1, with 0 being the most dissimilar and 1 being the most similar to the multivariate mean habitat characteristics of the target species based on the calibration data set. I used ArcGIS 9.1 (ESRI, 2005) to provide a spatial model (niche map) of the similarity to the species mean for each cell.

I refined the Mahalanobis statistic by partitioning it into separate components (Dunn and Duncan, 2000; Rotenberry et al., 2002, 2006). This partitioning is based on a principal components analysis of the selected model variables in the calibration data set. Each of the partitions are additive, orthogonal variable combinations that explain increasingly more variance until the final partition, the full model (labeled with the lowest partition number [1]), captures

Table 1
Variables used in the development of niche models for each of the reptile species included in this report. Median calibration and validation HSI values provide an indication of model accuracy; those values closer to 1.0 indicate models which have identified the original observation locations (and validation locations) as close to the multivariate statistical mean for the habitat where that species is known to occur.

Independent Variables	Desert Tortoise	Common Chuckwalla
Ruggedness 3×	X	
Ruggedness 20×	X	X
Slope		X
North slope aspect	X	X
East slope aspect	X	
Mean minimum temperature Jan	X	
Mean maximum temperature Jul	X	X
Mean annual precipitation	X	X
% Soil sand	X	X
% Soil water holding capacity	X	
Partition selected	8	1
Median calibration HSI	0.928	0.737
No. of observations	205	62
Median validation HSI	0.945	n/a
No. of observations	48	n/a

the full range of variance exhibited in the calibration data. The partition labeled with the highest number (equal to the number of variables being analyzed), is associated with the combination of habitat variables that have the least variation among locations, indicating minimum habitat requirements. The assumption is that variables with low variance are more likely to represent essential attributes explaining a species' distribution than those that take on a wide range of values where a species is present. I calculated Mahalanobis distances and their partitions with SAS code provided in Rotenberry et al. (2006).

2.3. Model variables

To avoid model over-fitting, I maintained a variables-to-observations ratio of approximately 1:10 (one variable per ∼10 observations) (Osborne and Costello, 2004). Forty independent observations were used as a minimum threshold for modeling, allowing the inclusion of at least four independent variables for the creation of each niche model. Only those observations that were spatially independent were included; no more than one observation per 200 × 200 m cell was used to construct the niche model. This spatial independence helped avoid biases or over-weighting observations from easy access or especially high visitation areas.

I constructed partitioned Mahalanobis D^2 models with different suites of abiotic variables derived from GIS layers readily available from internet sources in 2008; soils (Natural Resources Conservation Service, 2008); ruggedness (Sappington et al., 2007; United States Geological Survey, 2009); and climate (PRISM Climate Group, 2004). Habitat variables considered for modeling were (1) the median terrain slope value for 18 × 18 neighborhood of 10 m cells (Slope), (2) mean maximum temperatures in July from 1971 to 2000 (Max Temperature July), (3) mean minimum January temperatures for the same period (Min Temperatures January), (4) mean annual precipitation from 1971 to 2000 (Mean Precipitation), (5) median value for 18 × 18 of Sappington analysis (Sappington et al., 2007) results from 3 × 3 10 m neighborhood (Ruggedness 3 × 3 [fine-scale slope steepness]), (6) Sappington analysis for 18 × 18 10 m neighborhood (Ruggedness 20 × 20 [broad-scale slope steepness]), (7) median departure from a north slope aspect within a 20 × 20 m neighborhood analysis using 10 m cells (North Slope Aspect), (8) median departure from a east slope aspect within a 20 × 20 m neighborhood analysis using 10 m cells (East Slope Aspect), (9) soil composition including percent sand, percent clay, and percent silt, and (10) mean soil water content as a fraction of volume.

All variables were included in the initial model run; thereafter variables were removed individually when they were determined to be redundant (high correlation with other variables), when they did not contribute to an improved HSI score, or due to small observation numbers and the need to meet the 1:10 ratio. In all cases multiple variable combinations were attempted until a maximum HSI value was determined.

2.4. Niche model validation

There were only sufficient spatially independent observations to allow the creation of both a calibration and a validation data set for the desert tortoise. The validation data set was created by randomly selecting 48 tortoise observations from the total non-redundant (only 1 data point/200 × 200 m cell) observation data set of 253. To compare among models and multiple partitions within models, each with different combinations of environmental variables, the performance of each model-partition was evaluated in predicting suitable habitat at calibration and validation locations. For each model (combination of environmental variables and partitions) I calculated an HSI value for every point in the species calibration and validation data sets. Whether or not there were sufficient observations to create a validation data set, I examined the median HSI value for the calibration data set points, and then visually inspected the habitat suitability maps for high performing model-partitions. When a validation data set was available, I also examined the median validation HSI values for each model-partition, in both cases identifying the model-partition with the highest calibration median HSI values as the best performing niche model.

2.5. Modeling climate sensitivity

When I shifted either mean maximum July temperature or mean precipitation independently the resulting niche model indicated much lower available suitable habitat areas than when the same temperature and precipitation values were shifted together. This result was likely an artifact of the natural patterns of temperature and precipitation across a relatively confined desert landscape; hotter temperatures were invariably correlated with drier conditions. Shifting temperature without a corresponding shift in rainfall resulted in conditions that were rare or non-existent across the greater Joshua Tree National Park landscape and so the temperature or precipitation alone shifted models yielded unrealistic estimates of how climate change may impact these species. Therefore I only considered the model results with temperature and precipitation shifted together.

Using the best performing niche model, I then fit the model based on current environmental conditions onto new map-points data sets, iteratively shifting underlying the map-points values for Max Temperature July and Mean Precipitation. Climate variables were changed incrementally, increasing mean maximum temperature in July by 1 °C and decreasing mean precipitation by 25 mm, increasing 2 °C and reducing precipitation by 50 mm, and then increasing 3 °C, and reducing rainfall by 75 mm. For each new model the area of suitable habitat in ha for HSI values ≥ 0.6 was calculated and the distribution of that suitable habitat was mapped.

3. Results

3.1. Niche model results

For the desert tortoise, the niche model with the highest HSI value, and so the best performing model, was component 8 (Table 1). The highest eigenvectors (≥0.6) were mean maximum temperature

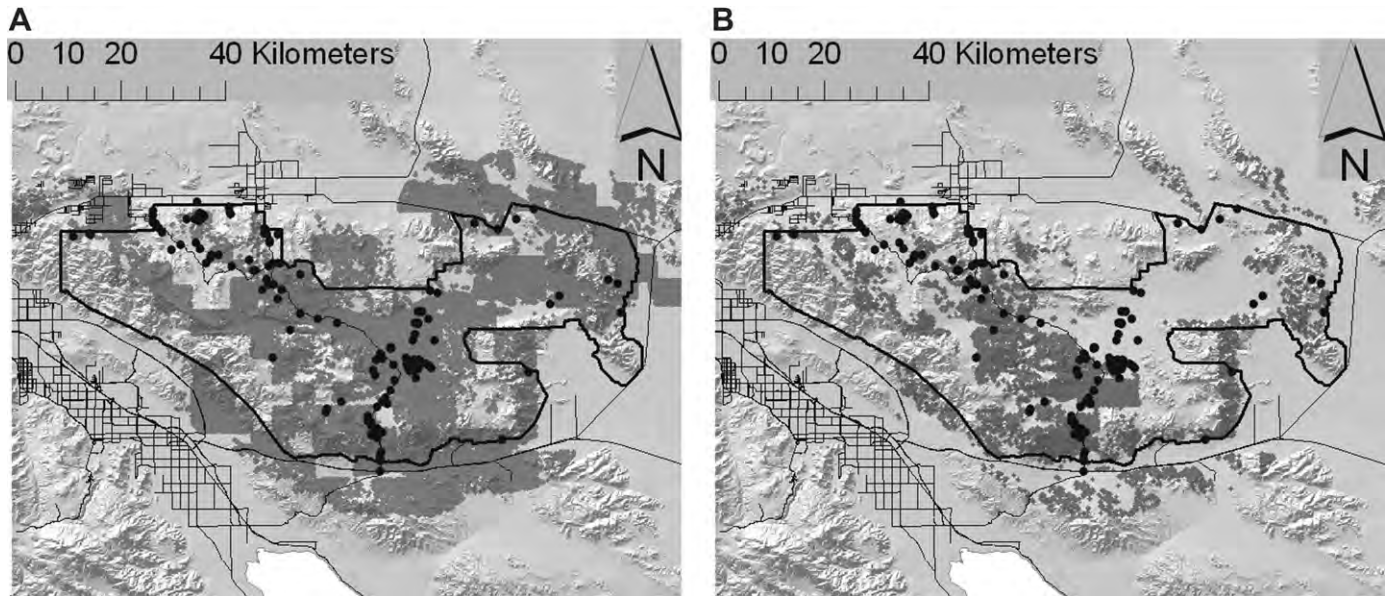**Fig. 2.** Modeled (HSI ≥ 0.6) current suitable habitat (A) and the projected extent of suitable habitat under a mean climate shift of +2 °C and −50 mm of annual rainfall (B) for desert tortoises. Black circles indicate tortoise locations used for the modeling. Heavy black bordered area indicates the boundary of Joshua Tree National Park.

in July, and two measures of slope ruggedness; the tortoise niche model was therefore largely a measure of mean maximum summer temperatures and topographic ruggedness. The highest HSI value for the chuckwalla niche model was the full model (the additive combination of all components); each of the six variables were weighted highly and contributed to the model results. The map output of the niche models represents the distributions of those unique multivariate combinations across the Park's landscape (Figs. 2A and 3A).

3.2. Assessing climate-change sensitivity

Using the niche models described above I then incrementally shifted the underlying conditions simulating climate change. At each increment niche models for the desert tortoise and chuckwalla responded to shifts in temperature and precipitation with decreases in the area of suitable habitat available within the Park, and by shifting to higher elevations and increasingly away from their Sonoran Desert distribution (Table 2). At moderate predictions of climate change (+2 °C, −50 mm precipitation) desert tortoises' suitable habitat was reduced by nearly 88% in the Sonoran Desert portions of Joshua Tree National Park, and nearly 66% in the Mojave Desert regions. Under those same conditions the chuckwallas' suitable habitat was reduced by nearly 92% in the Sonoran Desert portions, but increased by 120% in the Mojave Desert region. The mapped representation of the climate shifted niche models (+2 °C, −50 mm) precipitation illustrates the pattern and magnitude of these shifts (Figs. 2B and 3B).
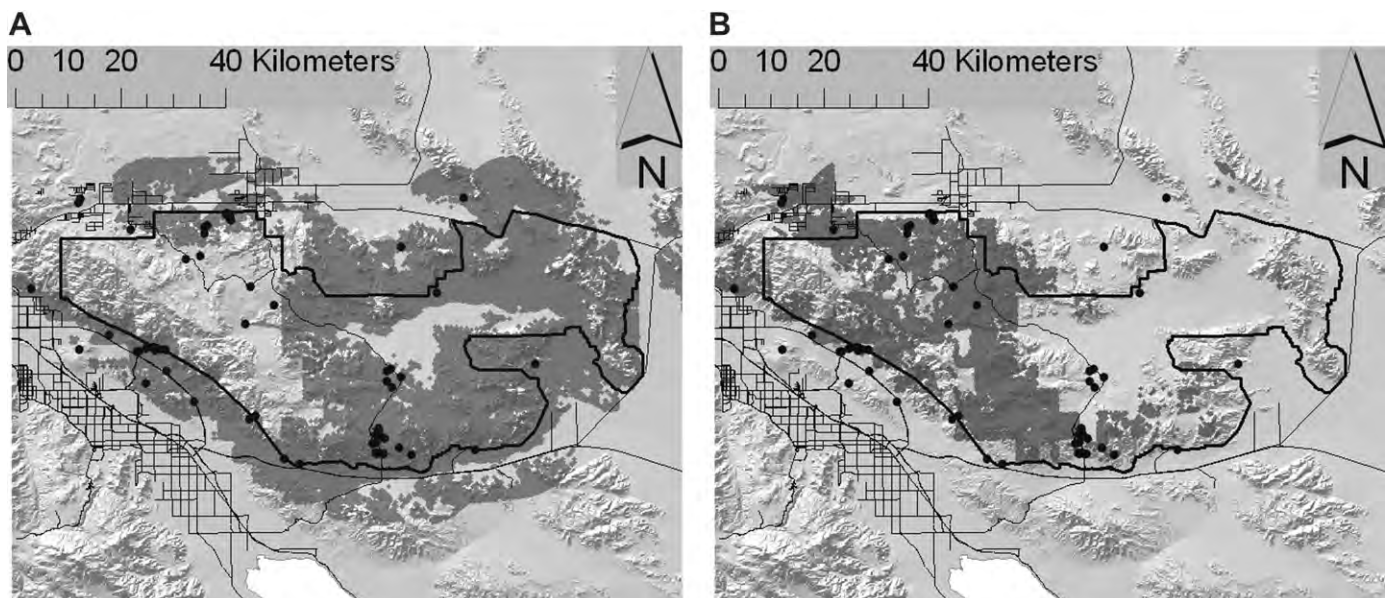

Fig. 3. Modeled (HSI ≥ 0.6) current suitable habitat (A) and the projected extent of suitable habitat under a mean climate shift of +2 °C and −50 mm of annual rainfall (B) for common chuckwallas. Black circles indicate tortoise locations used for the modeling. Heavy black bordered area indicates the boundary of Joshua Tree National Park.

Table 2
Estimated shifts in the area (ha) and mean elevation (m) of suitable habitat under a gradient of increasing severity of climate change (mean maximum July temperature increase [°C], and decrease in mean precipitation [mm]).

Species	Climate			
	Current	+1 °C, −25 mm	+2 °C, −50 mm	+3 °C, −75 mm
Desert Tortoise − Total	172,864	74,752	28,740	12,888
% of current modeled habitat	100	43	17	7
Sonoran Desert portion	138,656	52,656	17,084	6612
Mojave Desert portion	33,908	22,096	11,656	6276
Mean elevation	675 m	794 m	897 m	925 m
Common Chuckwalla − Total	219,332	112,860	66,932	57,184
% of current modeled habitat	100	51	30	26
Sonoran Desert portion	196,280	72,224	16,100	6260
Mojave Desert portion	23,052	40,636	50,832	50,924
Mean elevation	609 m	836 m	1059 m	1749 m

4. Discussion

Niche models presented here described climate and terrain envelopes, defined by species' current distributions within the study area. Fitting those envelopes to levels of climate change predicted for this region (Hayhoe et al., 2004; Seager et al., 2007) revealed species-specific responses. While the tortoises' relative habitat loss exceeded that for the chuckwalla, modeled niche spaces for both species responded to climate change simulations by shifting to or maintaining current habitat at higher elevations, which are currently cooler-wetter climate regimes.

Unlike high elevation and more tropical occurring reptiles which appear to be sensitive to even moderate increases in temperature (Huey et al., 2009; Sinervo et al., 2010), lower elevation desert species have evolved in environments that experience daily lethal surface temperatures through the summer months. These species have a large repertoire of behaviors to avoid high temperatures, including shifts in activity periods, seeking shelter below shrubs, beneath sand, in crevices, or burrows. Those behaviors may allow these species to adapt to temperature increases by shifting activity periods to earlier in the day or season and to otherwise avoid lethal temperatures. Non-lethal impacts of warming temperatures could include a shift in sex ratios to a higher frequency of female hatchlings, as incubation temperatures regulate sex ratios in hatchling desert tortoises (Lewis-Winokur and Winokur, 1995). Temperature regulation of sex ratios in chuckwallas has not been found.

Alternatively, the sparse precipitation in deserts regulates food and water resource availability (Noy-Meir, 1973; Bell, 1979; MacMahon, 1979) and so changes in annual rainfall, especially the increased duration and intensity of drought conditions, may have a more direct and negative impact on species distributions (Parmesan et al., 2000; Barrows et al., 2010). Although increased aridity is correlated with increased rainfall variability (Noy-Meir, 1973; Bell, 1979; MacMahon, 1979), climate change modeling as I have presented in this research considers only shifts in mean climate conditions, not extreme events such as extended droughts. When species-specific empirical data has been available to evaluate the impacts of extended droughts on species' demography, predictions of species' persistence were less optimistic than when considering mean shifts alone (Barrows et al., 2010). While there is disagreement among climate models, the mean climate change projection is for the southwestern U.S. is for increased aridity (Seager et al., 2007). Both tortoises and chuckwallas are large-bodied, long-lived (Curtin et al., 2009; Kwiatkowski et al., 2009). That longevity spanning at least a couple decades offers a potential buffer to periodic climate extremes as these species can curtail

reproduction until more favorable conditions return (Morris et al., 2008). However it is their ability to survive droughts will determine their ability to sustain populations if climate change predictions with respect to precipitation patterns are realized.

4.1. Desert tortoise drought strategies

Desert tortoises in the Mojave Desert are listed as threatened under the U.S. Endangered Species Act and as such have been a focus of protection and conservation related research. A large body of that research has addressed how desert tortoises deal with drought conditions (Peterson, 1996a, 1996b; Henen, 1997; Henen et al., 1998; Duda et al., 1999). In drought years tortoises increase time in burrows where they find higher humidity and moderate temperatures (Duda et al., 1999). The tortoises' large urine bladder enables them to consume large quantities of free water when available and to use that water to maintain hydration during periods when succulent plants or free water are not available (Peterson, 1996b). Drought conditions result in reduced tortoise activity (Duda et al., 1999) and lower metabolic and reproductive rates (Peterson, 1996a; Henen, 1997; Henen et al., 1998) although some breeding activity occurs even during periods of water stress (Henen, 1997). Despite these behavioral and physiological adaptations, during droughts tortoises experience as much as 40% loss of body mass and a 60% loss of water volume relative to body mass as well as large variations in blood osmolarity (Peterson, 1996b) and can have higher levels of mortality (Turner et al., 1984).

Desert tortoise diets are dominated by annual plants, perennial grasses and cactus (Turner et al., 1984; Jennings, 2002). Extended droughts would make these food resources largely unavailable (Wallace and Thomas, 2008). Tortoises do eat dry plant material and will increase lipid storage as a result of that consumption, but at the expense of loss in body water (Henen, 1997). Drinking free water during summer monsoon rains allows tortoises to avoid negative annual energy balances but such rains are unpredictable and increasingly so in the western portions of the tortoises' Mojave Desert distribution (Peterson, 1996a). The higher incidence of drought and the unpredictability of both annual plant growth and summer rains at lowest elevations within this portion of the Sonoran Desert may explain the tortoises' rarity or absence from those areas.

4.2. Common chuckwalla drought strategies

Like tortoises, during droughts chuckwallas reduce activity, reproduction, and abandon social interactions in order to minimize energy and water loss (Nagy, 1973; Smits, 1985). Common chuckwallas have also evolved divergent life history strategies based on the risk of extended drought at the locations where they occur (Tracy, 1999). At lower elevations where drought risk is higher chuckwallas reach sexual maturity faster and once mature divert energy into lipid storage more than toward continued growth. Those living at higher elevations have more dependable annual food resources, reach sexual maturity slower, but continue to grow after sexual maturity and achieve larger adult sizes than those at more arid locations. The greater stored fat of low elevation chuckwallas acts as a hedge against the likelihood of a subsequent poor resource year and so increases survivorship through those leaner periods (Case, 1976; Tracy, 1999). Chuckwallas also possess enlarged lymph sacs that store water (Norris and Dawson, 1964) which could allow them to reduce water deficits and, along with the use of efficient nasal salt glands that allow them to expel salt ions, maintain a more constant level of blood osmolarity even when employing evaporative cooling during periods of heat stress (Case, 1972).

Although both tortoise and chuckwallas are vegetarians, chuckwallas have a more varied diet. During years with high annual plant

productivity they consume those annual plants, but during dry years chuckwallas shift to consuming flowers and leaves from perennial woody shrubs and trees (Johnson, 1965; Nagy, 1973; Berry, 1974; Kwiatkowski and Sullivan, 2002). Those shrubs and trees often have deeper roots as well as other drought survival strategies and so can provide sustenance to the chuckwallas even in dry years. Such perennial food sources are reached by climbing into the shrubs and trees, a foraging mode unavailable to tortoises. Along with their physiological adaptations, utilizing woody plants for food and water resources during droughts may explain the chuckwallas' ability to sustain populations across a broad elevation range; that distribution is reflected in the niche model and climate response reflected in my analysis. This result is consistent with the hypothesis that having evolved in such a highly variable environment may afford some resilience to a changing climate (Huey et al., 2009).

4.3. Model caveats

My limitation on using abiotic independent variables for the development of niche models stemmed from available GIS layers as model inputs, as well as acknowledging the complexity and uncertainty as to how biotic variables would respond to climate change. The availability of annual and perennial plants, their density and species richness are clearly key components of these species' realized niche and ultimate distribution. Rainfall, temperature and slope characteristics may serve as a proxy for these biotic resources, with predictability of soil moisture during growing periods being a driver of vegetation characteristics. My levels of increasing aridity are based on analyses conducted by Seager et al. (2007) and Hayhoe et al. (2004). Those authors as well as the IPCC (2007) report acknowledge that not all climate models agree with the impact of climate change on precipitation in this region. The prognosis for impacts to the distribution for both the desert tortoise and common chuckwalla will improve if increases in aridity are less than those predicted by a majority of the climate models, and so are less than the increments used in my simulations.

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