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PAPER

# The range implications of lizard traits in changing environments

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## ABSTRACT

**Aim** Most predictions of species ranges are based on correlating current species localities to environmental conditions. These correlative models do not explicitly include a species' biology. In contrast, some mechanistic models link traits to energetics and population dynamics to predict species distributions. These models enable one to ask whether considering a species' biology is important for predicting its range. I implement mechanistic models to investigate how a species' morphology, physiology and life history influence its range.

**Location** North America.

**Methods** I compare the mechanistic model predictions with those of correlative models for eight species of North American lizards in both current environments and following a uniform 3 °C temperature warming. I then examine the implications of superimposing habitat and elevation requirements on constraints associated with environmental tolerances.

**Results** In the mechanistic model, species with a narrower thermal range for activity are both predicted and observed to have more restricted distributions. Incorporating constraints on habitat and elevation further restricts species distributions beyond areas that are thermally suitable. While correlative models generally outperform mechanistic models at predicting current distributions, the performance of mechanistic models improves when incorporating additional factors. In response to a 3 °C temperature warming, the northward range shifts predicted by the mechanistic model vary between species according to trait differences and are of a greater extent than those predicted by correlative models.

**Main conclusions** These findings highlight the importance of species traits for understanding the dynamics of species ranges in changing environments. The analysis demonstrates that mechanistic models may provide an important complement to correlative models for predicting range dynamics, which may underpredict climate-induced range shifts.

## Keywords

**Biophysical model, climate change, fundamental niche, habitat, life history, lizards, range shifts, North America, physiology, species distribution model.**

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## INTRODUCTION

Species have been observed to respond individually to past climate changes (mammals, FAUNMAP Working Group, 1996; butterflies, Parmesan *et al.*, 1999). The individualistic characteristics of these past range shifts include differences in the direction and distance that species distributions have shifted. Predictions of climate-induced range shifts are largely generated

using statistical models that correlate species localities to environmental conditions to define a species' environmental niche (Elith *et al.*, 2006). These models are inconsistent with individualistic range shifts to the extent that species with similar environmental niches are predicted to respond similarly to climatic changes (e.g. shift to the same degree along temperature isoclines). In a mechanistic model, climate changes are translated into changes in energetics and demography based on a species'

traits. Predictions that novel climates will cover extensive areas in the future also challenge model assumptions that the relationship between species localities and multiple environmental variables will remain constant (Williams & Jackson, 2007). In a mechanistic approach, these environmental variables are generally individually incorporated in biophysical models based on their known influence on an organism's physiology. This approach is consistent with a growing emphasis on considering organismal physiology when predicting responses to climate change (Addo-Bediako *et al.*, 2000; Helmuth *et al.*, 2005; Ghalambor *et al.*, 2006; Calosi *et al.*, 2008).

Correlative models generally perform well in predicting current species current ranges using only readily available data on the localities of species and environmental conditions (Elith *et al.*, 2006). Yet the models can exhibit weak performance in predicting past range shifts (Araújo *et al.*, 2005; Strasburg *et al.*, 2007). Mechanistic models, which describe the environmental dependence of energetics, physiological processes and demographics to directly estimate the parameters, are emerging to complement correlative models (Kearney & Porter, 2004; Buckley & Roughgarden, 2005; Crozier & Dwyer, 2006; Morin *et al.*, 2007; Buckley, 2008). The predictions of these models correspond more to an organism's fundamental niche (i.e. the regions where an organism is suited to live) rather than the realized niche (i.e. where the species actually lives), which corresponds to the predictions of correlative models (Hutchinson, 1957; Pulliam, 2000; Soberón, 2007; Kearney & Porter, 2009).

Mechanistic models require a comprehensive understanding of an organism's biology as well as detailed morphological and physiological data (Kearney & Porter, 2009). Most implementations of mechanistic models involve extensive empirical data collection for single species. Here I apply an existing mechanistic model (Buckley & Roughgarden, 2005; Buckley, 2008) to species of North American lizards. I parameterize the model using the considerable morphological, physiological, and life-history data available in the literature. I examine how interspecific trait differences enable species to occupy ranges that differ in extent and environmental conditions and how these trait differences can lead to differential future range shifts. I previously applied a foraging energetic model to examine how geographic trait variation between lizard populations yields differential current range predictions and differential responses to future climate change (Buckley, 2008). While this previous study of intraspecific trait variation suggested the occurrence of local adaptation, here I am interested in how interspecific trait differences enable lizard species to occupy different ranges. I thus use trait means across species.

Previous studies have established the strong role of environmental conditions in setting range limits in ectotherms (Buckley & Jetz, 2007; Cunningham *et al.*, 2009). Here I investigate how additional constraints such as habitat suitability and elevation limitations restrict ranges beyond those that are climatically suitable in both correlative and mechanistic models (Gaston & Chown, 1999; Wilson *et al.*, 2005). Whereas correlative models implicitly include a variety of abiotic and biotic constraints, mechanistic models represent a null model for the influence of

environmental conditions on the energetics of an organism. One can thus examine the implications of successively superimposing additional constraints such as habitat requirements onto the energetic constraints. Of particular interest is whether energetic constraints or habitat and elevation constraints result in the narrow distributions of several of the examined lizard species.

I compare the range predictions of mechanistic and correlative distribution models in current climates and following a uniform 3 °C temperature increase. The comparison of correlative and mechanistic models in this paper serves to: (1) address how trait differences translate into range predictions in mechanistic models and whether a trait-based perspective predicts different shifts in response to climate change than correlative models; and (2) how habitat suitability and elevation limitations influence correlative and mechanistic range predictions based on environmental conditions. I emphasize these comparisons rather than model performance. Because the predictions of correlative models correspond to the realized niche whereas the predictions of mechanistic models correspond to the fundamental niche, correlative models are generally expected to outperform mechanistic models at predicting current distributions.

## METHODS

### The foraging energetic model and parameterization with trait data

I applied a foraging energetic model (Buckley, 2008) to eight lizard species in North America that use a territorial sit-and-wait foraging strategy to pursue insect prey (Vitt & Pianka, 2005). The model was empirically tested for Caribbean *Anolis* lizards along elevation gradients (Buckley & Roughgarden, 2005). This implementation of the model closely follows that for populations of the eastern fence lizard, *Sceloporus undulatus* (Buckley, 2008; see also Appendix S1).

Energetic yield,  $E(d)$ , was calculated using an optimal foraging model for a territorial central place forager.  $E(d)$  ( $J s^{-1}$ ) is partially a function of metabolic rate and running velocity, both of which are estimated based on body size (snout–vent length, SVL). Energetic yield is also a function of prey density and prey size. The intrinsic rate of population increase,  $r_0$ , is calculated as births minus deaths,  $bE(d) - \lambda$ . Here,  $b$  is the reproductive rate per unit net energetic yield ( $b = mt_f$ ) and  $\lambda$  represents mortality and the reproductive cost of metabolism while not foraging [ $\lambda = \mu + m(24 \times 60 \times 60 - t_f)e_w$ ]. The parameter  $m$  is the quantity of eggs produced per joule multiplied by the probability of surviving to adulthood (eggs  $J^{-1}$ ),  $t_f$  is the time spent foraging (s),  $\mu$  is the daily mortality rate ( $day^{-1}$ ) and  $e_w$  is the resting metabolic rate. The influence of environmental temperature on population dynamics is determined by foraging time.

Morphological, physiological and life-history data for the eight analysed North American lizard species are presented in Table 1. The chosen species are those for which complete data were available, except *Urosaurus graciosus*. I attempted to locate all applicable data for each species and used the means of studies

**Table 1** The eight lizard species exhibit a wide range of life-history strategies as reflected in their morphological (SVL), physiological ( $T_{\min}$ ,  $T_{\text{mean}}$ ,  $T_{\text{max}}$ ) and life-history traits ( $S_{\text{ann}}$ ,  $S_{\text{mat}}$ , Mat, Egg and Prey).

Species	SVL (mm)	$T_{\min}$ (°C)	$T_{\text{mean}}$	$T_{\text{max}}$	$S_{\text{ann}}$ (%)	$S_{\text{mat}}$	Mat (months)	Egg (g)	Prey (mm)	References
<i>Holbrookia maculata</i>	52.4	30.0	34.4	39.0	0.40	0.16	11	0.24	7.0	1–4
<i>Phrynosoma platyrhinos</i>	76.6	25.0	34.9	40.0	0.65	0.10	22	0.70	7.2	2, 5–7
<i>Sceloporus graciosus</i>	55.5	24.5	33.9	38.2	0.57	0.12	23	0.18	4.6	7–11
<i>Sceloporus magister</i>	86.0	31.0	34.8	37.0	0.42	0.23	24	0.73	8.0	12–16
<i>Sceloporus undulatus</i>	63.0	25.0	34.8	38.9	0.28	0.09	14	0.33	10.1	2, 10, 17–18
<i>Urosaurus graciosus</i>	52.5	32.0	36.1	39.5	<i>U. ornatus</i> data used				5.2	6, 16
<i>Urosaurus ornatus</i>	51.2	28.0	36.0	41.0	0.30	0.09	10	0.23	4.9	16, 19–20
<i>Uta stansburiana</i>	45.7	24.5	35.4	40.6	0.11	0.13	9	0.20	5.7	2, 7, 8, 12, 21

SVL, snout–vent length.  $T_{\min}$ ,  $T_{\text{mean}}$ ,  $T_{\text{max}}$ , minimum, mean and maximum body temperatures, respectively;  $S_{\text{ann}}$ , annual survival;  $S_{\text{mat}}$ , survival to maturity; Mat, age of maturity; Egg, egg size; Prey, prey size.

References: 1, Sena (1978); 2, Barbault & Maury (1981); 3, Droge *et al.* (1982); 4, Jones & Ballinger (1987); 5, Medica *et al.* (1973); 6, Pianka & Parker (1975); 7, Vitt (1977); 8, Tinkle & Hadley (1975); 9, Rose (1976); 10, Van Berkum (1988); 11, Tinkle *et al.* (1993); 12, Brattstrom (1965); 13, Vitt & Ohmart (1974); 14, Tinkle (1976); 15, Huey *et al.* (2001); 16, Vitt *et al.* (1981); 17, Derickson (1976); 18, compiled in Buckley (2008); 19, Vitt & Congdon (1978); 20, Dunham (1982); 21, Tinkle (1967).

on different populations when possible. I include *U. graciosus* despite the lack of demographic data for the species because I wish to consider related and narrowly distributed species. I thus use demographic data for the closely related *Urosaurus ornatus* to parameterize the model for *U. graciosus* to see whether other traits are capable of predicting their differential ranges. The data vary between species in methodology, data quality and sample size. Another limitation is that data for different traits were gathered from different populations despite intraspecific differences in life-history strategies (Buckley, 2008).

SVL (mm) was compiled from the references as noted. I compiled data on mean adult female SVL when available and otherwise used the mean SVL across the sexes. I used a well-established relationship to convert lizard SVL to mass (g) (Pough, 1980):  $M = 3.1 \times 10^{-5} \times \text{SVL}^{2.98}$ . Maximum velocity ( $\text{m s}^{-1}$ ) was calculated as a function of body mass using a regression that was empirically derived across lizard species (Van Damme & Vanhooydonck, 2001):  $\log_{10} V = 0.044 + 0.2 \log_{10} M$ . Lizards were assumed to pursue prey at 70% of their maximum velocity (Irschick & Losos, 1998).

I used minimum and maximum voluntary temperatures [ $T_{\min}$  and  $T_{\text{max}}$  (°C), the range of recorded body temperatures of active individuals] to define the activity window for the lizards. The body temperature range for each species were reported in a single study and collected with variable methodology. Metabolic rates are contingent on whether lizards thermoregulate. The majority of field and laboratory research suggests that desert lizards successfully maintain their optimal body temperatures when environmental temperatures fall within the temperature range suitable for them to be active (Adolph & Porter, 1993; Christian, 1998; Huey *et al.*, 2003). I therefore focused on analyses that assume species thermoregulate to achieve their optimal performance temperature (which I approximated as  $T_{\text{mean}}$ ).

The survival parameter  $\mu$  ( $\text{day}^{-1}$ ) was estimated using annual survival,  $S_{\text{ann}}$ , from Table 1.

As data on the energetic requirements for egg production are scarce, I based my estimate of  $m$  ( $\text{eggs J}^{-1}$ ) on life-history data for

*Sceloporus undulatus* in Kansas and *Sceloporus graciosus* in Utah (Derickson, 1976). *Sceloporus undulatus* expends 64.67 kJ on average to produce eggs and produces an average of 20.9 eggs each season, yielding an egg production rate of  $3.2 \times 10^{-4}$   $\text{eggs J}^{-1}$ . *Sceloporus graciosus* expends an average of 54.16 kJ to produce eggs and produces an average of 10.4 eggs each season, yielding an egg production rate of  $1.9 \times 10^{-4}$   $\text{eggs J}^{-1}$  (Derickson, 1976). Dividing the energy required to produce an egg by the egg size yielded an energetic cost of 1000  $\text{J g}^{-1}$  of egg. I multiplied this quantity by the species-specific egg size and survival to maturity to estimate  $m$  ( $\text{eggs J}^{-1}$ ).

### Energetic costs and intake

The resting (waiting) metabolic rate,  $e_w$  ( $\text{J s}^{-1}$ ), was calculated as a function of mass and temperature using a relationship from Grant & Porter (1992) based on data for numerous species at several temperatures compiled by Bennett & Dawson (1982):

$$e_w = \frac{20.2}{3600} \times 10^{(0.038T_b - 1.77)} M^{0.82}$$

where  $T_b$  is body temperature (°C) and  $M$  is mass (g). To calculate  $e_w$ , I multiplied this expression by a factor of 1.5, which is the activity scope appropriate for a non-foraging iguanid lizard (Congdon *et al.*, 1982). For the active metabolic rate  $e_p$  ( $\text{J s}^{-1}$ ), I assumed an activity scope of 3 as suggested by Nagy (2005).

Data on geographic and climatic gradients of insect abundance and size distributions are limited, although insect abundance does tend to increase with increasing precipitation (Dunham, 1978). I use mean prey abundance ( $a = 0.01$  insects  $\text{m}^{-1} \text{s}^{-1}$ ) across four populations of *S. undulatus* (compiled in Buckley, 2008) as an estimate of prey abundance across all species as data are most readily available for this species. Abundance was estimated using sticky traps and counts included only those insects estimated to be of suitable prey size. I converted the insect density ( $\text{m}^{-2} \text{s}^{-1}$ ) to the number of insects

encountered ( $\text{m}^{-1} \text{s}^{-1}$ ) by assuming that lizards forage within 0.5 m of each side of the linear transect.

I calculated the energetic content per insect,  $e_i$  (J), using empirical data on mean prey size for each species (Table 1). Insufficient data were available to include a prey size distribution. The ratio of predator to prey length for those species with both metrics available is 10.2. I used this ratio to estimate that an insect's height and width are 1/5 of its length for three lizard species with only mean prey volume available (*Sceloporus magister*, 21.7 mm<sup>3</sup>; *U. graciosus*, 5.9 mm<sup>3</sup>; *U. ornatus*, 5.0 mm<sup>3</sup>; Vitt *et al.*, 1981). I used this geometry to estimate prey length (Table 1). I examined the sensitivity of the results to assuming differential prey size between species by parameterizing the models with the median prey size across species (6.33 mm,  $e_i = 33.8$  J). I converted insect length to mass using a regression for temperate deciduous forests from Schoener (1977) [ $M = 0.024 L^{2.35}$ ,  $n = 392$ , dry mass (mg) from length (mm)] and assumed an energy content of 23.85 J mg<sup>-1</sup> dry mass (Reichle, 1971; Andrews & Asato, 1977). I assumed that 76% of the energy available in an insect is in a form that could be assimilated by a lizard (Derickson, 1976). I discounted energy content per insect by multiplying by the proportion of prey caught. As no data were available on the proportion of prey caught, this factor is the only free parameter in the model. I assumed that 20% of insects are caught.

### Distribution data

Polygon lizard distribution data were derived from Peterson North America field guides and digitized by NatureServe (<http://natureserve.org/>). Extent of occurrence maps group known occurrences with polygons and include multiple polygons when known range discontinuities exist. Species occurrences were mapped using georeferenced museum specimens from HerpNet (<http://herpnet.org/>) and the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>). The occurrences are inherently spatially biased by the museums reporting georeferenced specimens.

I used habitat associations listed in the NatureServe Explorer (<http://natureserve.org/>, Table S1) that were compiled from the literature to define the species habitat associations. I assessed habitat availability using a 200-m resolution land-cover map generated by the National Atlas (<http://www.nationalatlas.gov/>). The map is based on the 1992 National Land Cover Database (NLCD) derived from Landsat Thematic Mapper imagery. The NatureServe habitat classes correspond closely to the 21 land-cover categories used by the NLCD. A grid cell was deemed to contain suitable habitat if at least 5% of its area was covered by any one class of suitable habitat for a species. I used georeferenced specimen localities from HerpNet to define a species' elevation range. I identified the 2.5% to 97.5% elevation quantiles for specimens to define the elevation range (Table S1 in Supporting Information). It is unclear whether this elevation range is an artefact of thermal constraints on ranges or whether the range reflects an independent factor such as changes in habitat availability and dispersal limitations with elevation.

I used the GTOPO30 (1-km spatial resolution, [http://eros.usgs.gov/#/Find\\_Data/Products\\_and\\_Data\\_Available/GTOPO30](http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/GTOPO30)) topographic map to assess elevation ranges. A grid cell was deemed to fall within a species' elevation range if the cell's mean elevation did so.

### Environmental data

I applied the foraging energetic model to individual equal-area projection and equal-area (343 km<sup>2</sup>) grid cells equivalent to 10' near the equator. I assumed that lizards are able to forage during daylight hours within their voluntary temperature range. Operative environmental temperatures,  $T_e$ , were calculated using a biophysical model (outlined in Campbell & Norman, 2000; lizard implementation in Buckley, 2008). Operative environmental temperature is the equilibrium temperature of an animal with specified thermal and radiative properties in a given environment and is calculated as air temperature plus or minus a temperature increment determined by absorbed radiation, wind speed and animal morphology (Bakken *et al.*, 1985). The approach is similar to, but is somewhat less detailed than, the ecophysiological models of Porter and colleagues that have been successfully applied to lizards at the landscape scale (Porter *et al.*, 2002; Kearney & Porter, 2004; Kearney *et al.*, 2009).

I used satellite-derived data to parameterize the environmental variables in the biophysical model for hourly air and soil temperature, annual mean wind speed, elevation and quarterly mean albedo (see Appendix S1). I derived mean values within the grid cells. The primary data source was New *et al.* (2002), which provides mean data from 1961 to 1990 with 10' resolution. To investigate responses to climate change, I assumed a uniform 3 °C increase, which is representative of midrange scenarios for the next century (Solomon *et al.*, 2007). I used a uniform warming to avoid confounding spatial patterns of temperature change with trait differences between species.

### Model comparison

Analysing model performance for mechanistic models is more complicated than doing so for traditional presence/absence ecological models because I wanted to compare predicted fundamental niches with observed realized niches. I minimized the penalty for predicting occurrences in areas outside a species' realized niche by testing for correct observed presences and predicted absences. The sensitivity index is the proportion of true positives correctly predicted (true positives predicted divided by the total number of true positives; Manel *et al.*, 2001). The specificity index is the proportion of predicted absences that were real (true negatives predicted divided by the total number of predicted negatives; Manel *et al.*, 2001). Overall performance is the proportion of cases correctly predicted.

I used specimen locality information to generate MAXENT correlative models (Phillips *et al.*, 2006) for comparison with the predictions of the mechanistic models. MAXENT derives the distribution, maximizing information entropy subject to constraints set by the association between the presence points and

the environmental variables. Twenty per cent of the specimen localities were withheld for model testing. Models were constructed with 500 iterations and a 0.00001 convergence threshold. The utilized environmental variables were the 19 bioclimatic variables derived from temperature and precipitation that are available in the WorldClim 10' dataset (Hijmans *et al.*, 2005). I used a resolution of 10' to correspond to the New *et al.* (2002) data used in the biophysical model.

## RESULTS

### Performance of correlative and mechanistic models in current environments

I investigated the proportion of grid cells occupied by neither, one or both of the predicted fundamental niches and the observed realized niche (Figs 1 & 2). As expected, the foraging energetic model including only climate often predicts that more areas are suitable than are actually occupied. Accordingly, model sensitivity, the proportional prediction of actual presences by grid cell, is fairly high and ranges from 0.87 to 1 (Table 2). However, overprediction leads to low values for specificity, the accuracy of predicted absences. The biological importance of this metric is uncertain because I am comparing the predicted fundamental niche with the observed realized niche. Accordingly, negative predictive power ranges from 0.03 to 0.77. The overall predictive performance, the proportion of cases correctly predicted, ranges from 0.13 to 0.77.

Range predictions from correlative maximum entropy models with both the 11 bioclimatic variables related to temperature and the full 19 bioclimatic variables (Fig. 3) enable a comparison with the mechanistic model. This confirms that the realized niches predicted by correlative models exhibit much less overprediction than the mechanistic models. While the correlative model predictions based on the 11 temperature-related variables and the full 19 bioclimatic variables are similar, a greater degree of overprediction (with low probability of occurrence) occurs when only temperature-related variables are incorporated. Whereas the mechanistic model primarily recognizes latitudinal range boundaries, the correlative model also recognizes longitudinal boundaries. The correlative model's recognition of longitudinal boundaries is weakened when restricting the analysis to the temperature-related variables as temperature gradients primarily occur latitudinally.

The foraging energetic model is fairly sensitive to parameter changes, but changes act consistently across species and do not influence range comparisons (Buckley, 2008). The most uncertain parameters are insect abundance,  $a$  (insects  $m^{-1} s^{-1}$ ), and the energetic content per insect,  $e_i$  (J). Abundance predictions respond approximately linearly to changes in both of these parameters. The range responses corresponding to 50% changes in insect abundance,  $a$ , and energetic input per insect,  $e_i$ , are depicted in Fig. S1. Decreasing the insect abundance by 50% results in a mean range loss across species of  $78 \pm 7\%$  (mean  $\pm$  SE, median = 82%), whereas increasing the insect abundance by 50% results in a mean range gain of  $67 \pm 30\%$  (median = 31%).

Changing the energetic content per insect by 50% results in a mean range loss of  $51 \pm 12\%$  (median = 51%) or gain of  $287 \pm 134\%$  (median = 114%). The narrowly distributed species tend to experience small range losses but large range expansions when halving or doubling the parameters. The range implications of using mean prey size rather than species-specific estimates are limited (Fig. S1).

### Importance of considering traits in distribution models

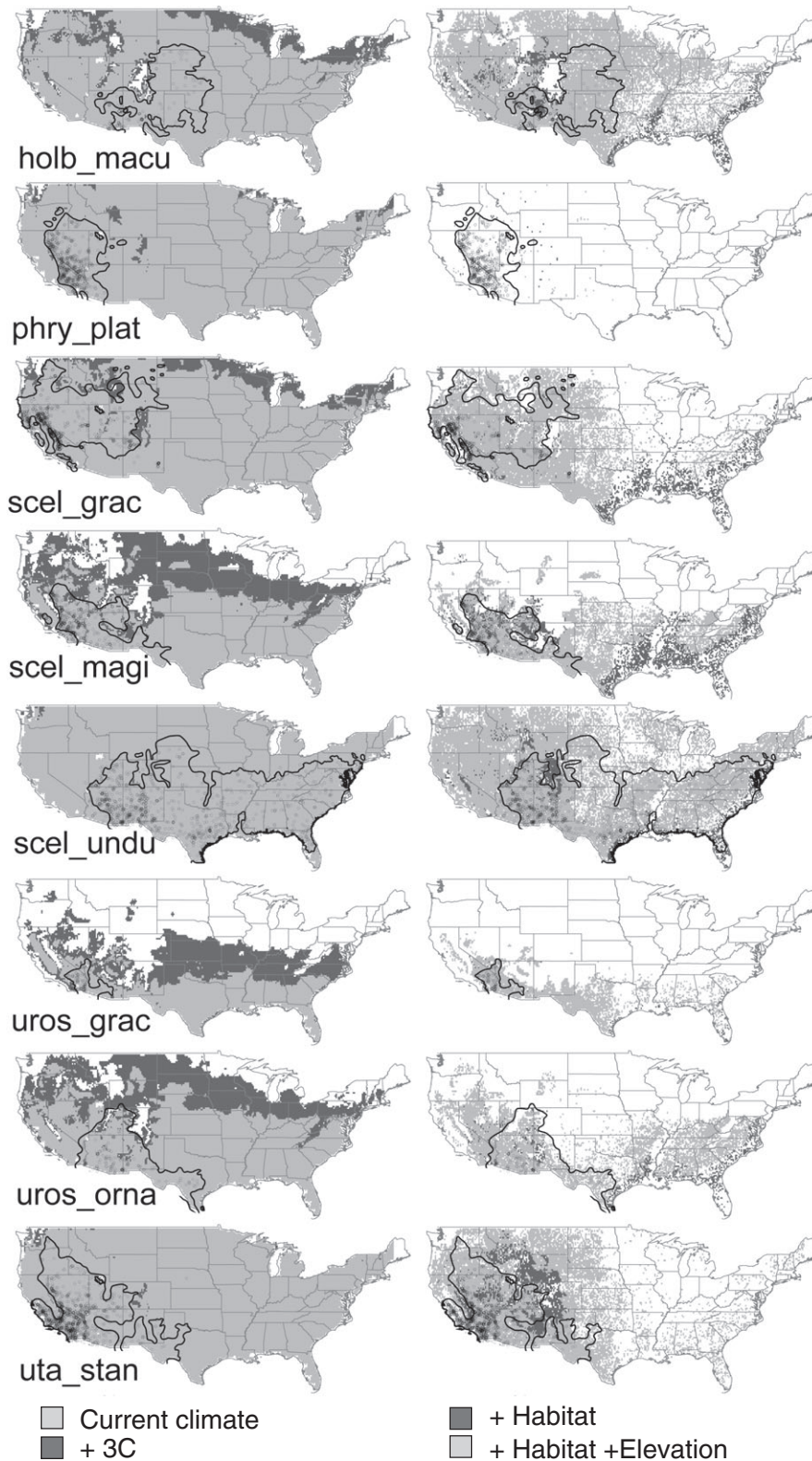
The ranges predicted by the foraging energetic model for the eight lizard species are strongly dependent on the breadth of their voluntary temperature ranges and energetic rates as a determined by body size (Fig. 1). As expected, species with the most southerly restricted ranges (*Holbrookia maculata*, *S. magister*, *U. graciosus*, *U. ornatus*) have the highest minimum voluntary temperatures. The species with southerly restricted ranges are less distinguished by mean and maximum temperatures than by minimum temperatures (Table 1, Fig. S2). Other species with restricted ranges such as *Phrynosoma platyrhinos* are predicted to be widely distributed. This vast overprediction leads to the question of whether other constraints such as habitat associations or the availability of appropriate food restrict the ranges below those which is thermally suitable.

The mechanistic model predicts that the thermally suitable ranges will respond individualistically to a 3 °C warming due to differential thermal breadth and metabolic rates (Figs 1 & 4). Predicted shifts are individualistic in that the extent of shift varies between species, but all species are predicted to extend their northern range boundary while the southern range boundary remains fixed. The predicted percentage change in range size is not a simple function of initial range size. I examined the percentage range expansion for those species that were initially predicted to occupy less than 90% of the prediction area to allow the potential for range expansion (Table 2). The average percentage range expansion among these five species is 48%. Although the three most narrowly distributed species do experience the greatest range expansion, the proportional range expansion varies considerably between species. The species with the largest proportional range change is *U. graciosus* at 99%, followed by *S. magister* at 63% and *U. ornatus* at 49%. I examine the sensitivity of the predictions to the assumption of constant insect abundance in Fig. S3.

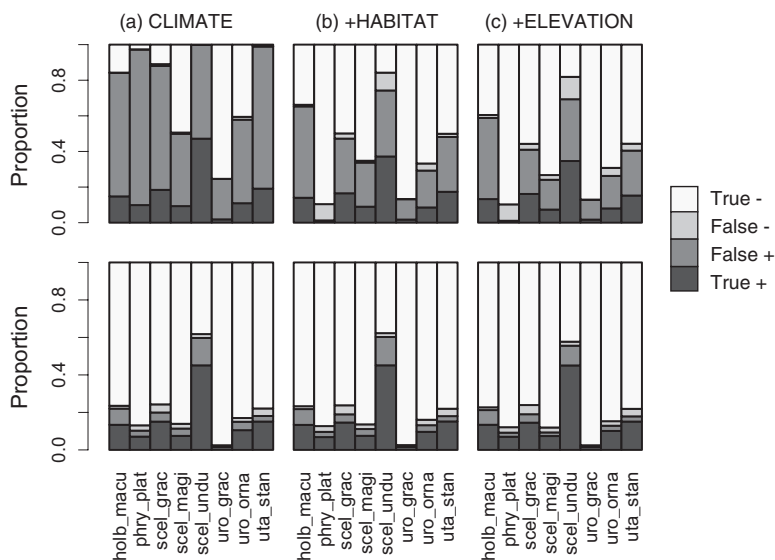
In comparison to the mechanistic model, the correlative model predicts some range contraction and much smaller range expansions (Table 2). The most extensive range expansion predicted by the correlative model with temperature and precipitation variables is 6%. The largest predicted expansion increases somewhat (6%) when precipitation variables are omitted from the model.

### Superimposing range constraints beyond environmental tolerance

I next superimposed habitat restriction onto the predicted ranges to see how habitat associations alter the thermally



**Figure 1** Range predictions for the lizard species from the foraging energetic model. Predictions are based on energetics alone under current climates (left, light grey) and following a uniform 3 °C temperature increase (left, dark grey). Predictions are also depicted for additionally including habitat associations (right, dark grey) and habitat associations and elevation constraints (right, light grey) for current climates in the model. Observed localities of the species (o) and atlas range polygons are included (black line). holb\_macu, *Holbrookia maculata*; phry\_plat, *Phrynosoma platyrhinos*; scel\_grac, *Sceloporus graciosus*; scel\_magi, *Sceloporus magister*; scel\_undu, *Sceloporus undulatus*; uros\_grac, *Urosaurus graciosus*; uros\_orna, *Urosaurus ornatus*; uta\_stan, *Uta stansburiana*.



**Figure 2** A comparison of observed and predicted ranges for the mechanistic and correlative models with (a) climate alone and (b) additionally habitat associations and (c) habitat associations and elevation constraints. The cumulative proportions of grid cells included are shown by both the observed and predicted range (true +), only the observed range (false -), only the predict range (false +) and neither range (true -). *holb\_macu*, *Holbrookia maculata*; *phry\_plat*, *Phrynosoma platyrhinos*; *scel\_grac*, *Sceloporus graciosus*; *scel\_mag*, *Sceloporus magister*; *scel\_und*, *Sceloporus undulatus*; *uro\_grac*, *Urosaurus graciosus*; *uro\_orna*, *Urosaurus ornatus*; *uta\_stan*, *Uta stansburiana*.

suitable range (Fig. 1). While many of the species have broad habitat associations resulting in minimal range implications (Table S1), the predicted range for *P. platyrhinos* is dramatically reduced due to its association with open sand and rock habitat. When accounting for habitat restrictions, the specificity and overall prediction success of the range prediction for *P. platyrhinos* increases to 0.90 and 0.99, respectively (Table 2). However, the range is now being underpredicted as only 11% of specimen occurrences are predicted. Small patches of appropriate habitat are probably available which are not reflected in the land-cover classification. Those species with broad habitat associations such as *S. graciosus* and *S. undulatus* are also those species that are broadly distributed.

Finally, I examined how superimposing elevation restrictions further limits the range beyond the areas that are thermally suitable and contain suitable habitat (Fig. 1). I used the 2.5 and 97.5% quantiles of specimen elevations to restrict the elevation range of each species. This approach is somewhat circular, as thermal constraints are directly related to elevation constraints. The elevation constraints generally have minimal range implications, suggesting that thermal constraints adequately restricted elevation ranges. The elevation constraints did eliminate some areas previously predicted to be suitable in the east, but this may be an artefact of biotic constraints restricting ranges – and specimen localities from which elevation ranges were derived – to the west. For *Uta stansburiana*, range predictions along the continental divide are somewhat improved when including elevation restrictions (Table 2).

Including habitat and elevation in the correlative model influences range predictions to a much lesser extent (Table 2, Fig. 3). Including habitat does not influence model performance, while additionally including elevation improves performance to a small degree.

## DISCUSSION

A vast quantity of lizard trait data exist in the literature. Yet few techniques exist to aggregate these data into demography. Such aggregation is essential for understanding the different combinations of traits that enable different lizard species to persist and to predict distributions. This analysis demonstrates that energetic implications of morphological, physiological and life-history traits broadly account for different distributions among lizard species. Including habitat and elevation constraints further refines the predicted distributions. However, the correlative models tend to outperform the mechanistic models at predicting current distributions. The performance of the mechanistic model approaches that of the correlative model when habitat and elevation are included. In contrast, including these additional factors has little influence on the performance of correlative models.

The mechanistic model largely predicts that climate change will expand ranges by extending the foraging window. The duration of foraging is a primary determinant of energetic yield and ultimately range extent (Adolph & Porter, 1993). The underlying assumption of the model is that lizards are able to successfully thermoregulate to their optimal performance temperature. While this is largely the case for most temperate regions in current climates (Adolph & Porter, 1993; Huey *et al.*, 2003), the potential for lizard thermoregulation in warmed climates is uncertain, particularly in tropical climates (Huey *et al.*, 2009; Kearney *et al.*, 2009). Additional energetic costs may be incurred for metabolism in warmer temperatures (Angilletta, 2001). Our results support previous findings that climate change may be more detrimental to tropical than temperate ectotherms despite the larger temperature changes projected in temperate areas (Deutsch *et al.*, 2008; Huey *et al.*, 2009).

**Table 2** Estimates of model performance for the eight lizard species when parameterizing the mechanistic models with (a) traits, (b) traits and habitat associations and (c) traits, habitat associations and elevation constraints is somewhat lower than the performance of corresponding correlative models.

	holb_macu	phry_plat	scel_grac	scel_magi	scel_undu	uro_grac	uro_orna	uta_stan
<i>Mechanistic</i>								
(a) Climate								
Prop. specimens predicted	1.00	1.00	0.95	0.97	1.00	0.98	0.95	1.00
Sensitivity	0.99	1.00	0.95	0.93	1.00	0.99	0.87	1.00
Specificity	0.18	0.03	0.14	0.55	0.00	0.77	0.46	0.01
Overall performance	0.30	0.13	0.29	0.59	0.47	0.77	0.51	0.20
Prop. range expansion	0.15		0.13	0.63		0.99	0.49	
(b) Climate + habitat								
Prop. specimens predicted	0.95	0.11	0.87	0.90	0.86	0.89	0.77	0.89
Sensitivity	0.94	0.08	0.85	0.90	0.79	0.93	0.68	0.91
Specificity	0.40	0.99	0.62	0.72	0.30	0.88	0.76	0.62
Overall performance	0.48	0.90	0.66	0.74	0.53	0.88	0.75	0.67
(c) Climate + habitat + elevation								
Prop. specimens predicted	0.91	0.10	0.84	0.81	0.79	0.89	0.69	0.81
Sensitivity	0.89	0.07	0.83	0.74	0.73	0.92	0.64	0.80
Specificity	0.46	1.00	0.69	0.81	0.34	0.89	0.79	0.69
Overall performance	0.53	0.90	0.72	0.81	0.53	0.89	0.77	0.71
<i>Correlative</i>								
(a) Climate								
Prop. specimens predicted	0.98	0.98	0.98	0.98	0.99	1.00	0.97	0.99
Sensitivity	0.90	0.72	0.78	0.75	0.96	0.83	0.84	0.79
Specificity	0.90	0.96	0.94	0.96	0.72	0.99	0.95	0.96
Overall performance	0.90	0.94	0.91	0.94	0.83	0.99	0.94	0.93
Prop. range expansion	0.03	0.03	0.01	0.06	0.02	0.03	0.04	0.03
Prop. range contraction	0.00	0.00	0.02	0.01	0.00	0.01	0.01	0.00
<i>Temperature only</i>								
Prop. specimens predicted	0.95	0.97	0.96	0.97	0.99	0.98	0.95	0.98
Sensitivity	0.94	0.78	0.77	0.81	0.97	0.89	0.79	0.82
specificity	0.81	0.91	0.88	0.90	0.60	0.98	0.90	0.79
Overall performance	0.83	0.90	0.86	0.89	0.78	0.98	0.89	0.80
Prop. range expansion	0.03	0.06	0.03	0.09	0.02	0.06	0.06	0.05
Prop. range contraction	0.01	0.02	0.04	0.02	0.01	0.00	0.03	0.02
(b) Climate + habitat								
Prop. specimens predicted	0.97	0.98	0.97	0.97	0.99	1.00	0.94	0.98
Sensitivity	0.90	0.69	0.75	0.75	0.96	0.82	0.77	0.79
Specificity	0.90	0.97	0.95	0.96	0.71	0.99	0.96	0.96
Overall performance	0.90	0.94	0.91	0.94	0.83	0.99	0.94	0.93
(c) Climate + habitat + elevation								
Prop. specimens predicted	0.95	0.98	0.98	0.96	0.99	1.00	0.97	0.98
Sensitivity	0.90	0.71	0.75	0.74	0.95	0.80	0.81	0.79
Specificity	0.91	0.98	0.94	0.98	0.80	0.99	0.97	0.97
Overall performance	0.91	0.95	0.91	0.95	0.87	0.99	0.95	0.93

The proportion (prop.) range expansion following a 3 °C temperature increase is greater for mechanistic models than for correlative models.

holb\_macu, *Holbrookia maculata*; phry\_plat, *Phrynosoma platyrhinos*; scel\_grac, *Sceloporus graciosus*; scel\_magi, *Sceloporus magister*; scel\_undu, *Sceloporus undulatus*; uro\_grac, *Urosaurus graciosus*; uro\_orna, *Urosaurus ornatus*; uta\_stan, *Uta stansburiana*.

Distribution models that explicitly incorporate trait differences among species predict that the extent of response to environmental change varies between species. The present analysis adds to growing evidence that species respond individualisti-

cally to temperature and that considering traits and life histories is essential for understanding ranges (reviewed in Helmut *et al.*, 2005). Differences between the predictions of correlative and mechanistic models suggest that temperature may constrain



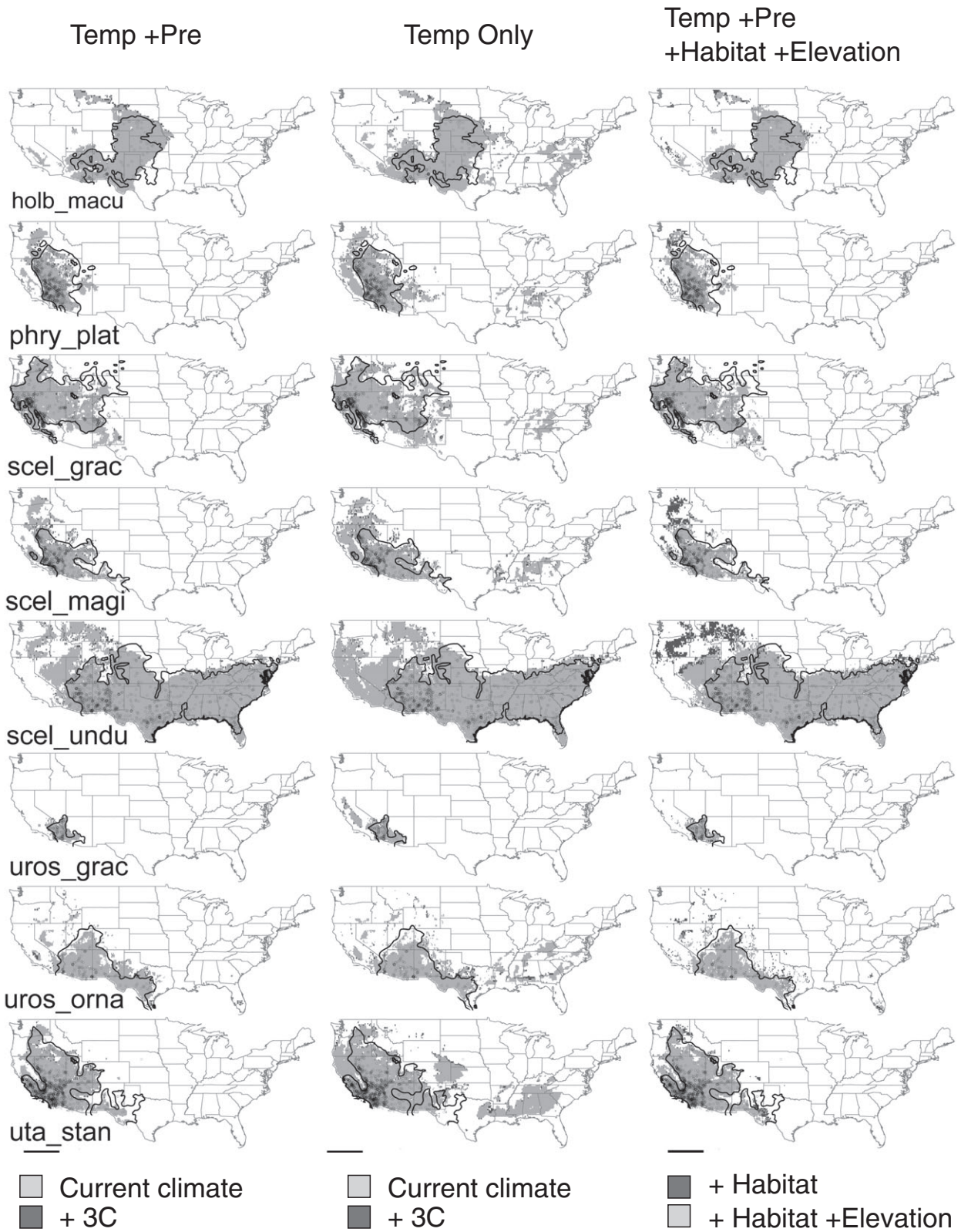
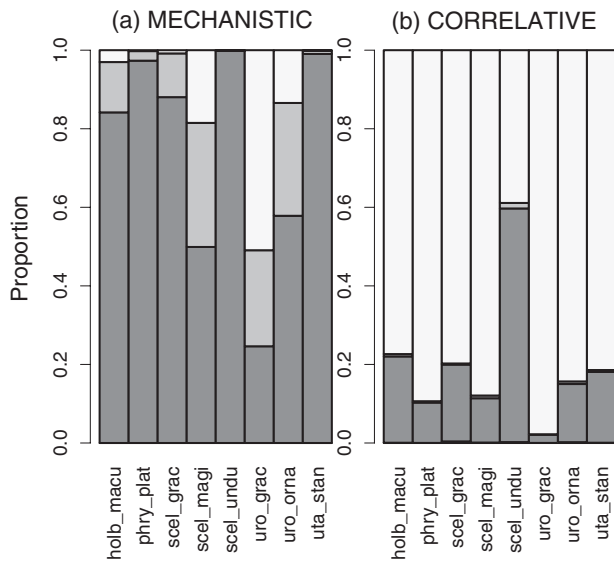


Figure 3 Range predictions for the lizard species from a correlative MAXENT model. Predictions are based on parameterization with temperature and precipitation variables (left), temperature variables only (middle) and temperature and precipitation variables plus habitat and elevation (right). Observed localities of the species (o) and atlas range polygons are included (black line). holb\_macu, *Holbrookia maculata*; phry\_plat, *Phrynosoma platyrhinos*; scel\_grac, *Sceloporus graciosus*; scel\_magi, *Sceloporus magister*; scel\_undu, *Sceloporus undulatus*; uros\_grac, *Urosaurus graciosus*; uros\_orna, *Urosaurus ornatus*; uta\_stan, *Uta stansburiana*.



**Figure 4** The proportion of total area predicted to be occupied (dark grey) in current environmental conditions and the predicted proportional range increase following a 3 °C warming (light grey). holb\_macu, *Holbrookia maculata*; phry\_plat, *Phrynosoma platyrhinos*; scel\_grac, *Sceloporus graciosus*; scel\_magi, *Sceloporus magister*; scel\_undu, *Sceloporus undulatus*; uro\_grac, *Urosaurus graciosus*; uro\_orna, *Urosaurus ornatus*; uta\_stan, *Uta stansburiana*.

distributions by altering the balance of energy acquisition and use (as set by physiologically constrained foraging duration and food abundance) rather than a direct influence of temperature. This indirect influence of temperature on distributions results in the prediction that species will respond differentially to a given change in temperature. If distribution limits were directly related to temperature, we would expect the ranges for all species to shift to an equal extent to follow a temperature isocline. In contrast to the mechanistic model, the correlative model predicts that species distributions will expand to a small and similar extent between species. The correlative model additionally predicts range contractions. Our analysis suggests that correlative models may underpredict climate-induced range shifts. Applying correlative and mechanistic models to forecast and hindcast distributions will be essential to understanding which type of model predicts more realistic range shifts.

A striking difference between the model predictions is that the correlative models recognize longitudinal range limits in addition to latitudinal limits, while the mechanistic models primarily recognize latitudinal range limits. This difference probably results from predictions of the realized and fundamental niches, respectively. For example, the closely related *Sceloporus* species may have nearly disjoint ranges due to species interactions (Buckley, 2008). Biotic constraints can be attributed to environmental conditions in correlative models. Whether these environmental correlates are coincidental or whether they correspond to underlying limiting processes will determine the robustness of the statistical model predictions.

The overprediction of the mechanistic model observed for most species suggests that there is considerable work required to refine the predictions of mechanistic distribution models. However, it is unclear what portion of the overprediction results from prediction of the fundamental niche versus problems with the model. Including limitations posed by habitat specificities and elevation ranges on the thermally suitable ranges predicted by the mechanistic models does reduce overprediction, particularly for species with specific habitat requirements. The similar performance of the correlative models parameterized with different sets of variables suggests that the correlative models may not capture how different variables differentially constrain ranges as is achieved when the constraints are explicitly specified in a mechanistic model.

Variation in lizard body size and thermal physiology along latitudinal and elevation gradients may cause divergence from the predictions, which are based on mean morphology and physiology (Sinervo, 1990). For example, the only prey size data I was able to locate for *S. undulatus* are from a Chihuahuan desert lizard community, where prey size appears to be large relative to the lizard's body size. This results in northerly range predictions for the species as the species gains a large amount of energy from large prey items in the model when it is sufficiently warm to forage. Indeed, trait differences between populations of *S. undulatus* produce differential range predictions and range shifts when using the mechanistic model described here (Buckley, 2008). Implementing mechanistic models requires substantial trait and demographic data which can be limiting. Parameterizing the models sometimes requires using data from closely related species (as was the case for *U. graciosus* here), which can induce error.

The model should be viewed as a simplified model for the influence of temperature on species ranges. I do not consider the influence of temperature on growth rates and time to maturation (Angilletta *et al.*, 2004) or on egg viability and energy assimilation (Porter *et al.*, 2002). I exclude other potentially important environmental constraints such as water availability, which was predicted by correlative models to be the major threat to European reptiles (Araújo *et al.*, 2006). I lack sufficient empirical data to model how prey availability varies with environmental conditions (Crozier & Dwyer, 2006). Mechanistic models based on population dynamics can be extended eventually to include these and other processes potentially constraining species ranges.

This study has emphasized how different suites of traits lead to different species distributions and range shifts rather than the predictive performance of mechanistic range models. The analysis has demonstrated the viability of using data from the literature for well-studied species to parameterize a mechanistic range model. It has also revealed data limitations such as the ability to estimate resource availability at broad scales. Parameter variation and errors in mechanistic models may be less likely to propagate than those in correlative models (Thuiller, 2004) because the model does not rely on the correlation structure between variables. Further, most of the uncertainty in the mechanistic model related to the different aspects of a single

parameter, namely insect abundance. Another parameterization challenge is assembling data collected at various spatial resolutions. I have attempted to minimize the errors introduced by scaling issues by standardizing all the data to a uniform grid cell size.

A growing interest in trait-based approaches may facilitate further implementations of mechanistic models through the development of online trait databases. Without conducting extensive empirical work to parameterize the model, mechanistic range models may be best suited for developing a qualitative understanding of range dynamics. Still, I believe this qualitative understanding is important, particularly when compared with the predictions of correlative models. This implementation of a mechanistic model represents a middle ground between highly detailed and carefully parameterized mechanistic models for single species and correlative models that can be readily implemented for many species but exclude species biology.

Correlative range models are generally more expedient and often exhibit more accurate predictions of current ranges than mechanistic distribution models. However, the assumptions of correlative models may be violated in changing environments (Kearney & Porter, 2009). Biotic constraints such as species interactions and dispersal limitations that limit specimen localities can shift in future climates. A further concern is that current climatic conditions may not fully reflect all the environmental conditions that are suitable for a species (Williams & Jackson, 2007). This concern is particularly acute given forecasts that the occurrence of novel climates will be widespread by 2100 (Williams & Jackson, 2007). Assessing whether correlative models are sufficient for predicting responses to climate change or whether mechanistic approaches are necessary requires data on historic ranges of lizards, which are currently limited. While correlative range models will remain an important predictive tool, this demonstration of the importance of considering species traits suggests the value in continuing to advance mechanistic range models.

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## REFERENCES

- Addo-Bediako, A., Chown, S. & Gaston, K. (2000) Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 739–745.
- Adolph, S.C. & Porter, W.P. (1993) Temperature, activity, and lizard life-histories. *The American Naturalist*, **142**, 273–295.
- Andrews, R.M. & Asato, T. (1977) Energy utilization of a tropical lizard. *Comparative Biochemistry and Physiology*, **58A**, 57–62.
- Angilletta, M.J. (2001) Variation in metabolic rate between populations of a geographically widespread lizard. *Physiological and Biochemical Zoology*, **74**, 11–21.
- Angilletta, M.J., Sears, M.W. & Steury, T.D. (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life history puzzle. *Integrative and Comparative Biology*, **44**, 498–509.
- Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, **33**, 1712–1728.
- Bakken, G.S., Santee, W.R. & Erskine, D.J. (1985) Operative and standard operative temperature: tools for thermal energetics studies. *Integrative and Comparative Biology*, **25**, 933–943.
- Barbault, R. & Maury, M.E. (1981) Ecological organization of a Chihuahuan desert lizard community. *Oecologia*, **51**, 335–342.
- Bennett, A.F. & Dawson, W.R. (1982) Metabolism. *Biology of the Reptilia*, Vol. 13 (ed. by C. Gans and F.H. Pough), pp. 127–223. Academic Press, London.
- Brattstrom, B.H. (1965) Body temperatures of reptiles. *American Midland Naturalist*, **73**, 376–422.
- Buckley, L.B. (2008) Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *The American Naturalist*, **171**, E1–E19.
- Buckley, L.B. & Jetz, W. (2007) Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1167–1173.
- Buckley, L.B. & Roughgarden, J. (2005) Effect of species interactions on landscape abundance patterns. *Journal of Animal Ecology*, **74**, 1182–1194.
- Calosi, P., Bilton, D. & Spicer, J. (2008) Thermal tolerance, acclimatory capacity and vulnerability to global climate change. *Biology Letters*, **4**, 99–102.
- Campbell, G. & Norman, J. (2000) *An introduction to environmental biophysics*. Springer, New York.
- Christian, K. (1998) Thermoregulation by the short-horned lizard (*Phrynosoma douglasi*) at high elevation. *Journal of Thermal Biology*, **23**, 395–399.
- Congdon, J.D., Dunham, A.E. & Tinkle, D.W. (1982) Energy budgets and life histories of reptiles. *Biology of the Reptilia*. Vol. 13 (ed. by C. Gans and F.H. Pough), pp. 233–271. Academic Press, New York.
- Crozier, L. & Dwyer, G. (2006) Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. *The American Naturalist*, **167**, 853–866.
- Cunningham, H., Rissler, L. & Apodaca, J. (2009) Competition at the range boundary in the slimy salamander: using reciprocal transplants for studies on the role of biotic interactions in spatial distributions. *Journal of Animal Ecology*, **78**, 52–62.
- Derickson, W.K. (1976) Ecology and physiological aspects of reproductive strategies in two lizards. *Ecology*, **57**, 445–458.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts

- of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences USA*, **105**, 6668–6672.
- Droge, D.L., Jones, S.M. & Ballinger, R.E. (1982) Reproduction of *Holbrookia maculata* in western Nebraska. *Copeia*, **1982**, 356–362.
- Dunham, A.E. (1978) Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology*, **59**, 770–778.
- Dunham, A.E. (1982) Demographic and life-history variation among populations of the iguanid lizard *Urosaurus ornatus*: implications for the study of life-history phenomena in lizards. *Herpetologica*, **38**, 208–221.
- Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- FAUNMAP Working Group (1996) Spatial response of mammals to late Quaternary environmental fluctuations. *Science*, **272**, 1601–1606.
- Gaston, K. & Chown, S. (1999) Elevation and climatic tolerance: a test using dung beetles. *Oikos*, **86**, 584–590.
- Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, **46**, 5–17.
- Grant, B.W. & Porter, W.P. (1992) Modeling global macroclimatic constraints on ectotherm energy budgets. *American Zoologist*, **32**, 154–178.
- Helmuth, B., Kingsolver, J.G. & Carrington, E. (2005) Biophysics, physiological ecology, and climate change: does mechanism matter? *Annual Review of Physiology*, **67**, 177–201.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Huey, R.B., Pianka, E.R. & Vitt, L.J. (2001) How often do lizards 'run on empty'? *Ecology*, **82**, 1–7.
- Huey, R.B., Hertz, P.E. & Sinervo, B. (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *The American Naturalist*, **161**, 357–366.
- Huey, R., Deutsch, C., Tewksbury, J., Vitt, L., Hertz, P., Álvarez Pérez, H. & Garland, T. (2009) Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1939–1948.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.
- Irschick, D.J. & Losos, J.B. (1998) A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution*, **52**, 219–226.
- Jones, S.M. & Ballinger, R.E. (1987) Comparative life histories of *Holbrookia maculata* and *Sceloporus undulatus* in western Nebraska. *Ecology*, **68**, 1828–1838.
- Kearney, M. & Porter, W.P. (2004) Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology*, **85**, 3119–3131.
- Kearney, M. & Porter, W.P. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.
- Kearney, M., Shine, R. & Porter, W. (2009) The potential for behavioral thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proceedings of the National Academy of Sciences USA*, **106**, 3835–3840.
- Manel, S., Williams, H.C. & Ormerod, S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, **38**, 921–931.
- Medica, P.A., Turner, F.B. & Smith, D.D. (1973) Effects of radiation on a fenced population of horned lizards (*Phrynosoma platyrhinos*) in southern Nevada. *Journal of Herpetology*, **7**, 79–85.
- Morin, X., Augspurger, C. & Chuine, I. (2007) Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? *Ecology*, **88**, 2280–2291.
- Nagy, K.A. (2005) Field metabolic rate and body size. *Journal of Experimental Biology*, **208**, 1621–1625.
- New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Pianka, E.R. & Parker, W.S. (1975) Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. *Copeia*, **1975**, 141–162.
- Porter, W.P., Sabo, J.L., Tracy, C.R., Reichman, O.J. & Ramanakutty, N. (2002) Physiology on a landscape scale: plant–animal interactions. *Integrative and Comparative Biology*, **42**, 431–453.
- Pough, F.H. (1980) The advantages of ectothermy for tetrapods. *The American Naturalist*, **115**, 92–112.
- Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- Reichle, D.E. (1971) Energy and nutrient metabolism of soil and litter invertebrates. *Productivity of forest ecosystems* (ed. by P. Devigneaud), pp. 465–475. UNESCO, Paris.
- Rose, B.R. (1976) Habitat and prey selection of *Sceloporus occidentalis* and *Sceloporus graciosus*. *Ecology*, **57**, 531–541.
- Schoener, T.W. (1977) Length–weight regressions in tropical and temperate forest-understory insects. *Annals of the Entomological Society of America*, **73**, 106–109.
- Sena, A.P. (1978) Temperature relations and the critical thermal maximum of *Holbrookia maculata maculata* (Reptilia Iguanidae). *Southwestern Naturalist*, **23**, 41–50.
- Sinervo, B. (1990) Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). *Oecologia*, **83**, 228–237.

- Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115–1123.
- Solomon, S., Qin, D., Manning, M. *et al.* (2007) Technical summary. *Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), pp. 996. Cambridge University Press, Cambridge.
- Strasburg, J.L., Kearney, M., Moritz, C. & Templeton, A.R. (2007) Combining phylogeography with distribution modeling: multiple Pleistocene range expansions in a parthenogenetic gecko from the Australian arid zone. *PLoS ONE*, **2**, e760.
- Thuiller, W. (2004) Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology*, **10**, 2020–2027.
- Tinkle, D.W. (1967) The life and demography of the side-blotched lizard, *Uta stansburiana*. *Miscellaneous Publications Museum of Zoology, University of Michigan*, **132**, 1–182.
- Tinkle, D.W. (1976) Comparative data on the population ecology of the desert spiny lizard, *Sceloporus magister*. *Herpetologica*, **32**, 1–6.
- Tinkle, D.W. & Hadley, N.F. (1975) Lizard reproductive effort: caloric estimates and comments on its evolution. *Ecology*, **56**, 427–434.
- Tinkle, D.W., Dunham, A.E. & Congdon, J.D. (1993) Life history and demographic variation in the lizard *Sceloporus graciosus*: a long-term study. *Ecology*, **74**, 2413–2429.
- Van Berkum, F.H. (1988) Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *The American Naturalist*, **132**, 327–343.
- Van Damme, R. & Vanhooydonck, B. (2001) Origins of inter-specific variation in lizard sprint capacity. *Functional Ecology*, **15**, 186–202.
- Vitt, L.J. (1977) Observations on clutch and egg size and evidence for multiple clutches in some lizards of southwestern United States. *Herpetologica*, **33**, 333–338.
- Vitt, L.J. & Congdon, J.D. (1978) Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *The American Naturalist*, **112**, 595–608.
- Vitt, L.J. & Ohmart, R.D. (1974) Reproduction and ecology of a Colorado River population of *Sceloporus magister* (Sauria: Iguanidae). *Herpetologica*, **30**, 410–417.
- Vitt, L.J. & Pianka, E.R. (2005) Deep history impacts present day ecology and biodiversity. *Proceedings of the National Academy of Sciences USA*, **102**, 7877–7881.
- Vitt, L.J., Van, Sels, R.C. & Ohmart, R.D. (1981) Ecological relationships among arboreal desert lizards. *Ecology*, **62**, 398–410.
- Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475–482.
- Wilson, R.D., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R. & Monserrat, V. (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**, 1138–1146.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Sensitivity analysis of the dynamic model predictions.

**Figure S2.** Principal components analysis of lizard traits.

**Figure S3.** Sensitivity analysis for changes in insect abundance during climate change.

**Table S1.** Species habitat specificities and elevation range.

**Appendix S1.** Supplementary methods.

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## BIOSKETCH

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