E-Article

Linking Traits to Energetics and Population Dynamics to Predict Lizard Ranges in Changing Environments

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abstract: I present a dynamic bioenergetic model that couples individual energetics and population dynamics to predict current lizard ranges and those following climate warming. The model predictions are uniquely based on first principles of morphology, life history, and thermal physiology. I apply the model to five populations of a widespread North American lizard, *Sceloporus undulatus*, to examine how geographic variation in traits and life histories influences ranges. This geographic variation reflects the potential for species to adapt to environmental change. I then consider the range dynamics of the closely related *Sceloporus graciosus*. Comparing predicted ranges and actual current ranges reveals how dispersal limitations, species interactions, and habitat requirements influence the occupied portions of thermally suitable ranges. The dynamic model predicts individualistic responses to a uniform 3°C warming but a northward shift in the northern range boundary for all populations and species. In contrast to standard correlative climate envelope models, the extent of the predicted northward shift depends on organism traits and life histories. The results highlight the limitations of correlative models and the need for more dynamic models of species' ranges.

Keywords: bioenergetic model, climate change, fundamental niche, population dynamic model, range shifts, species' ranges.

Understanding the factors that determine a species' range is a central objective in ecology and evolutionary biology, with important applications to predicting species distributions in unsampled regions and in response to environmental change (Holt and Keitt 2005). Predicting range shifts is particularly challenging because ranges are influenced by environmental suitability, species interactions, and dispersal limitations (Case et al. 2005). Here I use first principles of organism morphology and thermal physiology to predict current distributions and those following a uniform 3°C climate warming. Climate warming has been implicated in ongoing population declines (Pounds et al. 1999), phenological shifts (Root et al. 2003), morphological changes (Chamaillé-Jammes et al. 2006), and range shifts (Parmesan et al. 1999).

Two distinct methods are primarily employed to predict range shifts in response to climate change: climate envelope (or environmental niche) and ecophysiological models. Climate envelope models correlate species distributions to the underlying environment (Pearson and Dawson 2003). Range shifts are predicted by assuming that species follow their climate envelope to maintain constant climatic conditions. Climate envelope models are sufficiently general to supply valuable range information, with only limited data on current species distributions. However, envelope models do not incorporate population dynamics and thus have limited capacity to predict extinctions. The predictive power of climate envelope models is limited by several additional factors: (i) they are based on the assumption that species will respond uniformly and linearly to shifts in climatic variables, (ii) envelopes can confound the influences of species interactions and climate on current distributions, and (iii) envelopes do not consider biogeographic dispersal limitations (Pearson and Dawson 2003).

Recent developments in applying ecophysiological models at the landscape scale have begun to address the above limitations (Porter et al. 2000, 2002, 2006; Kearney and Porter 2004). These models can produce spatially explicit maps of parameters, such as potential activity hours and food requirements to meet energetic costs, but require assumptions about potential energy intake to predict distributions (Kearney and Porter 2004). For some species with extensive data, population dynamics can be modeled to predict ranges (Crozier and Dwyer 2006). Here I extend a simplified ecophysiological model to incorporate population dynamics.

This dynamic bioenergetic model represents a novel approach to predicting climate-induced range shifts that cou-

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Table 1: Geographic life-history variation for *Sceloporus undulatus* and *Sceloporus graciosus*

	Location	SVL (mm)	$Age_{maturity}$ (month)	$S_{maturity}$ (%)	S_{annual} (%)	a (insects m^{-1} s^{-1})	References
S. undulatus:							
A	Keith County, NE	55	9.5	.09	.33	.005	Jones et al. 1987; Niewiarowski and Roosenburg 1993
B	Burlington County, NJ	73	20	.23	.44	.016	Niewiarowski and Roosenburg 1993; Niewiarowski 1994
C	Pinos Altos, NM	63	18	.02	.32	.011	Vinegar 1975; Ballinger 1977
D	Lordsburg, NM	68	12	.03	.20	.011	Vinegar 1975; Ballinger 1977
E	Schleicher County, TX	57	12	.06	.11	.007	Tinkle and Ballinger 1972; Dunham 1978; Ruby and Dunham 1987
S. graciosus:							
F	Washington County, UT	55.5	23	.12	.57		Tinkle et al. 1993

Note: SVL = snout-vent length; $S_{maturity}$ = survival to maturity; S_{annual} = annual survival; a = insect abundance.

ples the energetic implications of morphology (body size) and physiology (voluntary temperature range) to a population dynamic model. The model predicts an organism's fundamental thermal niche (i.e., the regions where an organism is suited to live) rather than the realized niche (i.e., where the species actually lives), as predicted by climate envelope models (Pulliam 2000; Kearney and Porter 2004; Kearney 2006). The model builds on approaches linking biophysical models to distributions (Porter et al. 2002; Kearney and Porter 2004) and linking individual energetics to population dynamics to predict population growth as a function of activity hours (Adolph and Porter 1993). The model is among the first to integrate individual energetic and population dynamic models parameterized with spatial environmental data to predict distribution and abundance. The goals of the model are (*a*) to use easily obtainable morphological and physiological parameters to produce mechanistic predictions of species' ranges and (*b*) to include population dynamics as a basis for future examinations of extinction risk and the influence of species interactions, adaptation, and dispersal limitations.

Climate-induced range shifts are likely to disrupt ecological communities and cause movement into unsuitable or human-modified habitat, leading to largely unquantified biodiversity implications (Sala et al. 2000). The degree to which evolutionary and behavioral adaptation will moderate these range shifts is little understood (Etterson and Shaw 2001; Norberg et al. 2001). Correlative approaches to predicting climate-induced range shifts are unable to assess the potential moderating effects of adaptation (Pearson and Dawson 2003). Examining the range implications of current geographic trait variation addresses the potential for adaptation to moderate range shifts. I do so by examining the range implications of geographic trait variation for five populations near the range periphery of the well-studied eastern fence lizard, *Sceloporus undulatus* (Angilletta et al. 2004*a*; Niewiarowski et al. 2004). I use existing trait and life-history data for single populations in Nebraska, New Jersey, Texas, and New Mexico (two populations).

I then compare the range dynamics of *S. undulatus* to those of the closely related sagebrush lizard, *Sceloporus graciosus*. Comparing the dynamic model predictions to current ranges addresses how species interactions, habitat requirements, and dispersal limitations determine the occupied portion of the fundamental thermal niche. The comparison highlights the limitations of correlative approaches and the importance of dynamic approaches to species' ranges.

Methods

The Dynamic Bioenergetic Model

The model is appropriate for sit-and-wait predators with territorial foraging ranges. The basic model is detailed by Roughgarden (1997). The model was extended to include temperature dependence and was empirically tested for Caribbean *Anolis* lizards along elevation gradients (Buckley and Roughgarden 2005, 2006). The model is analogous to the neighborhood model, where plants interact with their adjacent neighbors (Pacala and Silander 1985). Lizards are assumed to forage on a linear transect, which simplifies the spatial dynamics and does not influence presence/absence predictions.

I model lizards as optimal foragers that maximize energetic yield per unit time. The foraging energetic yield, $E(d)$ (J), of foraging within a radius, d (m), is derived as the energetic input less the energetic cost divided by the total foraging time:

$$E(d) = \frac{e_i - e_w t_w(d) - e_p t_p(d)}{t_w(d) + t_p(d)},$$

where e_i (J) is the energy per insect; e_w (J s^{-1}) and e_p (J s^{-1}) are the energy per unit time expended waiting and pursuing, respectively; and t_w (s) and t_p (s) are time expended waiting and pursuing, respectively. The pursuit and waiting times are a function of prey density, a (insects m^{-1} s^{-1}), and lizard velocity, v (m s^{-1}; $t_w = 1/ad$ and $t_p = d/v$; Roughgarden 1997).

At low densities, lizards forage within the solitary foraging radius, d_s (m), which optimizes $E(d)$. Density dependence occurs when crowding forces the territory size to be less than the energetically optimal d for solitary lizards. This reduces energetic yield for each lizard. A specified transect length, L (1,000 m), is partitioned between N foragers (Roughgarden 1997). Population dynamics are modeled by calculating the change in population per unit time (the production function, ΔN) as the product of the population growth rate, based on birth minus death, and the population size, N, as follows:

$$\Delta N = [bE(d) - \lambda]N,$$

where λ represents mortality and the reproductive cost of metabolism while not foraging and b is the reproductive rate per unit net energetic yield. The reproductive cost of metabolism discounts the translation of energy to offspring by the cost of maintaining the organism. All density dependence is included in the expression for $E(d)$, which can be substituted into the production function. Because the foraging energetic yield is dependent on N, one can explicitly solve for equilibrium population size (carrying capacity, K, where the population growth rate equals 0; i.e., $bE(d) - \lambda = 0$) and the initial rate of population growth (the intrinsic rate of population increase, r_0):

$$K = \frac{L\left[be_i av + \sqrt{(be_i av)^2 - 4av(be_p + \lambda)(be_w + \lambda)}\right]}{2v(be_w + \lambda)},$$

$$r_o = -\lambda + b\frac{e_i - e_w/(ad_s) - e_p d_s/v}{1/(ad_s) + d_s/v},$$

where t_f is the duration of foraging, $b = mt_f$, and $\lambda = \mu + m(24 \times 60 \times 60 - t_f)e_w$. The parameter μ is the daily mortality rate and m is the quantity of eggs produced per joule times the probability of surviving to adulthood (eggs J^{-1}). Abundance is unstable and does not reach an equilibrium in the absence of density dependence. I therefore assume that species do not persist in the absence of density dependence. This corresponds to requiring a minimum population density to reproduce and maintain a viable population.

Morphological and Physiological Parameterization

I examined five populations of *S. undulatus* and one population of *S. graciosus* for which life-history and prey abundance data were available (compiled in Niewiarowski et al. 2004; table 1). Population data for snout-vent length (SVL [mm]), survival to maturity ($S_{maturity}$ [%]), annual survival (S_{annual} [%]), and insect abundance (a [insects m^{-1} s^{-1}]) are compiled in table 1. Insect abundance data was unavailable for the *S. graciosus* population. I assume that lizards initiate foraging when operative environmental temperatures fall within the observed field body temperature range. Because geographic variation in field body temperatures and voluntary thermal ranges has not been documented among the majority of populations of *S. undulatus* (Sears and Angilletta 2004), I use a single value for the minimum and maximum field body temperatures, $T_{b\,min}$ and $T_{b\,max}$ (°C), respectively. The mean body temperature across temperate *Sceloporus* spp. is 35°C, with only limited variation (Andrews 1998). For *S. undulatus*, I use the 20% and 80% quantiles of field body temperatures for lizards from New Jersey and South Carolina ($T_{b\,min}$ = 32.0°C, $T_{b\,max}$ = 35.6°C, n = 485; M. Angilletta, personal communication; data compiled in Angilletta et al. 2002). For *S. graciosus*, I use the 20% and 80% quantiles of field body temperatures for lizards from Utah ($T_{b\,min}$ = 29.0°C, $T_{b\,max}$ = 37.0°C, M. Sears, personal communication; data compiled in Sears 2005). I assume that lizards thermoregulate to their preferred body temperature (PBT). The PBT for the *S. undulatus* populations is 35.2°C (n = 152; Crowley 1985). For *S. graciosus*, I approximate the PBT as the mean field body temperature for the California populations (PBT = 34.5°C, n = 280; Adolph 1990). These thermal constraints are similar to those used in the ecophysiological models developed by Porter and colleagues and applied to *S. undulatus* (Adolph and Porter 1993; 32°C < T_b < 37°C) and *S. gracious* (Sears 2005; 29°C < T_b < 37°C). These ranges are identified as the PBT range (Adolph and Porter 1993). The model and parameterization here assume that lizards are active once they reach their minimum activity temperature and can then thermoregulate to approach their PBT (for a discussion of this assumption, see Buckley and Roughgarden 2005).

I used empirical data for *S. undulatus* to convert lizard SVL to mass (M [g]; Tinkle and Ballinger 1972): $M = 3.55 \times 10^{-5}(\text{SVL})^{3.00}$ (F = 4,845, df = 1, 45, $P < 1 \times 10^{-16}$, r^2 = 0.99). The regression is based on means of male and female lizards binned by size from populations in Texas (n = 154), South Carolina (n = 237), Ohio (n = 161), and Colorado (n = 168). There is no significant effect of population when it is included in the model. The relationship is similar to but has a significantly shallower slope and higher intercept than a relationship for both sexes

from South Carolina and New Jersey (M. Angilletta, personal communication; $M = 3.715 \times 10^{-6}(\mathrm{SVL})^{3.49}$, $F = 3{,}732$, df $= 1, 91$, $P < 1 \times 10^{-16}$, $r^2 = 0.98$, $n = 93$). The relationship is also similar to an intraspecific relationship based on 636 measurements from 47 species (Pough 1980): $M = 3.1 \times 10^{-5}(\mathrm{SVL})^{2.98}$. I chose the Tinkle and Ballinger (1972) relationship for its broader geographic coverage and larger sample size.

Maximum velocity (v) was calculated as a function of M (Van Damme and Vanhooydonck 2001): $\log_{10} v = -0.013 + 0.435 \log_{10} M - 0.129 \log_{10} M^2$. The regression accounts for 58% of the variation in v (when two chameleon outliers are removed, $n = \sim 125$). Lizards were assumed to pursue prey at 70% of their maximum velocity (Irschick and Losos 1998). The velocities were checked against repeated measures for 13 individuals of *S. undulatus* (M. Angilletta, personal communication; data compiled in Angilletta et al. 2002). The interspecific data was used because the small number of *S. undulatus* individuals had little variation is mass, resulting in a scaling relationship of only weak confidence.

Life-History Parameterization

The survival parameter μ (day^{-1}) was estimated using S_{annual} from table 1. To estimate m, I use life-history data for *S. undulatus* in Kansas and *S. graciosus* in Utah (Derickson 1976). *Sceloporus undulatus* exerts an average of 64.67 kJ to produce eggs and produces an average of 20.9 eggs each season, yielding an egg production rate of 3.2×10^{-4} eggs J^{-1}. *Sceloporus graciosus* exerts 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 1.9×10^{-4} eggs J^{-1} (Derickson 1976). Multiplying these values by the population-specific S_{maturity} from table 1 yields m (eggs J^{-1}).

Energetic Costs and Intake

The resting (waiting) metabolic rate, e_{w}, was calculated as a function of mass and temperature by using repeated measures for 15 *S. undulatus* from New Jersey and South Carolina ($F = 20.01$, df $= 9, 162$, $P < 1 \times 10^{-16}$, $r^2 = 0.53$; M. Angilletta, personal communication; data compiled in Angilletta 2001*b*)

$$\ln(e_{\mathrm{w}}) = -10.0 + 0.51 \ln(M) + 0.115 T_{\mathrm{b}}.$$

Population and individual were controlled for but were not significant factors. The scaling slope is less than that generally observed for lizards (Nagy 2005). The metabolic rate was multiplied by a factor of 1.5, which is the activity scope appropriate for an iguanid lizard (Congdon et al. 1982). I assume that e_{p}, the active metabolic rate, is a constant times the resting metabolic rate, and I assume the activity scope is the factor of 3, as suggested by Nagy (2005). Energetic costs are contingent on whether lizards thermoregulate. The majority of both field and laboratory research suggests that lizards are able to successfully maintain their optimal body temperatures (Avery 1982; Adolph and Porter 1993; Huey et al. 2003). I therefore focus on analyses assuming that species thermoregulate to their PBT.

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 thus gathered location-specific estimates for insect prey abundance from the literature (table 1). Abundance was estimated using sticky traps, and counts included only those insects estimated to be of suitable prey size. I convert the insect density (m^{-2} s^{-1}) to number of insects encountered (m^{-2} s^{-1}) by assuming that lizards forage within 0.5 m to each side of the linear transect. For most of the analyses, the mean insect abundance across populations is used. Mean abundance is also used for *S. graciosus* because no population-specific data is available.

I calculate the energetic content per insect, e_{i}, by using field data for *S. graciosus* and *S. occidentalis* from northern California (Rose 1976). *Sceloporus occidentalis*, the western fence lizard, is closely related and morphologically similar to *S. undulatus*. Using a single study ensures consistent methodology and analysis. Insufficient data were available to include a prey size distribution. The mean prey length, L, is 4.6 mm for *S. graciosus* and 5.4 mm for *S. occidentalis*. I convert insect length to mass using a regression for temperate deciduous forests from Schoener (1977; $M = 0.024L^{2.35}$, $n = 392$, dry mass [mg] from length [mm]) and assume an energy content of 23.85 J mg^{-1} dry mass (Reichle 1971; Andrews and Asato 1977). I assume that 76% of the energy available in an insect is in a form that could be assimilated by a lizard (Derickson 1976). This yields e_{i} values of 20.66 J for *S. graciosus* and 30.12 J for *S. occidentalis*. While prey size has been observed to vary with SVL for some lizards, no such relation has been found for many temperate lizards. There was only a weak prey size–body size relationship for *Sceloporus* in the Chihuahuan Desert (Barbault and Maury 1981). I thus use a single prey size for all lizard populations.

Digestive efficiency, which is the percent of ingested energy that is assimilated, has been observed to strongly vary with environmental temperature. I use a regression for digestive efficiency, DE (%), empirically derived for *Uta stansburiana* (Waldschmidt 1983; Waldschmidt et al. 1986) and applied in the ecophysiological model for *S. undulatus* by Grant and Porter (1992):

$$\mathrm{DE} = \left\{\sin\left[\frac{\pi(85.34 - 0.05T_{\mathrm{b}} + 0.000074T_{\mathrm{b}}^3)}{180}\right]\right\}^2.$$

Energetic intake from foraging is constrained by the percent of prey captured and the maximum daily insect consumption. By assuming that 50% of insects are captured, I introduce the only free parameter in the model. I multiply this factor by insect abundance to yield realized insect abundance. I convert the insect catch ($\mathrm{m^{-2}\ s^{-1}}$) to number of insects ($\mathrm{m^{-1}\ s^{-1}}$) by assuming that lizards forage within 0.5 m to each side of the linear transect. The maximum number of insects consumed in a day is constrained by gut capacity and passage rate of food, which is highly temperature dependent (Angilletta 2001*a*). I used feeding trial data collected for *S. undulatus* to constrain maximum daily energy intake, $C_{\max}$ (J). I linearly interpolated between the maximum consumption data for 20°C (94 J $\mathrm{g^{-1}\ d^{-1}}$), 30°C (270 J $\mathrm{g^{-1}\ d^{-1}}$), 33°C (511 J $\mathrm{g^{-1}\ d^{-1}}$), and 36°C (421 J $\mathrm{g^{-1}\ d^{-1}}$; Angilletta 2001*a*). The total daily foraging intake is the product of $E(d)$ and the daily foraging time, t_{f} (s). I introduce a factor, $0 < a_{\mathrm{factor}} \leq 1$, that is multiplied by a to form the realized abundance, that is, the insect abundance that a lizard can actually use without exceeding its maximum daily energy intake. To solve for a_{factor} such that $E(d)t_{\mathrm{f}} < C_{\max}$, I first solve for the energetically optimal foraging radius for a solitary anole, d_{s}, which maximizes $E(d_{\mathrm{s}})$:

$$d_{\mathrm{s}} = \frac{-(e_{\mathrm{p}} - e_{\mathrm{w}}) + \sqrt{(e_{\mathrm{p}} - e_{\mathrm{w}})^2 + ave_{\mathrm{i}}^2}}{ae_{\mathrm{i}}}.$$

Substituting this expression into the expression for $E(d_{\mathrm{s}})$, one can then solve for a_{factor}:

$$a_{\mathrm{factor}} = \frac{-C_{\max}v - t_{\mathrm{f}}ve_{\mathrm{w}}}{ad_{\mathrm{s}}(C_{\max}d_{\mathrm{s}} - t_{\mathrm{f}}ve_{\mathrm{i}} + d_{\mathrm{s}}t_{\mathrm{f}}e_{\mathrm{p}})}.$$

Multiplying a by this factor constrains the maximum daily foraging intake.

Environmental Conditions and Observed Distributions

I applied the dynamic bioenergetic model to individual 0.5° grid cells. I assume that lizards are able to forage during daylight hours within their voluntary temperature range. Operative environmental temperature, T_{e}, is calculated using a biophysical model (appendix). 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; Campbell and Norman 2000). The approach is similar to but 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. 2000, 2002, 2006; Kearney and Porter 2004). Lizards are considered active when the operative temperatures (calculated at the two extremes of full sun and full shade, where observed radiation equals zero) fall within the observed field body temperature range.

All spatial analyses were conducted in ArcGIS using an equal-area projection and equal-area (3,091 $\mathrm{km^2}$) grid cells equivalent to 0.5° near the equator. I use satellite-derived data to parameterize the environmental variables in the biophysical model related to air temperature, soil temperature, wind, elevation, and albedo. I derive mean values within the grid cells. The primary data source is from New et al. (2002), who provided mean data from 1961 to 1990 with 10′ resolution. Within the daylight window, temperatures are checked hourly (data from 1961 to 1990 with 10′ resolution; New et al. 2002). The hourly air temperature for an average day of each month, calculated using the monthly mean daily temperature and the monthly mean diurnal temperature range, is T_{a} (K; Campbell and Norman 2000). To investigate responses to climate change, I assume 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 highlight species' individualistic responses. Additionally, I use data for annual mean elevation, $E(m)$, and wind speed, u ($\mathrm{m\ s^{-1}}$; data from 1961 to 1990 with 10′ resolution; New et al. 2002).

Seasonal surface albedo, ρ (%), is derived seasonally, with 1° resolution based on vegetation and cultivation intensity maps and satellite imagery (Matthews 1985). Albedo values are provided for winter, spring, summer, and autumn (January, April, July, and October, respectively, in the Northern Hemisphere). I use a given seasonal albedo value for the month in which the seasonal period begins as well as the subsequent 2 months. The albedo values indicate the seasonal percentage of incoming radiation reflected into space, integrated across the electromagnetic spectrum.

I use hourly soil surface temperature data (at a depth of 3 cm and a resolution of 1/8°) derived from ground-based data and a biophysical soil model to estimate monthly means for daily soil temperature and for the diurnal soil temperature range (Mitchell et al. 2004). The Noah Land Surface Model captures the surface energy balance to estimate soil temperature (Ek et al. 2003). The Noah model output was regionally validated using local data collection. Soil surface temperatures reach a maximum at approximately 1400 hours and are assumed to reach a minimum at 0200 hours, according to a sinusoidal

approximation (Campbell and Norman 2000). I thus average the maximum daily temperature and diurnal temperature range ($T_{1400\ \text{hours}} - T_{0200\ \text{hours}}$) over the 5 days in the middle of each month.

Polygon lizard distribution data was derived from North America field guides (Conant and Collins 1998; Stebbins 2003) and digitalized by NatureServe (http://www.natureserve.org). The 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://www.herpnet.org) and the Global Biodiversity Information Facility (http://www.gbif.org). The occurrences are inherently spatially biased by the museums reporting georeferenced specimens.

Climate Envelope Model

For comparison, I ran climate envelope models to predict current ranges and those following 3°C warming. The climate envelopes were based on the annual mean of monthly estimates of minimum, mean, and maximum temperature using DesktopGarp (genetic algorithm for rule-set production) available from the University of Kansas Center for Research (Peterson and Vieglais 2001). The specimen localities were used to develop models for *S. undulatus* ($n = 3{,}936$) and *S. graciosus* ($n = 4{,}429$). I used 70% of points for training in 10 runs for each species. I used 100 maximum iterations and a 0.001 convergence limit with all available rule types. The best model was selected by DesktopGarp using χ^2 and omission criteria. This implementation of climate envelope models using only temperature is a simplification over most implementations and is not intended to be representative. Rather, the implementation was designed to enable comparisons based exclusively on temperature.

Model Comparison

Analyzing model performance is less straightforward than doing so for traditional presence/absence ecological models because the comparison is between predicted fundamental thermal niches and observed realized niches. The sensitivity index is the proportion of true presences correctly predicted (true presences predicted divided by the total number of true presences; Manel et al. 2001). The specificity index is the proportion of true absences correctly predicted (true absences predicted divided by the total number of true absences; Manel et al. 2001). The overall predictive success combines the first two metrics by calculating the percentage of all cases that are correctly predicted (true presences plus true absences divided by total cases; Manel et al. 2001).

Results

Substantial variation in morphology, life history, and prey abundance is present among the geographically distinct populations (table 1). While the large body sizes in the New Jersey population are consistent with Bergmann's clines (Angilletta et al. 2004*a*), the body sizes of the other northern population, Nebraska, are the smallest of any population. Lizards in the Nebraska population are the fastest to mature to adulthood, while those in the New Jersey population exhibit delayed maturation. The probability of surviving to maturity and annual survival in Nebraska is only slightly higher than that of southern populations. In contrast, the probability of surviving to maturity is nearly 25%, and the annual survival is also high in New Jersey. Notably, insect abundance is also the lowest in Nebraska and the highest in New Jersey.

Range predictions that are based on population-specific body size and species' mean life history are variable between populations and do not correspond to whether a population is from the northern or southern extent of the species' range (fig. 1, left column). Populations with larger body sizes are predicted to have more northerly ranges but lower abundance. Model predictions improve when population-specific survival parameters (m and μ) are included (fig. 1, middle column). The populations from the northern extremity of *Sceloporus undulatus*'s range, those in Nebraska and New Jersey, are predicted to have more northerly range extents than those populations in the southern extent of the range.

I compare the performance of these models to that of the climate envelope model (fig. 1*F*) for the Nebraska and New Jersey populations. I first evaluate the models' performance in predicting which grid cells contain *S. undulatus* localities. The climate envelope model correctly predicted a higher proportion of cells containing specimens (sensitivities: 96% climate envelope, 77% dynamic model for Nebraska, 85% dynamic model for New Jersey). However, the climate envelope model substantially overpredicts the distribution of *S. undulatus*, yielding low specificities (percent prediction of true absences, specificity = 31%). Despite the dynamic models predicting fundamental thermal niches rather than realized niches, the dynamic models for the Nebraska and New Jersey populations provide greater specificities (respective specificities = 59% and 51%). The overall predictive success is higher for the dynamic models for the Nebraska (63%) and New Jersey (58%) populations than for the climate envelope model (44%).

Because the specimen localities are certainly incomplete, I compare the performance of the models for the northern populations at predicting which grid cells fall within the range polygons across the entire United States. This per-

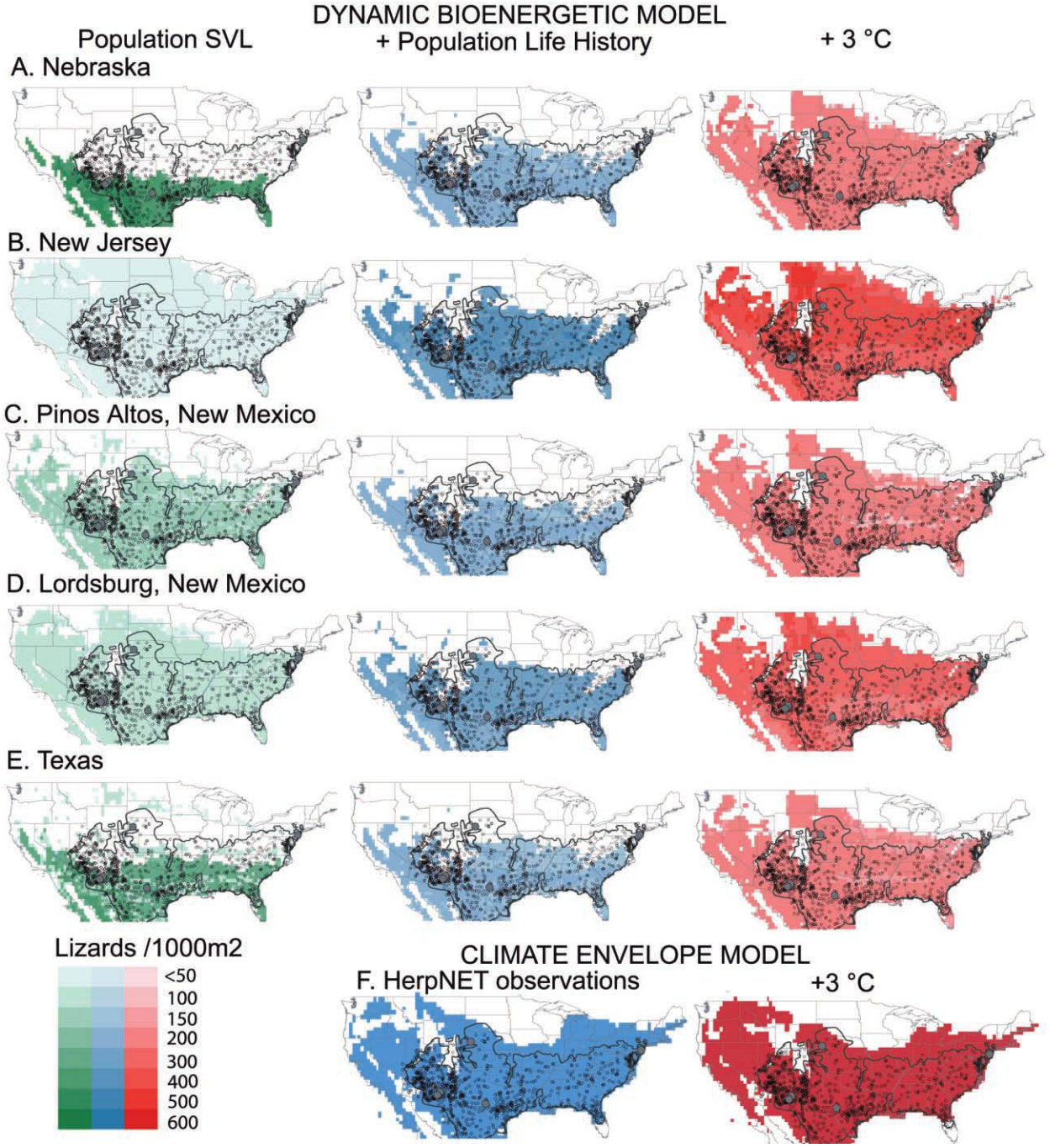

Figure 1: Density predictions (lizards 1,000 m^{-2}) for *Sceloporus undulatus* from the dynamic bioenergetic model are compared to those from a climate envelope model (*inset*) for current climates and a uniform 3°C temperature increase. Predictions for the dynamic model are depicted for the model parameterized with population-specific snout-vent length (SVL) and mean life history (*green*); population-specific SVL and life history (*blue*); and population-specific SVL and life history under a 3°C temperature increase (*red*). Locations of the focal populations, species localities, and atlas range polygons are included.

formance assessment does not appropriately account for patchy distributions. The dynamic model for Nebraska (fig. 1*A*) exhibits 76% sensitivity, 76% specificity, and an overall performance of 76%. The dynamic model for New Jersey (fig. 1*B*) exhibits 85% sensitivity, 69% specificity, and an overall performance of 77%. The climate envelope model has a higher sensitivity but a lower specificity and slightly lower overall model performance compared with the dynamic models (97% sensitivity, 45% specificity, and 69% overall performance).

I examine the range implications of incorporating population-specific insect abundance. Because data are lacking to parameterize the models with insect abundance across the range, I consider the influence of local insect abundance on the predicted range for the Nebraska and New Jersey populations. The low insect abundance observed for the Nebraska population contracts the predicted range below that which is observed (fig. 2*A*). High insect abundance in New Jersey extends the lizard's predicted range in the northeast to better correspond to the observed range (fig. 2*B*).

The range predictions for *S. undulatus* can then be compared to those for *Sceloporus graciosus*. While the two species are closely related and share similar morphology (Reeder 1995), the species have nearly disjoint ranges, with *S. graciosus* occurring primarily west of the continental divide. The two species are predicted to have similar thermally suitable ranges, with *S. graciosus* predicted to have a somewhat more substantial presence in the north due to a lower minimum body temperature (figs. 1, 3). This demonstrates how biotic factors influence occupancy of thermally suitable regions and highlights the limitations of correlative approaches.

Correlative predictions contrast dynamic predictions of range shifts. The climate envelope model predicts that the range boundaries shift poleward to maintain constant temperatures. While the populations of *S. undulatus* are predicted to differentially shift based on traits and life history, only a single range shift is produced by the climate envelope model. The range change predicted by the correlative model for *S. undulatus* is less than that predicted by the dynamic model for most populations (median 35.7% for the dynamic model and 9.5% for the climate envelope model; fig. 4). However, the climate envelope model predicts a greater range shift than the bioenergetic model for *S. graciosus* (37.0% and 24.6%, respectively; fig. 4). In contrast to the dynamic predictions, the correlative model predicts contraction of the southern range.

The model is fairly sensitive to parameter changes, but changes act consistently across species and do not influence range comparisons (Buckley and Roughgarden 2005). The most uncertain parameters are a and the proportion of insects caught, which is included in e_i. Abundance predictions respond approximately linearly to changes in both of these parameters, but using equilibrium abundance to define range boundaries results in some nonlinear responses. The range responses for *S. undulatus* corresponding to halving and doubling a and e_i are depicted in figure A1. Halving or doubling a results in a mean range loss of 15.7% ± 2% (mean ± SE, median = 13.5%) or a gain of 32.7% ± 3% (median = 30.0%). Halving or doubling e_i results in a mean range loss of 48.1% ± 4% (median = 46.3%) or a gain of 66.0% ± 4% (median = 64.3%). I also examined model sensitivity to the environmental temperature range within which lizards are able to forage (fig. A1). Assuming that lizards can forage when environmental temperature falls between the 10% and 90% quantiles (30.4°–36.4°C) of field body temperatures (rather than the 20% and 80% quantiles) results in a predicted range gain of 12.3% ± 1% (median = 13.1%).

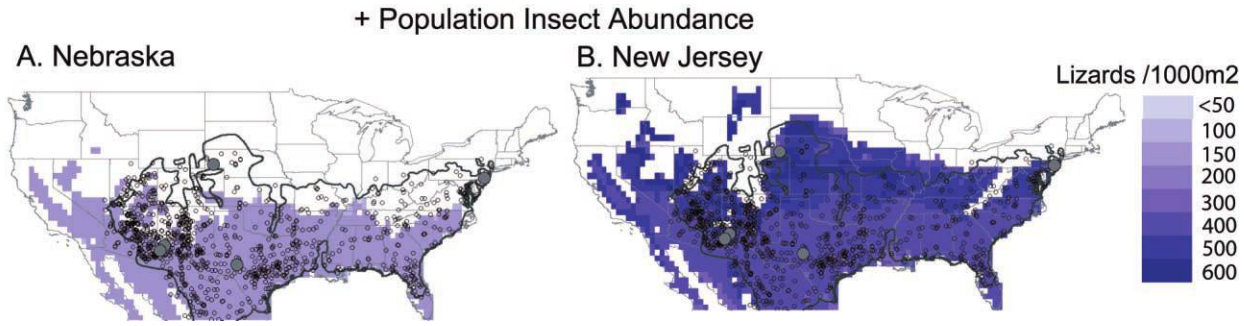

Figure 2: Incorporating population-specific insect abundance for the populations from the northern range extent improves predictions (lizards 1,000 m^{-2}) of the northern range boundary. While Nebraska (*A*) has relatively low insect abundance, New Jersey (*B*) has relatively high insect abundance. The insect abundance values apply only in the vicinity of the population.

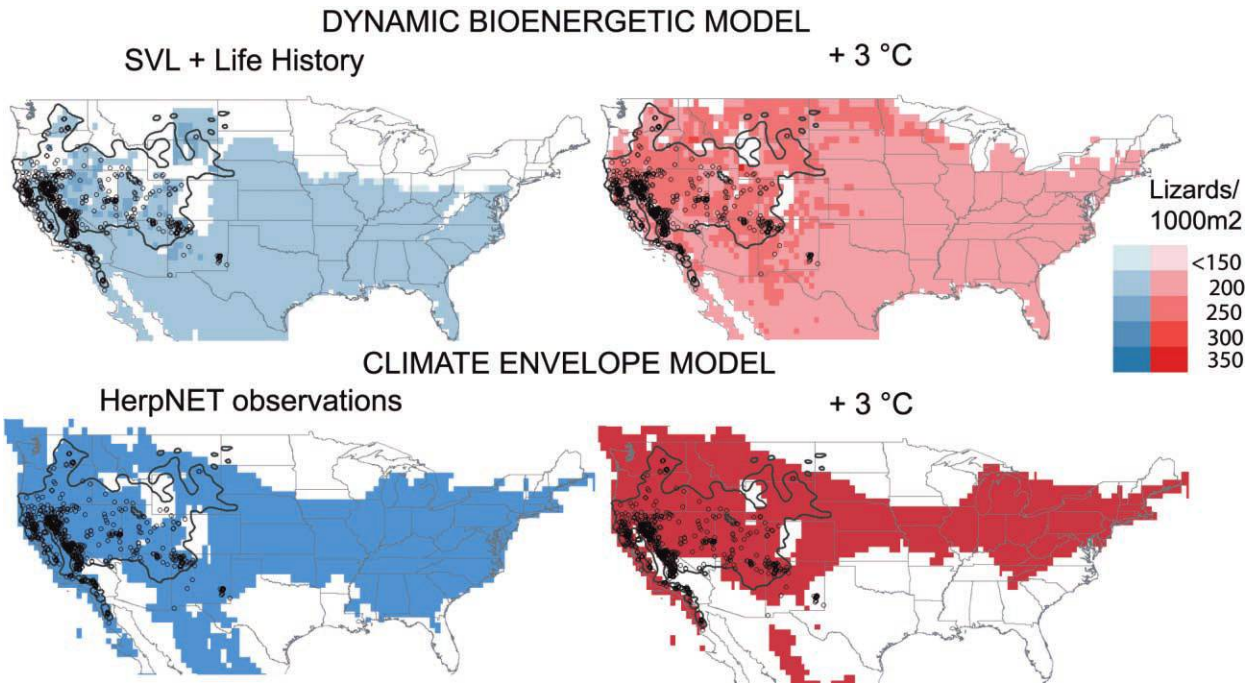

Figure 3: Density predictions (lizards 1,000 m^{-2}) for *Sceloporus graciosus* from the dynamic bioenergetic model are compared to those from a climate envelope model for current climates (*blue*) and a uniform 3°C temperature increase (*red*). The dynamic model is parameterized with population-specific snout-vent length and life history. Localities and atlas range polygons are included.

Discussion

This analysis adds to growing evidence that species respond individualistically to temperature and that considering traits and life histories is essential to understanding ranges (reviewed in Muth 1980; Porter et al. 2000; Kearney and Porter 2004; Helmuth et al. 2005). Individualistic range shifts have been widely observed in response to past climate changes (Graham et al. 1996). Dynamic models based in first principles of morphology, life history, and thermal physiology have the potential to identify which factors are the primary determinants of species distributions and how the factors interact in current and potential future climates. This analysis suggests that temperature constrains distributions by altering the balance of energy acquisition and use (as set by physiological-constrained foraging duration and food abundance) rather than a direct influence.

Examining range predictions suggests that factors such as species interactions and habitat suitability strongly influence current lizard ranges and limit the potential of correlative approaches for predicting future range shifts. *Sceloporus* spp. are closely related species (Reeder 1995), with similar thermal physiology, that occupy distinct ranges. *Sceloporus occidentalis* and *Sceloporus undulatus* (the western and eastern fence lizards, respectively) are sister species with sharply disjoint ranges. *Sceloporus* species with similar thermal physiology, such as *S. occidentalis* and *Sceloporus graciosus*, maintain sympatry through partitioning habitat, activity times, and prey (Rose 1976; Adolph 1990). *Sceloporus graciosus* typically lives at higher elevations than does sympatric *S. occidentalis* (Adolph 1990). This specific habitat use by *S. graciosus*, which results in shorter activity times for the species, is not fully captured by my model. *Sceloporus graciosus* exhibits a proportionally higher reproductive effort than most congeners, including *S. undulatus*, potentially due to lower predation pressure (Tinkle and Hadley 1975). This history of speciation and niche partitioning yields the disjoint ranges for *S. undulatus* and *S. graciosus* despite their similar fundamental thermal niches.

Some differences between *S. undulatus* populations in morphology and life history are genotypic and thus have significant range implications. In a reciprocal field transplant using *S. undulatus*, Nebraska hatchlings had reduced growth rates in New Jersey that were comparable to those of local hatchlings. In Nebraska, Nebraska hatchlings had higher growth rates than transplants from the New Jersey population. Potential activity time was found to be longer in Nebraska, suggesting that Nebraska hatchlings exhibit a stronger sensitivity to thermal opportunity (Niewiarowski and Roosenburg 1993). In a laboratory thermal

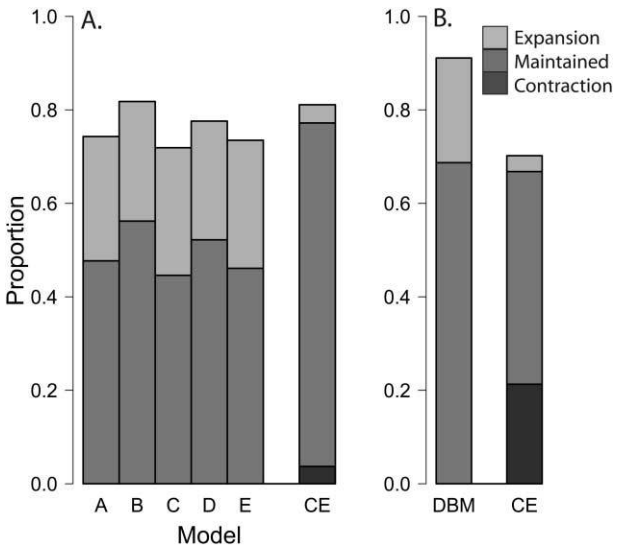

Figure 4: Range dynamics predicted by the dynamic bioenergetic model (DBM) and the climate envelope model (CE) for *Sceloporus undulatus* (*A*) and *Sceloporus graciosus* (*B*) following a uniform temperature increase of 3°C. The letters correspond to predictions of the DBM for the populations depicted in figure 1. The proportion of range area that represents maintained range, contractions, or expansions under a 3°C warming varies between populations of *S. undulatus*.

gradient, hatchling growth rates differed among three geographically distinct populations of *S. undulatus*, and *S. graciosus* grew more slowly than all three populations of *S. undulatus* (Ferguson and Brockman 1980). While laboratory rearing of *S. occidentalis* and *S. graciosus* revealed some life-history plasticity, genetically based differences in average reaction norms between populations and species were apparent (Sinervo and Adolph 1994).

These population and species differences in morphology, physiology, and life history both reflect past adaptation to local conditions and address the potential for adaptation to future environmental change. Current genetic diversity is likely to influence the potential to adapt to new environments. While sufficient genetic variation was observed between populations of *S. undulatus* for Leaché and Reeder (2002) to suggest that the species is composed of a least four geographically distinct lineages (eastern, western, central, and southwestern clades) that should be recognized as evolutionary species, the implications of this genetic diversity for life history is uncertain. Phylogenetic effects on life-history variation were found to be weak or absent among the populations of *S. undulatus* (Niewiarowski et al. 2004). Expanding understanding of the potential for plastic and genetic evolution through modeling and empirical work will be essential to predicting how adaptation will mediate climate-induced range shifts.

The model provides an initial step toward a dynamic understanding of the influence of temperature on species ranges. Crucial factors for lizard ranges such as water, prey availability, and species interactions were not thoroughly considered. Prey distributions often vary as a function of climate (Crozier and Dwyer 2006), but there is little predictive knowledge of the influence of current and potential future climates on insect abundances. The model also simplifies temperature's influence. Temperature modifies growth rates and time to maturation (Angilletta et al. 2004*b*) as well as egg viability (Porter et al. 2002). For example, *S. graciosus* requires lower egg incubation temperatures than *S. undulatus* (Ferguson and Brockman 1980).

In ecophysiological models, the duration of foraging is a primary determinant of energetic yield and ultimately range extent (Adolph and Porter 1993). Thus, climate change is largely predicted to expand ranges by extending the foraging window. The dynamic bioenergetic primary model assumes that lizards are able to successfully thermoregulate to their optimal performance temperature. While this is largely the case for most regions in current climates (Avery 1982; Adolph and Porter 1993; Huey et al. 2003), the potential for lizard thermoregulation in warmed climates is uncertain. While the dynamic bioenergetic model predicts northward range shifts following climate warming, whether ranges will expand is less certain. Northern boundaries tend to be determined by temperature-dependent energetics, but southern boundaries are often determined by biotic interactions (Dobzhansky 1950; Root 1988; but see Wilson 1991). The availability of habitat and the absence of dispersal barriers will determine whether lizards are able to shift poleward (Parmesan et al. 1999). Complex variation in thermal environments at local scales may limit poleward shifts and result in distribution mosaics (Helmuth et al. 2002). Additionally, physiological adaptation through changes in allele frequencies, phenotypic plasticity, and acclimatization will moderate range shifts (reviewed in Helmuth et al. 2005). A recent example provides evidence of the importance of considering species traits when investigating the implications of climate change: lizard body size increased in response to climate warming, which ultimately resulted in higher fitness (Chamaillé-Jammes et al. 2006).

The performance of the dynamic model is competitive with the climate envelope model, although the dynamic model does not require information about current distributions. While the dynamic model suggests that the implications of climate change may be more severe than anticipated from climate envelope approaches, assessing the relative accuracy of predictions requires (currently unavailable) data on historic lizard ranges. Notably, the variation between climate envelope model predictions using

different correlation algorithms is substantial (Pearson et al. 2006). Overpredictions by the climate envelope model highlight that such models rely heavily on environmental variables other than temperature to accurately predict current ranges. Including population dynamics in range models also enables examining density in addition to presence. The dynamic model's range of abundance predictions for *S. undulatus* (0–6,000 lizards ha^{-1}; fig. 1) is substantially broader and generally higher than observed densities (median = 20.1 lizards ha^{-1}, mean = 63.5 lizards ha^{-1}, range = 1–660 lizards ha^{-1}; Buckley et al. 2008). These higher-density predictions are consistent with not considering competition or predation in the model.

The dynamic predictions for current ranges and range shifts lend credence to the often discussed and historically substantiated potential for individualistic responses to environmental temperatures. These individualistic responses are incompatible with correlative approaches. Dynamic models with the potential to include species interactions and dispersal limitations are essential to understanding current ranges and the biodiversity implications of environmental change. Correlative approaches to species' ranges have provided and will continue to provide important information to ecologists and conservation practitioners, particularly when information and resources are limiting. The analysis highlights the importance of dynamic approaches to species' distributions. This dynamic approach based on first principles of morphology and physiology demonstrates that thermal breadth and metabolic rates constrain organisms' responses to current and potential future temperatures, which are in turn influenced by species interactions and dispersal barriers.

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APPENDIX

The Biophysical Model

I construct a biophysical model to calculate operative environmental temperature, T_e, which is air temperature, T_a (°C), plus or minus a temperature increment determined by absorbed radiation, wind speed, and animal morphology. The expression is derived from balancing an energy budget and represents the equilibrium temperature of an animal with specified thermal and radiative properties in a given environment. I follow the modeling approach contained in work by Campbell and Norman (2000) that is based on well-established biophysical equations. All equations are derived by Campbell and Norman (2000) unless indicated otherwise. 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. 2000, 2002, 2006; Kearney and Porter 2004).

Day Length and Sun Angles

I constrain the lizard's foraging to hours of daylight. I use the relations below to calculate day length and the time of solar noon. I first calculate the solar declination, δ (rad), the angular distance of the sun north or south of the earth's equator:

$$\delta = \arcsin\left[0.39795\cos\left(0.21631 + 2\arctan\left\{0.967\tan\left[0.0086(-186 + J)\right]\right\}\right)\right], \tag{A1}$$

where J is calendar day, with $J = 1$ at January 1. One can then calculate day length, h_{day} (h), using the CBM model (Forsythe et al. 1995):

$$h_{day} = 24 - \frac{24}{\pi}\arccos\left[\frac{\sin(6\pi/180) + \sin\phi\sin\delta}{\cos\phi\cos\delta}\right], \tag{A2}$$

where ϕ is latitude (rad).

The time of solar noon (h) is calculated as

$$t_0 = 12 - \mathrm{LC} - \mathrm{ET}, \tag{A3}$$

where LC is the longitude correction (h) and ET is the equation of time (h). The LC is a +1/15-h correction for each degree that a location is west of a standard meridian, which occurs at 0°, 15°, …, 345°. The ET corrects for the difference between sun time and clock time based on calendar day as follows:

$$\mathrm{ET} = \frac{-104.7 \sin f + 596.2 \sin 2f + 4.3 \sin 3f - 12.7 \sin 4f - 429.3 \cos f - 2.0 \cos 2f + 19.3 \cos 3f}{3{,}600}, \tag{A4}$$

$$f = \frac{\pi}{180}(279.575 + 0.9856J). \tag{A5}$$

The zenith angle, ψ (rad), is the sun angle measured from vertical,

$$\cos\psi = \sin\delta \sin\phi + \cos\delta \cos\phi \cos\frac{\pi}{12(h - t_0)}, \tag{A6}$$

where h is hour.

Air and Soil Temperature

Hourly air temperature is estimated on the basis of mean temperature for an average day of each month and on the diurnal temperature range for an average day of each month. Campbell and Norman (2000) derived a diurnal temperature function by fitting two terms of a Fourier series to the average of assembled and normalized hourly temperature data:

$$\Gamma = 0.44 - 0.46 \sin(0.9 + \omega h) + 0.11 \sin(0.9 + 2\omega h), \tag{A7}$$

where $\omega = \pi/12$. Hourly air temperature is

$$T_a = T_x - T_n(1 - \Gamma), \tag{A8}$$

where T_x and T_n are the maximum and minimum daily temperatures (°C), respectively.

Hourly surface soil temperature, T_s (K), is likewise estimated based on mean soil temperature for an average day of each month and on the diurnal temperature range for an average day of each month:

$$T_s = T_{Sa} + A_d \sin[\omega(h - 8)], \tag{A9}$$

where T_{Sa} is the average daily soil temperature (K), A_d is the amplitude of diurnal temperature fluctuation (K), and $\omega = \pi/12$. The model assumes uniform soil properties and sinusoidally varying surface temperature. The time variable in the sine function is phase adjusted by 8 h.

Radiation and Environmental Temperature

Central to the thermal influence of radiation is the Stefan-Boltzmann law, which expresses the total radiant energy over all wavelengths admitted per unit surface area of a blackbody radiator. The law yields the emitted flux density, B (W m^2),

$$B = \sigma(T_a + 273)^4, \tag{A10}$$

where σ is the Stefan-Boltzmann constant (5.67×10^{-8} W m^{-2} K^{-4}). Emissivity, $\varepsilon(\lambda)$, where λ is wavelength, is the fraction of blackbody emittance at a given wavelength emitted by the surface of a material. Gray bodies are those with no wavelength dependence of the emissivity. Thus, emitted energy of a gray body, Φ (W m^{-2}), is

$$\Phi = \varepsilon B. \tag{A11}$$

I assume lizards are a gray body, which is reasonable for most natural surfaces. The emissivity of most natural surfaces ranges from 0.95 to 1.0. I use the emissivity value of 0.965 measured by Bartlett and Gates (1967) for a *Sceloporus* lizard. However, the emissivity of a clear atmosphere is substantially lower. I use the approximation by Swinbank (1963) to estimate clear sky emissivity,

$$\varepsilon_{ac} = 9.2 \times 10^{-6}(T_a + 273)^2. \tag{A12}$$

I first consider convective heat transport between the lizard's body and the environment. The boundary conductance of air (mol m^{-2} s^{-1}) is expressed as

$$g_{Ha} = 1.4 \times 0.135\sqrt{\frac{u}{d}}, \tag{A13}$$

where u is wind velocity (m s^{-1}) and d is the characteristic dimension (m). Assuming that wind is blowing parallel to the axis of a cylindrical approximation of a lizard, d is the lizard's length (snout-vent length [m]). A factor of 1.4 is introduced to account for the increased convection due to environmental turbulence (Mitchell 1976). I additionally consider radiative conductance, the exchange of thermal radiation between the lizard and the environment proportional to temperature differences. The radiative conductance (mol m^{-2} s^{-1}) is expressed as

$$g_r = \frac{4\varepsilon\sigma(T_a + 273)^3}{c_p}, \tag{A14}$$

where c_p is the specific heat of air (29.3 J mol^{-1} K^{-1}).

I then turn to calculating the components of the radiant energy budget of a lizard. I estimate the solar (shortwave) component of this quantity by aggregating flux densities for four radiation streams: the direct irradiance on a surface perpendicular to the beam, S_p (W m^{-2}); the diffuse sky irradiance on a horizontal plane, S_d (W m^{-2}); the total irradiance of a horizontal surface, S_t (W m^{-2}); and the reflected radiation from the ground, S_r (W m^{-2}). Calculation of these flux densities requires the introduction of several additional quantities. The atmospheric transmissivity, τ, ranges between 0.6 and 0.7 for typical clear sky conditions (Gates 1980). I thus assume $\tau = 0.65$. The solar constant, S_{p0}, indicates extraterrestrial flux density to be 1,360 W m^{-2}. Optical air mass number, m_a, is the ratio of slant path length through the atmosphere to zenith path length and is a function of atmospheric pressure, p_a (kPa):

$$p_a = 101.3 \exp\left(\frac{-E}{8{,}200}\right), \tag{A15}$$

where E is the elevation in meters above sea level. I can then calculate m_a as

$$m_a = \frac{p_a}{101.3 \cos\psi}. \tag{A16}$$

Direct irradiance is a function of the distance a solar beam travels through the atmosphere; the transmittance of the atmosphere, τ; and the incident flux density, S_{p0}:

$$S_p = S_{p0}\tau^{m_a}. \tag{A17}$$

Sky diffuse radiation can be approximated using an empirical relation (Liu and Jordan 1960),

$$S_d = 0.3(1 - \tau^{m_a})S_{p0}\cos\psi. \tag{A18}$$

Solar irradiance is the sum of diffuse sky irradiance and the beam irradiance on a surface:

$$S_t = S_d + S_p \cos \psi. \tag{A19}$$

Finally, reflected radiation is the product of albedo, ρ_S, and the total shortwave irradiance:

$$S_r = \rho_S S_t. \tag{A20}$$

Albedo was empirically derived from satellite images and is the surface reflectance for the solar waveband.

The longwave component of a lizard's radiant energy budget can be estimated using the Stefan-Boltzmann law (eq. [A10]). The longwave flux density from atmosphere, L_a (W m^{-2}), is computed as

$$L_a = \varepsilon_{ac}\sigma(T_a + 273)^4, \tag{A21}$$

where ε_{ac} is clear sky emissivity. The longwave flux density from the ground is

$$L_g = \varepsilon_s \sigma T_s^4, \tag{A22}$$

where ε_s is surface emissivity.

I can then aggregate short- and longwave radiation to compute absorbed radiation:

$$R_{abs} = \alpha_S(F_p S_p + F_d S_d + F_r S_r) + \alpha_L(F_a L_a + F_g L_g), \tag{A23}$$

where α_S and α_L are the absorptivities in the solar and thermal wavebands, respectively, and F_p, F_d, F_r, F_a, and F_g are view factors between the surface of the lizard and sources of radiation. Solar absorptivity, α_S, is approximately 0.9 for lizards (Gates 1980). Because absorptivity in a given waveband is equal to emissivity in that waveband, I use the thermal absorptivity, α_L, of 0.965, as measured by Bartlett and Gates (1967).

View factors refer to the fraction of radiation that is intercepted by the lizard. The beam view factor, F_p, for a lizard is the ratio of the projected area perpendicular to the solar beam, A_p, to the total animal area, A, $F_p = A_p/A$. I use an empirically derived relationship that was developed for a standing *Callisaurus* (Muth 1977). I assume a relative azimuth angle of 90°, which indicates that the long axis of the lizard is perpendicular to incoming solar radiation:

$$A_p = \frac{[(-1.1756 \times 10^{-4})\psi^2 + (-9.2594 \times 10^{-2})\psi + 26.2409]A}{100}. \tag{A24}$$

Roughgarden et al. (1981) provide an expression for total area based on empirical lizard data from Norris (1965) and Porter and James (1979):

$$A = 0.121 m^{0.688}, \tag{A25}$$

($r^2 = 0.996$), where m is mass in grams, and the relation holds for a variety of lizards from 2 to 50 g. For diffuse shortwave and longwave radiation, the sky can be approximated as a hemisphere. The diffuse radiation view factor, F_d, for a standing lizard was found to be 0.8 by Bartlett and Gates (1967). We assume that one-half of thermal radiation is received from both the ground and the sky. The atmospheric thermal radiation factor, F_a, is thus 0.5, and the ground thermal radiation factor, F_g, is 0.5. I likewise assume that the reflected solar radiation view factor, F_r, is 0.5. The operative environmental temperature is calculated within each grid cell as

$$T_e = T_a + \frac{R_{abs} - \varepsilon_s \sigma (T_a + 273)^4}{c_p(g_r + g_{Ha})}. \tag{A26}$$

Biophysical Model Testing

While biophysical models have been tested locally, tests of landscape-scale patterns of foraging duration have been limited. I compared annual foraging duration predictions (H) of the described bioenergetic model (Campbell and

Norman 2000) to those of the biophysical models by Porter and colleagues (Adolph and Porter 1996) for populations of *Sceloporus undulatus*. I used data from the immediate vicinity of the site (rather than averaged over a grid cell) for a more representative comparison. While there is reasonable relative agreement between the predictions, the Campbell and Norman model predicts substantially shorter foraging durations ($H_{\text{Campbell and Norman}} = -94.9 + 0.39H_{\text{Porter}}$, $F = 7.16$, df $= 1, 11$, $P < .05$, $r^2 = 0.34$). Notably, when Angilletta et al. (2004*a*) made relatively small changes to the Porter et al. ecophysiological model, the predicted foraging duration changed substantially from those reported by Adolph and Porter (1996; $P < .01$, $r^2 = 0.71$).

All these biophysical models consist of well-established physical equations; thus, the models are likely to predict similar operative environmental temperatures. Porter's model incorporates thermoregulatory behavior to assess whether a lizard is able to maintain its preferred body temperature in a given location. Thus, the thermal constraints for foraging are differentially incorporated in the two models. This is consistent with the models predicting different but correlated foraging durations. Examining sensitivity to thermal constraints for foraging (e.g., comparing predictions for the 20% and 80% quantiles of body temperatures and the corresponding 10% and 90% quantiles; fig. A1) in the Campbell and Norman model should thus accurately portray foraging durations. Further testing of biophysical models at landscape scales will be necessary to produce accurate predictions of foraging duration.

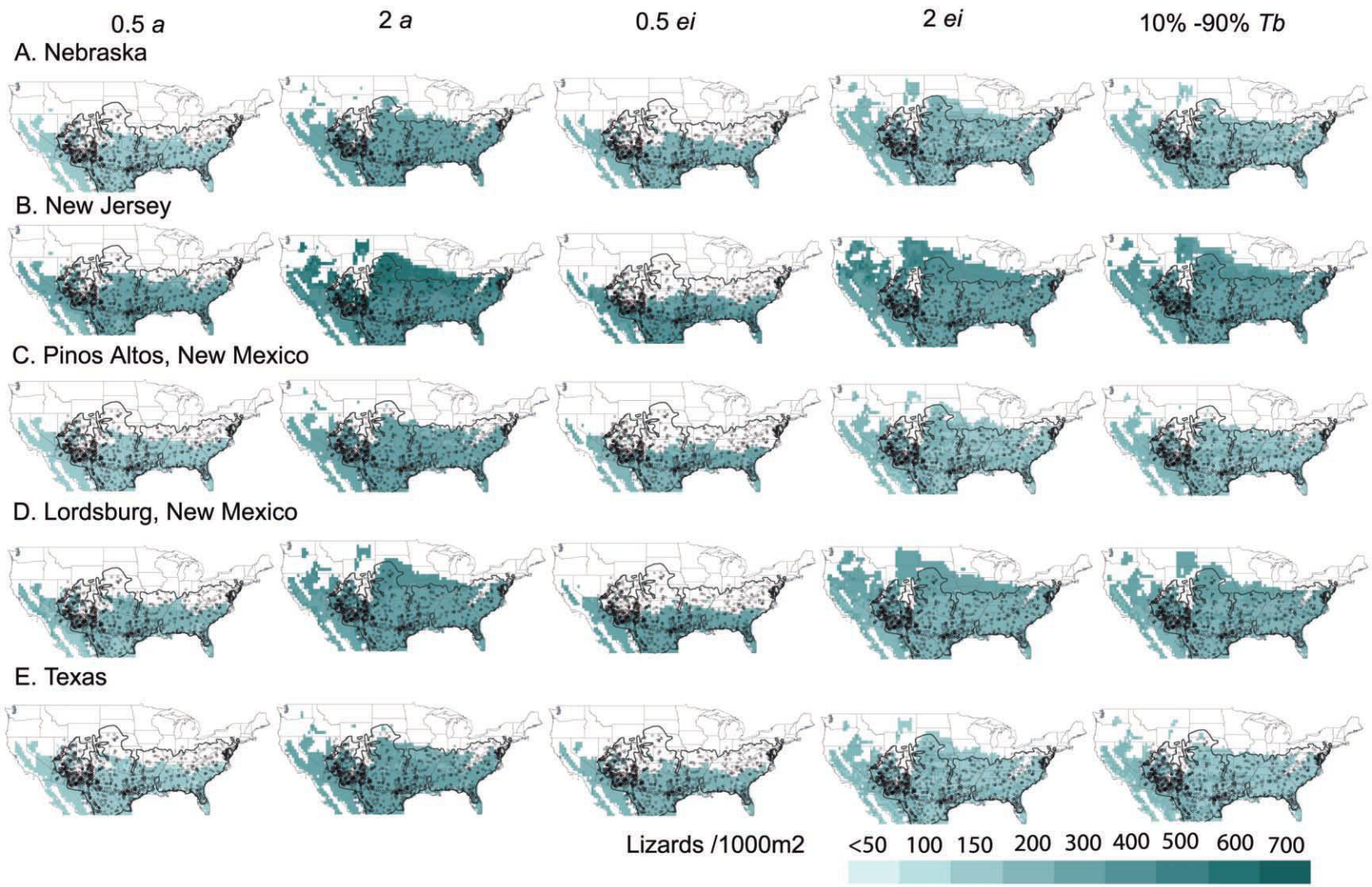

Figure A1: Sensitivity analysis of the dynamic model predictions for *Sceloporus undulatus* shows that relative density predictions (lizards 1,000 m^{-2}) remain constant when parameters are varied. The range implications of halving and doubling the parameters for insect abundance, a (insects m^{-1} s^{-1}), and the energetic content per insect, e_i (J), are presented. The range implications of assuming that lizards forage at temperatures within the 10% and 90% quantiles of their body temperature are also depicted.

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