

Costs and Benefits of Thermoregulation Revisited: Both the Heterogeneity and Spatial Structure of Temperature Drive Energetic Costs

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ABSTRACT: In recent years, ecologists have stepped up to address the challenges imposed by rapidly changing climates. Some researchers have developed niche-based methods to predict how species will shift their ranges. Such methods have evolved rapidly, resulting in models that incorporate physiological and behavioral mechanisms. Despite their sophistication, these models fail to account for environmental heterogeneity at the scale of an organism. We used an individual-based model to quantify the effects of operative environmental temperatures, as well as their heterogeneity and spatial structure, on the thermoregulation, movement, and energetics of ectotherms. Our simulations showed that the heterogeneity and spatial structure of a thermal landscape are as important as its mean temperature. In fact, temperature and heterogeneity interact to determine organismal performance. Consequently, the popular index of environmental quality (d_e), which ignores variance and spatial structure, is inherently flawed as a descriptor of the thermal quality of an environment. Future efforts to model species' distributions should link thermoregulation and activity to environmental heterogeneity at fine scales.

Keywords: thermoregulation, climate, activity, ectotherm, temperature, heterogeneity.

Predicting ecological responses to climate change is one of the greatest challenges of the 21st century. To forecast these responses, ecologists rely on computational methods that leverage climatic and biological data to infer the distributions of species. Current models, based on the concept of the ecological niche (Crozier and Dwyer 2006; Kearney et al. 2008; Holt 2009; Buckley 2010; Angilletta and Sears 2011), successfully integrate principles of biophysical,

population, and spatial ecology (Kearney and Porter 2009; Buckley et al. 2010). These models predict the duration that a species can be active in a particular area; this duration reflects the sum of all periods when the preferred temperature of a species falls within the range of body temperatures permitted by access to sun and shade. Once activity has been calculated, one can determine whether an animal can obtain the energy needed to survive and reproduce. By aggregating estimates of fitness across a landscape, one arrives at a predicted distribution for the species.

Despite their sophistication, these models fail to represent thermal heterogeneity on the scale of the organism (Sears et al. 2011; Potter et al. 2013), which fundamentally biases their predictions. Typically, topographical features are considered constant throughout an area as large as 1 km² (or larger). Consequently, all individuals within that area are predicted to be either active or inactive at a particular time. As an example from our own work (Buckley et al. 2010), climatic data resolved to 1 km² were used to predict the distribution of *Sceloporus undulatus*, a species of small lizards that occurs in the United States. Since climatic data were coarsely resolved, the predicted distribution varied widely according to our assumptions about heat fluxes over homogeneous surfaces. Moreover, failing to include spatial variation—by ignoring topography—overestimated constraints on thermoregulation (Sears et al. 2011). These problems are by no means unique to this example. A general mismatch between the resolutions of climatological data and organismal processes introduces great uncertainty about the persistence of species in future climates (Potter et al. 2013).

An ignorance of spatial heterogeneity has plagued studies of thermoregulation for decades. Since the 1990s, researchers have inferred the potential for thermoregulation from the mean temperatures available to organisms. Specifi-

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cally, quantitative analyses are based on an index of thermal quality, d_c , which equals the absolute difference between the operative temperature of the environment and the preferred temperature of the species (Hertz et al. 1993). Typically, samples of d_c are averaged over space to obtain a simple descriptor of thermal quality (e.g., Blouin-Demers and Nadeau 2005). Unfortunately, this descriptor carries no information about the heterogeneity or spatial structure of temperatures in the landscape. Yet, this heterogeneity and spatial structure determine whether an organism can maintain its preferred temperature and the cost it incurs when doing so. Therefore, a successful theory of thermoregulation must consider the abundance and distribution of thermal resources in space (Angilletta 2009).

Individual-based modeling provides a framework for analyzing the behaviors of organisms in spatially explicit landscapes. Given the thermal landscape associated with a particular topography and climate, one can model the temperatures of individuals. The thermoregulatory performance in the landscape determines activity and energetics, which can ultimately be used to calculate the demographics of a population (Buckley 2008; Buckley et al. 2013). Using this approach, we examined how features of the thermal landscape influence the thermoregulation and energetics of ectotherms. By modeling the movements and heating of small animals in two-dimensional landscapes, we quantified the body temperatures resulting from thermoregulatory decisions. Surface activity depended on the distributions of suitable thermal patches, and energetic expenditure was driven by body temperatures and movement distances. We also simulated thermoregulatory behavior for individuals of different sizes because larger animals heat and cool more slowly. These simulations quantified how heterogeneity and spatial structure of temperatures affect the performance of organisms, which is necessary for understanding the energetic cost of thermoregulation.

Methods

We simulated thermoregulatory behaviors of animals in two-dimensional landscapes. These landscapes differed in the availability of preferred temperatures (availability), the spatial arrangement of temperature (dispersion), and the thermal variance of temperature (variance). Each landscape consisted of a tiled grid of cells (64×64). Within the grid, each cell was classified as either preferred or non-preferred with respect to temperature. The mean operative temperature of a preferred cell was 34°C (similar to the preferred temperature of a *Sceloporus* lizard), whereas the mean temperature of the non-preferred cell equaled or exceeded the preferred temperature (the mean for non-preferred cells ranged from 34° to 50°C in increments of 1°C). Thermal heterogeneity was created by increasing the

standard deviations associated with the mean temperatures in preferred and non-preferred cells (the standard deviation was 0.25° , 0.5° , 1.0° , or 2.0°C for preferred cells and 0.5° , 1.0° , 2.0° , or 4.0°C for non-preferred cells). For each distribution of operative temperatures, values were assigned to cells according to one of three spatial structures: 1 patch, 4 patches, and 16 patches of preferred temperatures (fig. 1).

Individuals were given a set of behavioral decisions to optimize thermoregulatory performance while moving through a spatially explicit environment. During a simulation, individuals sampled their environment for a location that offered operative temperatures resulting in body temperatures (T_b) within their preferred range (32° – 36°C). At the start, an individual with a T_b of 34°C was placed in a random location on the grid. Every minute, the individual searched locations and chose one that provided a T_b closest to 34°C . If its T_b was already within the preferred range, the individual remained still with a probability of 0.75. Note that this probability could be modified to capture the behavior of any organism (or behaviors other than thermoregulation). If T_b was outside of the preferred range, the individual moved with a probability of 1.0.

When moving, the individual searched for a preferred cell. The distance and the range of angles searched were drawn from beta and von Mises distributions, respectively. The beta distribution,

$$f(x|\mu, \kappa) = \frac{\Gamma(\alpha + \beta)}{\Gamma(\alpha)\Gamma(\beta)} x^{\alpha-1}(1-x)^{\beta-1},$$

required two parameters, α and β . This function was multiplied by a maximal distance to determine how far an animal would sample locations. We set α and β to 1 and 4, respectively, such that locations were sampled more intensely at closer proximity. Maximal distance was calculated as $8 \times [\log_{10}(\text{mass}) + 1]$, such that the largest animals could search farther (half the distance of the grid) than the smallest (one-eighth the distance of the grid). The von Mises function,

$$f(x|\mu, \kappa) = \frac{e^{x \cos(x-\mu)}}{2\pi I_0(\kappa)},$$

also required two parameters, κ and μ . The parameter κ determined the concentration of search angles. The parameter μ determined the angle with reference to a forward-facing direction. Both μ and κ were set to 0 and 1, respectively, such that animals oriented straight ahead and concentrated their searches in a forward direction, between $+\pi/2$ and $-\pi/2$ radians with respect to their orientation. The final term, I_0 , equals the modified Bessel function of zero order. For each sampled location, an individual evaluated the body temperature that would result from spend-

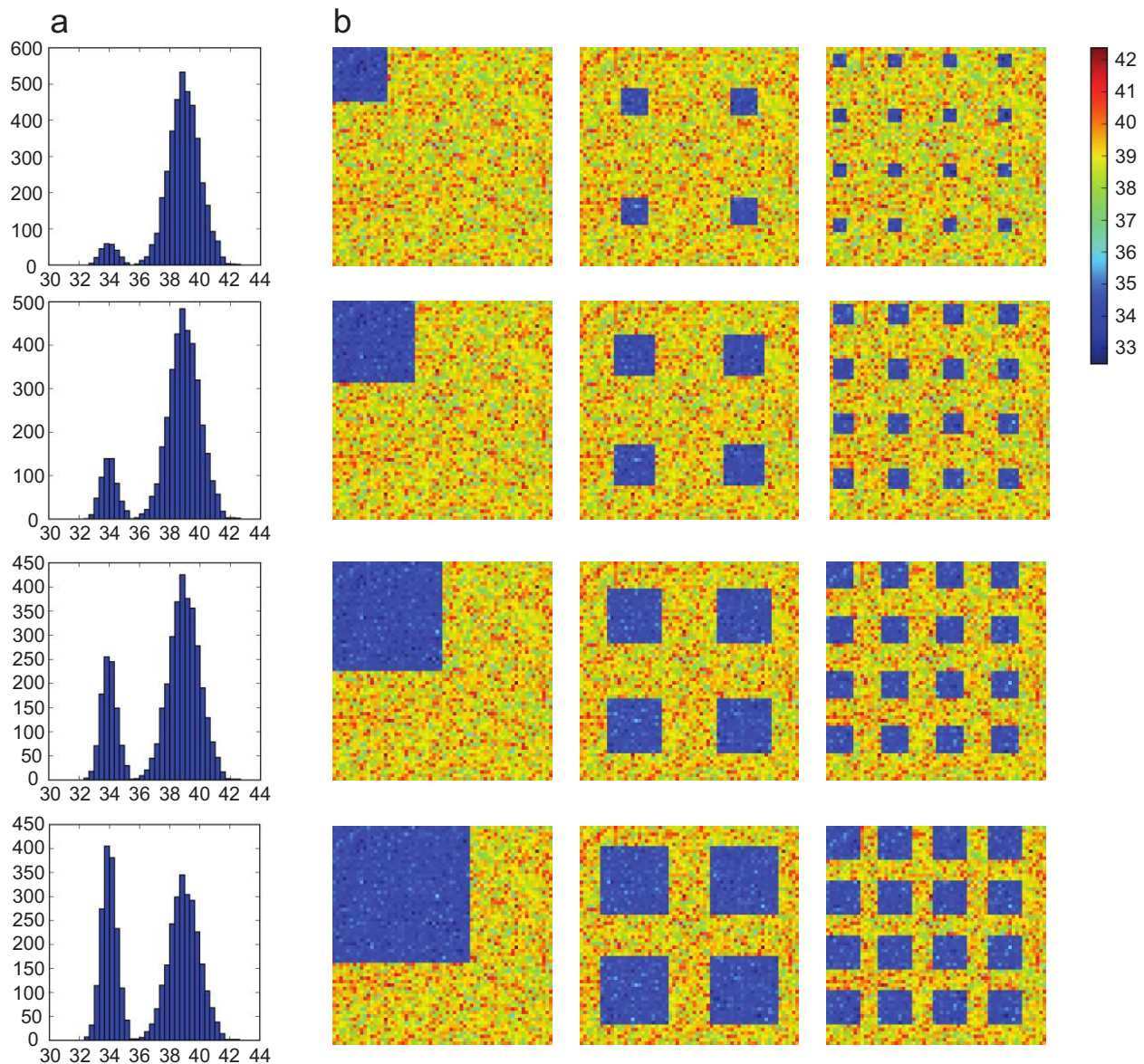


Figure 1: For our simulations, we created thermal landscapes that differed in composition and arrangement. *a*, Operative temperatures were drawn from bimodal distributions (*leftmost column*) and distributed among cells to create a spatial structure. *b*, Preferred patches—containing temperatures from the part of the distribution surrounding the lower mode—composed 6.25%, 14.1%, 25.0%, or 39.1% of the environment. Preferred patches were distributed within 1 large patch or spread evenly among either 4 or 16 smaller patches. Operative temperatures of the remaining cells were drawn from the part of the distribution surrounding the upper mode, which was hotter than preferred. To manipulate thermal heterogeneity within environments, we increased the standard deviation of temperature within preferred and nonpreferred cells from 0.5° to 4°C without changing the means (only one of those distributions is shown here).

ing 1 min in that location. This body temperature (T_{b2}) was given by

$$T_{b2} = T_c + e^{(-t/\tau)}(T_{b1} - T_c),$$

where T_{b1} equals the current T_b , T_c equals the operative temperature, t equals the duration at the operative temperature, and τ equals the thermal time constant of the

animal (depending on its mass and whether it was heating, $\ln \tau = 0.72 + 0.36 \ln \text{mass}$, or cooling, $\ln \tau = 0.42 + 0.44 \ln \text{mass}$; Grigg et al. 1979). Each minute, the animal evaluated six locations and chose the one that brought its body temperature closest to 34°C; when several locations would confer the same body temperature, the closest location was chosen. Once a location was chosen, ener-

getic expenditure (J/min) was estimated by $20.2 \times 10^{(0.038 \times T_b - 1.771)} \times \text{mass}^{0.82} \times \text{activity scope}$ (Grant and Porter 1992). To account for the cost of locomotion, we assumed that the activity scope increased by a factor of $4 \times (d/d_{\max})$, where d and d_{\max} equal the distance moved during the current time interval and the maximal distance per move, respectively. Thus, when the animal moved the maximal distance, its metabolic cost quadrupled.

For each combination of factors, we simulated 1,000 replicates of 15 min of activity. For comparison, we simulated 1,000 replicates of a thermoconforming animal in the same environments. A thermoconforming animal moved without regard for how movements affected its body temperature. In these simulations, all parameters were the same as they were for our simulations of thermoregulation, except that the animal moved to a new location chosen randomly with respect to operative temperature during 90% of the time intervals. For each simulation, we recorded the inaccuracy of thermoregulation (d_b), the total distance moved, and the net energetic expenditure. A full factorial ANOVA was used to quantify how the availability of preferred temperatures, the mean temperature of nonpreferred cells, the spatial structure of the landscape, the thermal heterogeneity, and the body mass of the organism affected each of the dependent variables. Analyses were performed using the R statistical software package (ver. 3.0.1). Simulations were coded in the run using Cython, version 0.20, based on Python 2.7.6 (<http://www.python.org>), NumPy 1.8.1 (<http://www.scipy.org>), and SciPy 0.13.3 (<http://www.scipy.org>). This code was run on a workstation composed of 16 2.9-GHz E5-2690 Xeon CPU cores (32 cores with hyperthreading) and 128 GB DDR3 1,600 MHz memory running Gentoo Linux. With this configuration, the script runs in approximately 14 min. Code for this simulation is available in the supplementary zip file and on GitHub (<https://github.com/thermalecology/AmNat>).¹

Results and Discussion

Both mean environmental temperatures and spatial heterogeneity greatly affected thermoregulation, movement, and energetics (for details, see table S1 in the supplementary PDF). As the availability of preferred temperatures increased from 6.25% to 39.1%, thermoregulatory performance improved, indicated by a closer match between body temperatures and preferred temperatures (fig. 2a). This effect was accentuated as preferred temperatures became more dispersed over space. When preferred temperatures were common, landscapes made up of either 4 or 16 favorable patches enabled accurate thermoregulation. Total

movement for individuals corresponded to the average distance between preferred patches; for example, distances were the smallest for environments with 16 patches (see figs. S1–S8 in the supplementary PDF). Consequently, energetic expenditure decreased as preferred patches became either more frequent or more dispersed. For a given mean temperature and spatial distribution of preferred patches, an increase in thermal heterogeneity improved thermoregulatory performance and lowered energetic expenditure (fig. 2b).

To assess the relative importance of mean environmental temperatures versus spatial heterogeneity and structure of environmental temperatures, we compared the magnitudes of effects among treatments (fig. 3). Effect sizes were put into three categories: (1) factors related to the mean operative temperature, consisting of the frequency of preferred temperatures and the mean temperature of nonpreferred patches, (2) factors related to spatial heterogeneity (availability, variance, and dispersion), and (3) interactions between factors related to mean operative temperatures and those related to spatial heterogeneity. Spatial heterogeneity was relatively more important to the thermoregulatory performance of larger organisms; this result makes sense because small animals, such as lizards, have a relatively short thermal time constant (Bell 1980; Fraser and Grigg 1984) and most movements result in thermal change (e.g., Christian and Tracy 1981; Christian et al. 2006). For an animal weighing 1 kg, structure and heterogeneity had nearly the same effects on thermoregulatory performance as the mean operative temperature; each of these categories accounted for just over 20% of the variation. The effects on the distance moved were quite small even for larger organisms, in which movement varied mainly according to the spatial structure of the environment. For large organisms, structure and heterogeneity had even greater effects on movements and energetics than did the mean operative temperature.

Based on our model, one cannot explain variation in thermoregulatory performance without considering the spatial heterogeneity of an environment. In fact, the spatial heterogeneity of microclimates appears to be just as important as the modal operative temperatures. Most models of habitat choice (reviewed by Brown 1998) define landscapes implicitly. Although an implicit landscape would simplify an analysis of costs and benefits, a spatially explicit description of operative temperatures enabled us to better estimate thermoregulatory performance and the energetic cost of behavioral thermoregulation. This cost largely accrues from the costs of transport (John-Alder and Bennett 1981), which should be correlated with the mean distance between preferred microclimates (Huey 1974). To illustrate the problem, we chose 100 random combinations of environmental temperature and thermal heterogeneity; these

1. Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

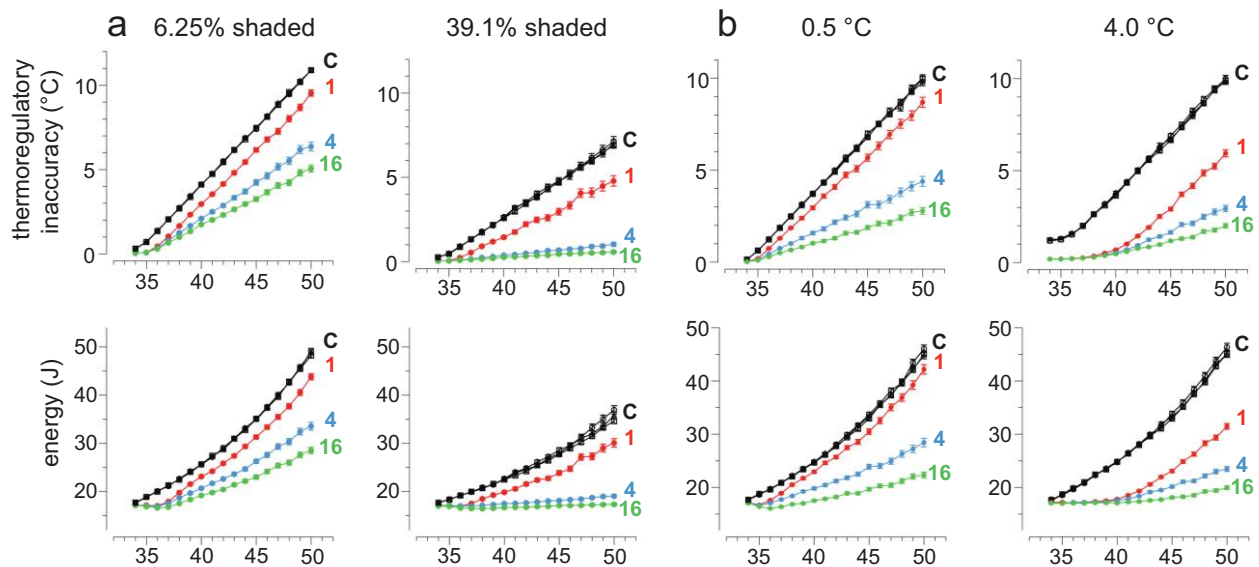


Figure 2: Thermoregulatory behavior and energetic costs are shown for a 10-g individual with respect to the extremes in the percent of favorable (shaded) patches and in the extent of environmental heterogeneity. More detailed results can be found in the supplementary PDF. *a*, As the proportion (from 6.25% to 39.1%) or dispersion of cells (1, 4, or 16 patches) containing preferred temperatures increased, individuals were able to thermoregulate more accurately and expend less energy. *b*, As the environment became more heterogeneous, individuals were able to thermoregulate more accurately, move shorter distances, and expend less energy. Here results are shown for an environment where 14.1% of the shaded cells fell within the preferred thermal range. Heterogeneity was manipulated by increasing the standard deviations of temperatures in the preferred and nonpreferred cells (e.g., standard deviations ranged from 0.5° to 4°C for operative temperatures for cells in the sun) without changing the means. Lines are labeled C (conforming individuals for all patch types), 1 (regulating individuals with one favorable patch, i.e., low dispersion), 4 (regulating individuals with 4 favorable patches, i.e., moderate dispersion), and 16 (regulating individuals with 16 favorable patches). All conformers were not labeled with respect to dispersion because of the overlapping performance among patch types.

simulations covered the ranges of parameter values described in “Methods.” For each combination of environments, we simulated 100 individuals and recorded their thermoregulatory performance, as indicated by the index d_b (fig. 4). Several problems arose. First, thermoregulatory performance would appear random without knowing the conditions of the environment. Second, large thermoconforming individuals would appear to thermoregulate when contrasted to smaller thermoconforming animals at the same environmental temperatures, only because of lags in heating and cooling.

The costs and benefits of thermoregulation should induce organisms in different environments to thermoregulate differently, with potential strategies ranging from pure thermoconformers to strict thermoregulators. Individuals who face a greater cost should thermoregulate less accurately (Huey and Slatkin 1976; Angilletta 2009). In contrast to this prediction, a meta-analysis of empirical studies (Blouin-Demers and Nadeau 2005) indicated that reptiles thermoregulated better in environments where thermoregulation seemed more costly. The failure to validate the theory likely reflects poor estimates of energetic costs of thermoregulation. Such costs were inferred from the index

of environmental quality known as d_e (Hertz et al. 1993). A larger value of d_e means that the environment is (on average) hotter or colder than the animal prefers. Nevertheless, d_e ignores the heterogeneity and spatial structure of the environment and thus cannot adequately portray the energetic cost of thermoregulation. Thus, the results in Blouin-Demers and Nadeau are likely biased not to find a cost of thermoregulation due both to differences in body size among species used in the meta-analysis as well as potential randomness and/or bias introduced by ignoring structure and heterogeneity (depending on how dissimilar environments were across studies). Our simulations showed that these factors can be as important as the mean operative temperature when examining thermoregulatory performance and energetic costs. Therefore, the use of d_e to estimate thermoregulatory costs, without controlling for spatial heterogeneity, will lead to erroneous conclusions. Our theoretical framework clearly partitions the impacts of mean temperature and spatial heterogeneity. Furthermore, our model shows that the null model for comparison—the relationship between d_e and d_b for a thermoconformer—changes systematically with the body size of the animal as a consequence of thermal inertia (i.e., larger animals heat

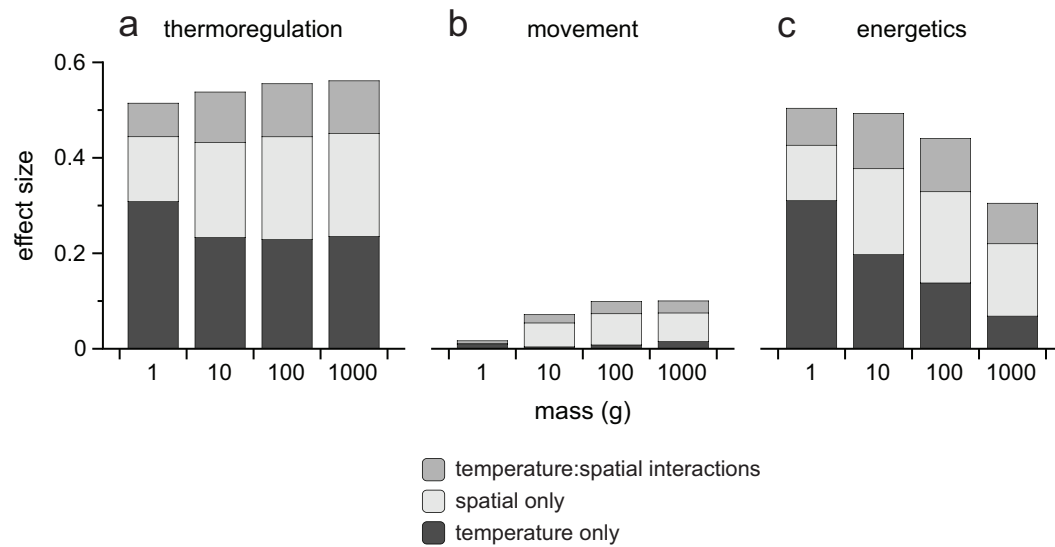


Figure 3: Relative impacts of mean operative temperature, spatial structure, and thermal heterogeneity on thermoregulation (i.e., thermoregulatory inaccuracy; *a*), movement while thermoregulating (*b*), and energetics (costs of thermoregulation; *c*). Effects were binned into three categories: (1) effects related to factors affecting mean operative temperature (temperature only), (2) effects related to spatial structure and thermal heterogeneity (spatial only), and (3) interactive effects between factors related to mean operative temperature and spatial structure or thermal heterogeneity. Effect sizes, calculated using ω^2 , were used to evaluate the relative importance of independent factors in our simulations (Graham 2001) instead of frequentist approaches (e.g., *P* values), which merely indicate whether an appropriate number of simulations was run to detect significant effects (White et al. 2014.).

and cool more slowly than smaller animals; similar to Seebacher and Shine 2004 and Christian et al. 2006). Thus, our model suggests that costs cannot be evaluated using simple indices of environmental quality.

A spatially explicit model also enables one to consider spatial correlations between temperature and other resources such as food and water. The distribution of these resources also influences the cost of thermoregulation. For example, consider the effects of water on the thermoregulatory behavior of ectotherms. Typically, less hydrated animals select lower temperatures (Smith et al. 1999; Ladyman and Bradshaw 2003; Tracy and Christian 2005). Whether a microclimate seems favorable or not could depend on its proximity to water as well as the organism's rate and tolerance of water loss (Cohen and Alford 1996). Physical processes link many abiotic variables to temperature in predictable ways (Campbell and Norman 1998). Thus, our spatially explicit approach enables researchers to link multiple resources in a model of habitat selection.

We can easily expand our theory of thermoregulation to consider costs of thermoregulation that arise from interactions within and among species. The quality of thermal patches depends on competition for resources within that patch (Magnuson et al. 1979; Huey 1982; Downes and Shine 1998; Stapley and Keogh 2004). Similarly, animals respond simultaneously to the thermal benefit and the predation risk (Loose and Dawidowicz 1994; Martin and

Lopez 1999; Gerald and Spezzano 2005; Downes 2008). An animal can also miss opportunities to capture prey, defend territories, and acquire mates by spending its time in specific microclimates. Although these costs have been considered by previous models (Mitchell and Angilletta 2009), a spatially explicit approach seems ideal for modeling organisms that move in response to one another (Mitchell and Lima 2002).

The predictions of our individual-based model could be tested in two ways. First, one could relate the thermoregulatory performance of free-ranging animals to the structure and heterogeneity of their thermal environments. In natural habitats, thermal heterogeneity is produced statically through vegetation and dynamically through differential heating of surfaces as the sun moves across the sky. Choosing habitats that varied in their vegetative structure and topographic relief might allow specific quantitative predictions to be made. For instance, flat habitats with sparse vegetation might be expected to produce higher costs than otherwise similar habitats with more vegetation dispersed through the habitat or over landscapes with increased topographic relief. In earlier work, we produced landscapes with realistic topographies to show how thermal heterogeneity influences thermoregulatory performance for a small lizard (Sears et al. 2011). By performing similar simulations using topographies of real landscapes, one could predict the thermoregulatory performance and en-

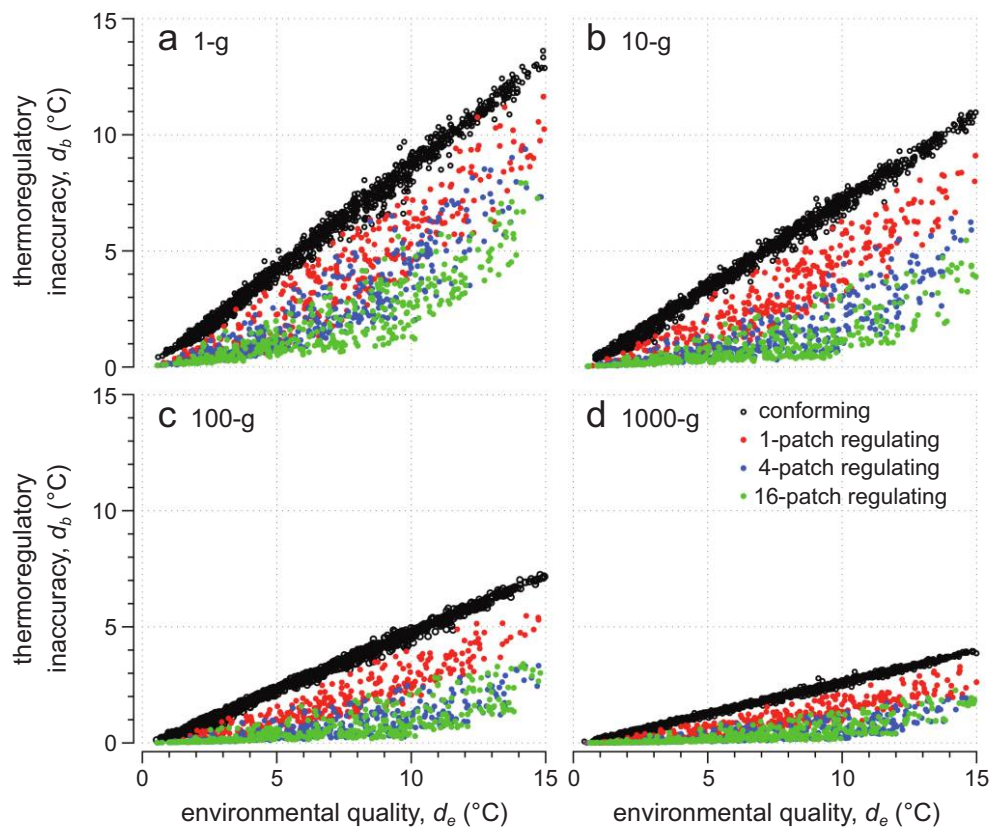


Figure 4: Results of environmental index d_e on realized body temperature d_b . Here we plotted the results of randomly configured environments with respect to spatial arrangement, environmental temperature, and within-patch heterogeneity. Results are shown for 1-g (a), 10-g (b), 100-g (c), and 1,000-g (d) animals. Without prior knowledge of environmental configurations, (1) thermoregulatory performance would appear random with respect to d_e and (2) null expectations for thermoregulatory performance change with the size of the animal (i.e., d_b becomes less sensitive to d_e as animal size increases).

ergetic expenditure of animals in these landscapes and compare these predictions to observed values for real animals. Second, one could manipulate the structure and heterogeneity of operative temperatures in artificial environments, such as indoor or outdoor arenas. The advantage of this approach is that one can manipulate the heterogeneity of the arenas to match the thermal landscapes used in our individual-based models. The thermoregulatory performance and energetic expenditure of real animals could be monitored within each arena to see whether they follow the predictions of the model. We do not believe that comparative or experimental tests of theory are too difficult; instead, such tests have not been conducted because researchers failed to recognize how critically thermoregulatory performance depends on spatial properties of thermal landscapes.

Our theory of thermoregulation has clear implications for predicting how organisms respond to climate change. Past responses include northerly shifts in species distributions (Walther et al. 2002), temporal advances in biological

events (Parmesan and Yohe 2003), adaptation of thermally sensitive traits (Bradshaw and Holzapfel 2008), shifts in body size (Caruso et al. 2014), and extinctions of populations (Sinervo et al. 2010). Consequently, researchers have sought to project future responses to anticipated changes in climate, often predicting unsettling views of the future for ectothermic organisms (Thomas et al. 2006; Deutsch et al. 2008; Sinervo et al. 2010). For instance, using estimates of the amount of time where environmental temperatures exceed critical thermal maxima, Sinervo et al. (2010) predicted that up to 39% of lizard populations would go extinct worldwide by 2080. These predictions stem from analyses of thermoregulation and energetics in either spatially implicit or homogeneous environments. Consequently, such analyses exaggerate the energetic costs of thermoregulation (and its consequences) if environments possess substantial heterogeneity, increased availability, or higher dispersion of thermal patches (see figs. 3, 4) with concurrent increases in the duration of activity (Sears et al. 2011). Indeed, previous approaches to modeling the activity of a thermoregulator

would consistently underpredict performance in a heterogeneous environment. For instance, a bioenergetic model failed to predict patterns of growth (based on activity) for sagebrush lizards (*Sceloporus graciosus*) along an elevational gradient, likely because the model ignored the effects of spatial heterogeneity and availability of environmental temperatures (Sears 2005). Considering that environmental temperatures in simple habitats can vary by more than 20°C at any given time (Sears et al. 2011), one might conclude that quantifying heterogeneity constitutes a major challenge for researchers interested in responses to climate change (Angilletta and Sears 2011). By contrast, species that inhabit flatter landscapes, which offer less heterogeneity (Sears et al. 2011), would be at higher risk than anticipated during warming climates. Other studies also suggest that less heterogeneous habitats impose greater stress during climate warming (Ackerly et al. 2010; Sears et al. 2011; Potter et al. 2013). Therefore, future research in ecological forecasting should link mechanisms that generate activity to the spatial heterogeneity of environments.

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