THERMAL AND ENERGETIC CONSTRAINTS ON ECTOTHERM ABUNDANCE: A GLOBAL TEST USING LIZARDS

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Abstract. Population densities of birds and mammals have been shown to decrease with body mass at approximately the same rate as metabolic rates increase, indicating that energetic needs constrain endotherm population densities. In ectotherms, the exponential increase of metabolic rate with body temperature suggests that environmental temperature may additionally constrain population densities. Here we test simple bioenergetic models for an ecologically important group of ectothermic vertebrates by examining 483 lizard populations. We find that lizard population densities decrease as a power law of body mass with a slope approximately inverse to the slope of the relationship between metabolic rates and body mass. Energy availability should limit population densities. As predicted, environmental productivity has a positive effect on lizard density, strengthening the relationship between lizard density and body mass. In contrast, the effect of environmental temperature is at most weak due to behavioral thermoregulation, thermal evolution, or the temperature dependence of ectotherm performance. Our results provide initial insights into how energy needs and availability differentially constrain ectotherm and endotherm density across broad spatial scales.

Key words: ectotherms; energetic constraints; energetic equivalence rule; environmental temperature; lizards; metabolic theory; population density.

INTRODUCTION

Energetic needs constrain population densities (Damuth 1981, 1987). This constraint is suggested by an inverse-scaling relationship between population density and mean adult body mass for interspecific comparisons (reviewed in White et al. 2007). This relationship reflects the greater metabolic energy needs of larger organisms (Bennett 1982, Nagy 2005). The decline in population density with respect to body mass approximately follows a −3/4 power law in mammals (Damuth 1981, 1987, Jetz et al. 2004), birds (Nee et al. 1991, Meehan et al. 2004), intertidal invertebrates (Marquet et al. 1990), land plants (Enquist et al. 1998), and marine phytoplankton (Belgrano et al. 2002). In this special case of a −3/4 scaling, populations are termed energy equivalent (Damuth 1981, 1987) because the metabolic rate of an individual, *B*, generally scales with body mass to the 3/4 power (Bennett 1982, Gillooly et al. 2001).

Rates of energy use by individuals are additionally strongly affected by temperature. For endotherms such as birds and mammals within the thermoneutral zone, metabolic rates vary little with ambient temperature (Calder 1984). In contrast, body temperature exerts an exponential effect on the metabolic rates of ectotherms,

with individuals in warmer environments requiring disproportionately more energy per unit time (Bennett 1982, Gillooly et al. 2001). Metabolic theory extends population energy-equivalence to apply to temperature gradients: for a given body mass, ectotherm population densities are predicted to decrease exponentially with increasing body temperature as single individuals require exponentially more energy (Gillooly et al. 2001, Savage et al. 2004; see Allen et al. 2002 for empirical examples). Animal abundances are not only constrained by energetic requirements, but also extrinsically by the amount of energy available in the environment (Kaspari et al. 2000, Meehan et al. 2004).

Few regional or global scale studies have investigated environmental constraints on vertebrate ectotherm groups (but see Currie and Fritz 1993, Allen et al. 2002) despite ongoing population declines (Gibbons et al. 2000) and potential susceptibility to environmental change (Pounds 2001). Can body size predict ectotherm population density? Do environmental temperatures additionally constrain densities? How much variation in ectotherm abundance can be explained by energy availability as approximated by net primary productivity? Here we evaluate these questions across 483 populations of lizards from across the world. Specifically, we examine how lizard population densities covary with (1) energy needs as determined by body mass; (2) energy needs as additionally determined by environmen-

tal temperature (modeled with several temporal resolutions); and (3) energy supply.

We are particularly interested in the potential metabolic effects of temperature on ectotherm abundances and present the first broad-scale test of this notion for terrestrial vertebrates. As average annual environmental temperatures simplify the temperatures experienced by organisms, we model diurnal and seasonal variation in environmental temperatures and integrate metabolic rates across hours, days, and months to calculate annual metabolic costs per individual (kJ/yr). These calculations may still only poorly reflect body temperatures as behavioral thermoregulation, a prominent feature in lizards, buffers against changes in environmental temperature (Hertz et al. 1993). Optimal or actual body temperature data is unavailable for most species. A strong and negative exponential relationship between environmental temperature and lizard abundances would support a metabolic constraint on ectotherm population densities and indicate only limited behavioral thermoregulation. A weak relationship would reject extending energetic-equivalence to temperature, point to behavioral thermoregulation, or both.

Methods

Metabolic cost calculations, B

Population density (N) is expected to be approximately proportional to individual energy use (B) and population energy availability (P; $N \propto P/B$). We define expressions for resting metabolic rates, BX (kJ/year per individual), which incorporate sequentially more refined environmental temperature estimates. This addresses whether metabolic rates track diurnal and seasonal temperature trends or whether thermoregulation buffers these trends. The coarsest population estimate incorporates average annual environmental temperature, T_a (K):

$$B0 = 526.0 \times b_0 M^{3/4} e^{-E/kT_a}$$

where b_0 is a constant, M is mass (g); e^{-E/kT_a} is the Boltzman factor, which accounts for temperature's influence on reaction kinetics (Gillooly et al. 2001); E is the activation energy; and k is the Boltzman constant. The factor converts from the initial unit (J/min) to kJ/yr. Gillooly et al. (2001) used empirical metabolic rate data for reptiles ($n = 105$ species) to estimate $b_0 = 4.58 \times 10^{11}$ and $E = 0.757$ eV. B is thus a function of mass and temperature. We increase the refinement of the B calculation by incorporating monthly ($B1$) and hourly ($B2$) temperatures:

$$B1 = 43.8 \times b_0 M^{3/4} \sum_{m=1}^{12} e^{-E/kT_m}$$

$$B2 = 1.83 \times b_0 M^{3/4} \sum_{m=1}^{12} \sum_{h=1}^{24} e^{-E/kT_{h,m}}$$

where T_m is the average temperature for each month m and $T_{h,m}$ is the temperature for hour h and month m (data from 1961 to 1990 with $10'$ latitude/longitude resolution [New et al. 2002]). $T_{h,m}$ is the hourly temperature for an average day of each month calculated using the monthly means for daily temperature and the diurnal temperature range (Campbell and Norman 1998).

Finally, we use the daylight period to define the lizard's activity window. Civil sunrise and sunset were calculated as a function of latitude and calendar day using the CBM day length model of Forsythe et al. (1995). We assume that the active metabolic rate is a constant, a, times the resting metabolic rate and that $a = 3$ (Nagy 2005). We assume that lizards are active for three-quarters of the daylight period (proportion activity is an approximate upper bound [Adolph and Porter 1993]):

$$B3 = 1.83 \times b_0 M^{3/4} \sum_{m=1}^{12}$$

$$\times \left[(3/4a + 1/4) \sum_{h=\text{sunrise}}^{\text{sunset}} e^{-E/kT_{h,m}} + \sum_{h=\text{sunset}}^{\text{sunrise2}} e^{-E/kT_{h,m}} \right].$$

The results are not affected qualitatively by doubling the metabolic factor or assuming lizards forage over the entire day length period, because constant factors affect all populations equally. An additional energetic model attempted to capture the metabolic consequences of hibernation by conservatively assuming that lizards are inactive when temperatures dropped below freezing. This assumption had little effect on relative estimates of annual metabolic costs (B), suggesting that examining hibernation is infeasible without species-specific physiological information.

The scaling exponents for both resting and field metabolic rates of lizards may diverge significantly from 3/4, with the majority of observations suggesting a steeper slope (e.g., field metabolic rate $\propto M^{0.889}$, $n = 55$ species, $r^2 = 0.94$ [Nagy 2005]). Here we follow predictions from recent theory on the scaling of metabolism and assume that $B \propto M^{3/4}$ (Gillooly et al. 2001). In our analysis, we find that the value of the scaling exponent within the biologically reasonably range of 0.6–0.9 has little influence on the effect of temperature, the scaling coefficient for productivity, and the fit of the combined model. The results are thus robust to the assumption that $B \propto M^{3/4}$. This indicates that we cannot resolve the exact scaling coefficient due to both biological and methodological sources of variation in population density.

Database

We gathered lizard population density data from the literature, expanding from Rodda et al. (2001) (see Appendix A for database details). The database consists
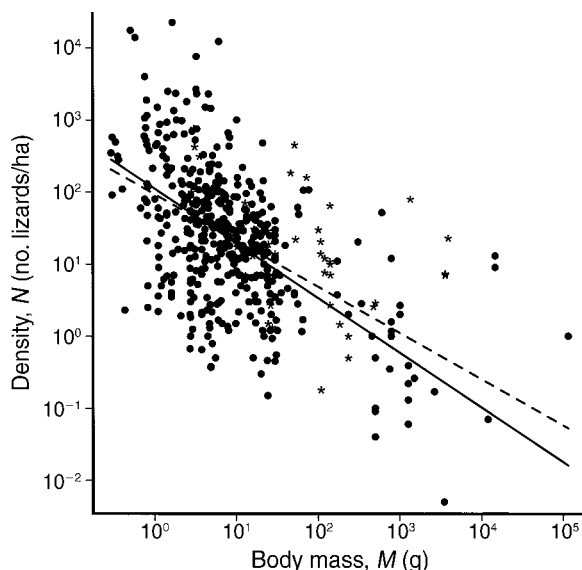
FIG. 1. The power law relationship between lizard population density, N, and body mass, M. We depict the regression for $M < 55$ g (solid line; $N \propto M^{-0.75}$, $n = 418$, $r^2 = 0.17$) and for all data (dashed line; $N \propto M^{-0.63}$, $n = 482$, $r^2 = 0.29$). Herbivores and omnivores are indicated with stars; carnivores are represented by solid circles.

of 483 populations of 246 lizard species representing 106 genera. Approximately half of the observations (253 populations) were subsets of studies of the entire lizard assemblage. We analyze the density ramifications of resource partitioning between lizards by including energy use by the lizard assemblage (minus the target species) as a covariate.

Mass and length (snout–vent length, SVL) data for the majority of populations were assembled from the source articles and regional guides by Rodda et al. (2001). The estimates account for the size distribution of sampled individuals and thus include some intraspecific variation. When these mass estimates were not available, we used a well-established relationship for lizards to convert mean adult SVL (mm) to mass (g): $M = 3.1 \times 10^{-5} \, SVL^{2.98}$ (Pough 1980). Environmental data were assembled in ArcGIS 9.0 (ESRI, Redlands, California, USA). Mean annual precipitation (mm) is reported with $10'$ latitude/longitude resolution from 1961 to 1990 (New et al. 2002). Net primary productivity is reported as the 18-year average of annual totals from the DOLY global model (Mg C per ha per year, 0.5° spatial resolution [Woodward et al. 1995]). Minimum net primary productivity (P_{min}) is the mean of the three-month period with the lowest average monthly DOLY productivity predictions (average over the 18-year period, Appendix A).

Analysis

We describe the relationships between environmental variables and density as power laws (slopes and 95% CI) because this form can describe a linear, accelerating, or

decelerating relationship. Consequently, all data were log-transformed. Generalized linear models were fit with maximum likelihood estimation using R (methods *available online*).[5] Akaike's information criterion (AIC) values were used to compare the fit of nested models (Burnham and Anderson 2002). The best model is that with the lowest AIC value. Models with deviations from the minimum AIC of less than 2 are competitive while those with deviations of more than 7 are considered inferior (Burnham and Anderson 2002). Likelihood ratio tests (LRT) were used to compare the population density models to the null model for density, N ($N \sim 1$). P values were calculated from the chi-square distribution.

Additional analyses accounted for potential spatial and phylogenetic autocorrelation using spatially autoregressive models and generalized-least squares regressions, respectively (Appendix B). Accounting for phylogeny is informative because most potential data biases (e.g., foraging strategy, diet, thermal physiology, morphology, sampling method) are phylogenetically conserved. We additionally analyzed whether foraging mode (searching or waiting predation) or diet (carnivorous or herbivorous/omnivorous) influence densities. We used phylogeny to assign foraging mode (Vitt and Pianka 2005) and data from the literature to assign diet (Appendix A).

RESULTS

We first evaluate how rates of energy use covary with lizard population densities. The density of lizards (no. lizards/ha) scales as a power law of mass (Fig. 1; least-squares model, $F_{1, 480} = 193.7$, $P < 1 \times 10^{-15}$, $r^2 = 0.29$). The slope (-0.63 ± 0.08 [mean $\pm$ 95% CI]) is significantly shallower than that anticipated if metabolic costs are the primary determinant of density and scale proportionally to $M^{-3/4}$. However, smoothing splines reveal that the slope shallows for masses greater than approximately 55 g. The density of species less than 55 g scales with the $-3/4$ slope predicted by metabolic theory (-0.75 ± 0.16, $F_{1, 418} = 86$, $P < 1 \times 10^{-15}$, $r^2 = 0.17$). This trend is consistent with larger species eating at a lower trophic rank on average and thus having the potential to reach higher population densities (Pough 1973). While only 5.9% of lizards in the database are herbivorous (or omnivorous), 35.5% of those with masses greater than 55 g are herbivorous (or omnivorous). Plant-eating lizards have significantly higher densities when diet is included as a factor along with mass ($N_{herb} \approx 2.45 \, N_{carn}$, $F_{2, 479} = 106.7$, $P < 1 \times 10^{-15}$, $R^2 = 0.31$). In this ANCOVA, the scaling slope is indistinguishable from $-3/4$ and the slopes are indistinguishable between diet classes. Among carnivores (including omnivores), whether the lizard is an active or waiting forager is not a significant determinant of density. Fig. 1 suggests a

[5] ⟨http://rweb.stat.umn.edu/R/library/stats/html/lm.html⟩

TABLE 1. Model coefficient estimates and fits for maximum-likelihood models explaining lizard population density (N, no. lizards/ha) as a function of body mass (M), metabolic costs (BX, where $B0$ incorporates the crudest, and $B3$ the most refined environmental temperature data), and minimum productivity (P_{min}).

| | Predicted | | Observed [estimate (SE)] | | | | |
Model	α_1	α_2	α_1	α_2	ΔAIC	I	r^2
A) Energetic use models							
M	−0.75		−0.63 (0.04)		161.4	0.23	0.29
$B0$	−1		−0.75 (0.06)		145.5	0.31	0.30
$B1$	−1		−0.80 (0.06)		162.2	0.27	0.30
$B2$	−1		−0.80 (0.06)		165.4	0.27	0.30
$B3$	−1		−0.80 (0.06)		173.7	0.26	0.31
B) Energetic use and availability models							
P_{min}		1		0.66 (0.07)	81.7	0.21	0.16
$M + P_{min}$	−0.75	1	−0.54 (0.04)	0.45 (0.06)	207.2	0.14	0.36
$B0 + P_{min}$	−1	1	−0.67 (0.05)	0.53 (0.06)	213.8	0.15	0.38
$B1 + P_{min}$	−1	1	−0.70 (0.05)	0.49 (0.06)	220.2	0.14	0.38
$B2 + P_{min}$	−1	1	−0.70 (0.05)	0.48 (0.06)	222.0	0.14	0.38
$B3 + P_{min}$	−1	1	−0.70 (0.05)	0.46 (0.06)	219.5	0.14	0.38

Notes: ΔAIC compares the AIC values for each nested model to the null model ($N \sim 1$) using likelihood ratio tests (LRT, ΔAIC = AIC$_{N \sim 1}$ − AIC). To illustrate, in the case of the energetic use and availability models, the models take the form $\log(N) = \alpha_1 \log(M) + \alpha_2 \log(P_{min})$ or $\log(N) = \alpha_1 \log(BX) + \alpha_2 \log(P_{min})$. All models are significantly better than the null model at $P < 0.001$. We used Moran's I tests to evaluate the spatial autocorrelation of the model residuals, with larger absolute values of I indicating higher spatial autocorrelation.

constraint on maximum population density (quantile regression slope for the 90% quantile = −1.09 ± 0.24).

Adding the effect of environmental temperature on metabolic rate and using sequentially more refined temperature measures only slightly improves the energetic models' abilities to predict densities (Table 1A). Incorporating a simple exponential effect of annual temperature ($B0$) does not predict densities as well as mass alone. Including environmental temperature does not significantly improve the explanatory power of the model until accounting for the diurnal temperature trend and activity period ($B3$; LRT = 7.1, $P < 0.01$). The scaling of B with population density is stable at −0.80 ± 0.12 and 29–31% of variation in population density is accounted for when metabolic costs are modeled using $B1$, $B2$, or $B3$. These slopes are significantly shallower than the slope of −1 that is anticipated if energetic needs fully account for density trends.

We next scrutinize this weak effect of environmental temperature. Controlling for the effect of body mass using either the observed or 3/4 scaling confirms that the temperature dependence of energetic needs has little explanatory power (slope = 2.2 ± 1.2 for 3/4 scaling, $F_{1, 479}$ = 3.2, $P < 0.1$). The relationship between mass-adjusted density and the inverse of temperature is highly scattered (Fig. 2). Minimum productivity (P_{min}) accounts for the scatter in the model residuals to a small degree (slope = 0.39 ± 0.12 for 3/4 scaling, $F_{1, 480}$ = 39.9, $P < 1 \times 10^{-9}$, r^2 = 0.07).

We finally assess whether additionally considering energy availability better accounts for densities. We evaluate three covariate proxies of energy availability (annual precipitation, annual net primary productivity, and minimum annual net primary productivity). While all three metrics account for similar amounts of density

variation, we use minimum productivity (P_{min}) to evaluate how body mass, temperature, and productivity combine to influence lizard densities as it reflects the annual bottleneck of energy availability. Minimum productivity, P_{min}, alone is a weak but significant density predictor (Table 1B, slope = 0.66 ± 0.14, $F_{1, 480}$ = 91.0, $P < 1 \times 10^{-15}$, r^2 = 0.16). Mass-adjusted density increases with P_{min} (slope = 0.41 ± 0.12, $F_{1, 480}$ = 45.0, $P < 1 \times 10^{-10}$, r^2 = 0.08).

In our database, population densities are more strongly influenced by total environmental resource availability than by the resource use of sympatric lizard species. When we analyze studies of entire lizard assemblages and include total energy use by sympatric lizard species ($\Sigma B2$, kJ·ha^{-1}·yr^{-1}) as a covariate, energy use by sympatric lizards has less influence on lizard population density than productivity (P_{min}). We do not find evidence that resource competition with other lizards constrains lizard population density. Rather, both lizard population density and the total energy use by other lizard species in the community increase with increasing total resource availability. In the model including population energy use, $B2$, and energy availability, P_{min}, the slope of the relationship between community energy use and lizard population density is weak but positive (slope = 0.11 ± 0.04, $F_{3, 251}$ = 24.6, $P < 0.01$, r^2 = 0.23).

Considering both energetic needs and availability [$N \sim M + P_{min}$, which statistically was fitted as $\log(N) = \log(M) + \log(P_{min})$ and corresponds to the predicted energetic model $N \propto P_{min}/M^x$] has substantially more predictive power than considering energetic needs alone ($N \sim M$; LRT = 23.9, $P < 1 \times 10^{-5}$). In contrast to our previous models not accounting for energy availability, $B0$ is a better predictor than mass, M, in multi-predictor
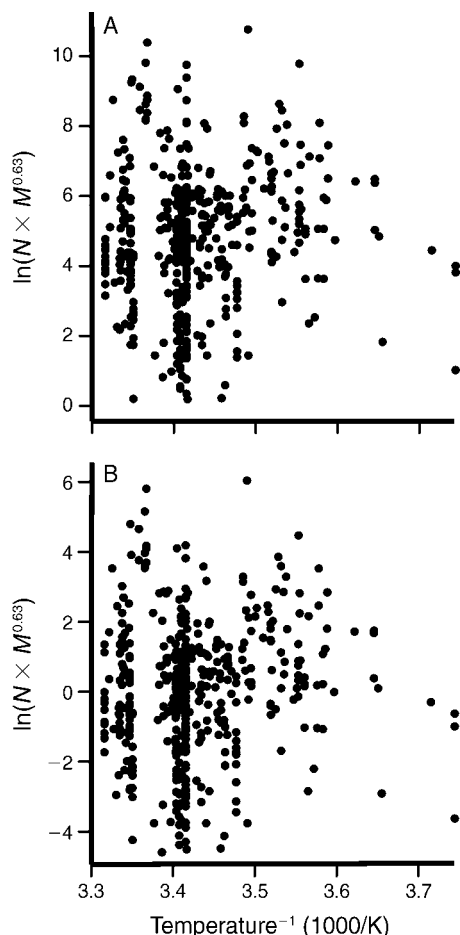
FIG. 2. Effect of the inverse of average annual ambient temperature (Kelvin) on the natural logarithm of mass-corrected lizard population density, $N \times M^x$ (where population density N is in units of lizards/ha, and mass M is in grams): (A) $x = 0.75$; (B) $x = 0.63$.

models including productivity (Table 1B). The best fitting model incorporates the diurnal temperature trend ($N \sim B2 + P_{min}$) and accounts for 38% of the variation in lizard population densities ($F_{2, 479} = 142.6$, $P < 1 \times 10^{-15}$). The energetic need effect ($B2$) has a slope of -0.70 ± 0.10, while that corresponding to energy availability (P_{min}) has a slope of 0.48 ± 0.12 (for individual contributions, see Fig. 3).

The regressions presented so far show relatively weak, but significant, spatial as well as phylogenetic autocorrelation (Appendix C). The multi-predictor models tend to have less autocorrelation, suggesting unobserved variables as the source of autocorrelation. Incorporating a spatially dependent error term substantially improves the explanatory power of the models (AIC) and succeeds in reducing the degree of spatial autocorrelation. Accounting for phylogenetic correlation improves the explanatory power of the models (AIC) only to a small degree. The major foraging strategy and diet divergence between the Iguania (primarily sit-and-wait foragers)

and Scleroglossa (primarily searching foragers [Vitt and Pianka 2005]) clades does not influence the scaling of energy use and supply. The coefficients for the spatial and phylogenetic models are similar, if somewhat lower, than the corresponding coefficients for the uncontrolled models. Thus, the scaling relationships between energy use and availability and lizard densities are robust to spatial and phylogenetic autocorrelation.
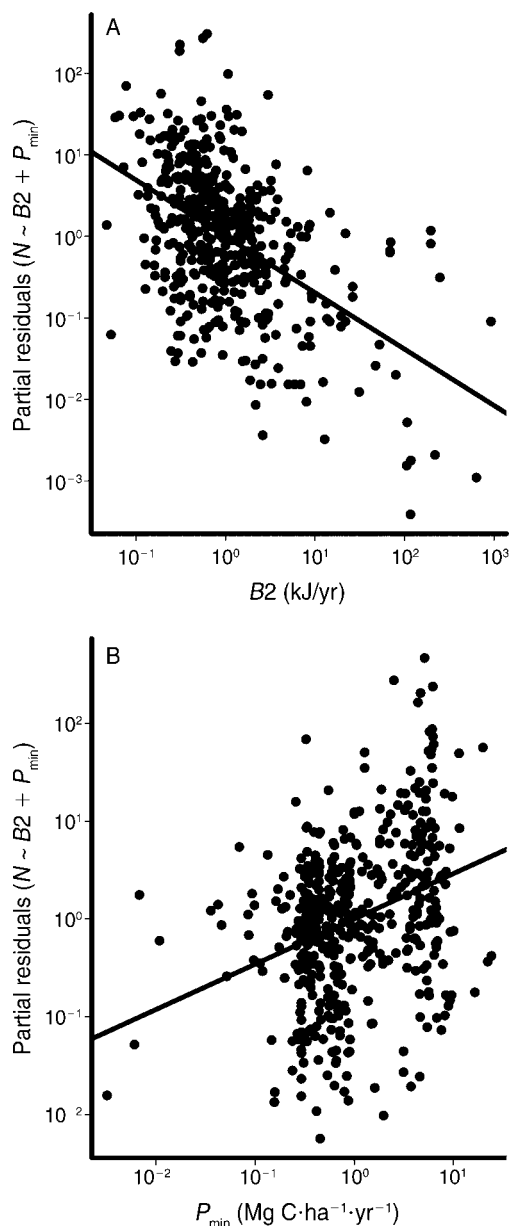

FIG. 3. Partial residual plots, including the partial fit, for the model $N \sim B2 + P_{min}$, which statistically was fitted as $\log(N) = \log(B2) + \log(P_{min})$. Partial residuals are plotted for (A) annual metabolic costs, $B2$ (calculated by summing over each hour of an average day of each month, partial $R^2 = 0.25$), and (B) three-month minimum annual net primary productivity, P_{min} (partial $R^2 = 0.11$).

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DISCUSSION

We showed that lizard population densities covary with mass-dependent individual energetic needs. Populations of species with masses below 55 g exhibit approximate energetic equivalence with respect to body mass. This finding augments the evidence for widespread energetic equivalence that has been gathered for taxa including plants, birds, and mammals (Damuth 1981, 1987, Marquet et al. 1990, Nee et al. 1991, Enquist et al. 1998). The observed slope across all populations (−0.63 ± 0.08) is shallower than the −3/4 scaling predicted by metabolic theory. The lesser slope is consistent with herbivorous lizards reaching higher abundances and tending to have larger body sizes (Pough 1973). Analogously, Damuth's (1987) found a statistically indistinguishable slope but higher intercept for mammalian herbivores compared to other mammal groups. Subsequent analyses of an extended dataset suggest that the slope for mammalian carnivores may be steeper (Marquet 2002), but that this steeper slope results from reduced prey availability for larger mammalian carnivores (Carbone and Gittleman 2002).

While individual energetics are a significant determinant of lizard population densities, the scatter in the relationship demonstrates that factors other than energetics reduce population densities below the levels that would be energetically permissible. Ecological factors including competition, predation, and life histories are the primary potential origins of density variation (as has been extensively documented on islands [e.g., Buckley and Jetz 2007]). However, competition does not emerge as a strong predictor of mainland lizard densities. While competition between lizard species inevitably constrains lizard density at many sites, it is not a ubiquitous effect for the lizard assemblages in our database. Other taxa (e.g., birds) may be stronger competitors for insect prey than other lizards. Temporal variability is unlikely to contribute substantially to the scatter in the lizard density relationship because lizard populations are markedly constant through time (mean SD of $\ln(N) = 0.29$, median $= 0.21$, $n = 29$ populations [Schoener 1985]).

Our results reject a strong influence of environmental temperature on lizard population densities. For lizards, there is no empirical support for a direct link between environmental temperature and ectotherm abundance, which underlies the metabolic explanation of broad-scale gradients in richness proposed by Allen et al. (2002, see Algar et al. [2007] for an assessment of metabolic explanations of reptile richness). This may be due to the lack of a mechanistic connection between body temperature, metabolic rate, and abundance; methodological limitations in assessing environmental temperature; or behavioral thermoregulation and thermal adaptation. The home ranges of lizards are substantially smaller than the spatial resolution of our temperature data (10′), which may obscure temperature's effect. Behavioral thermoregulation can effectively maintain preferred body temperatures (Hertz et al. 1993) such that temperature primarily influences net energetics through determining an ectotherm's activity window (Adolph and Porter 1993). If thermoregulation is prevalent, temperature would be expected to exert a greater influence on reptile distributions than densities (e.g., Kearney and Porter 2004). This suggests a potential decoupling of animal density and diversity that is inconsistent with the "more individuals" theory for diversity gradients (Currie et al. 2004).

Our observation of a weak influence of environment temperature on population density is despite considering diurnal and seasonal temperature fluctuations to better capture the potential energetic implications of environmental temperature. Additionally, regional environmental and historical differences can cause spatial autocorrelation and influence regression results. While spatial models of lizard density do reveal spatial autocorrelation, the influences of energy use and availability on lizard density are robust to autocorrelation. Model comparisons do suggest that nonspatial models overestimate the magnitude of scaling coefficients. However, non-perfect determination of the connectivity matrix and missing autocorrelated predictor variables may depress the magnitude of coefficients (Haining 2003). Hence, the spatial model coefficients should not provide a basis for rejecting a metabolic explanation for density scaling.

Density scales with productivity (P_{min}) with a slope significantly less than one for both bird communities and lizard populations, indicating a non-linear relationship between annual productivity and density (lizard slope for $N = 0.66 ± 0.14$; bird slope for $\Sigma N = 0.61 ± 0.19$ [Meehan et al. 2004]). Measurement error in productivity may depress the slopes (Frost and Thompson 2000). However, the decelerating relationship between productivity and density suggests that resource availability for particular groups of organisms is not directly proportional to annual production or that units of resources do not translate directly into increased population densities. Increased diversity and abundance of competitors may decrease the fraction of resources available to a single group of organisms in more productive environments (Currie 1991). The presence of predators may also increase with productivity (Post 2002).

Our database adds to the growing support of a strong role for individual energetics in constraining population densities (Currie and Fritz 1993). Our findings provide support for the balance of energy use and supply constraining ectotherm densities, but demonstrate that environmental temperature only weakly influences ectotherm density. This puts into question a simple metabolic explanation for ectotherm abundance and diversity gradients and calls for increasingly mechanistic modeling of temperature's influence on ectotherms at broad spatial scales. Extensions of these sorts of broadscale models may prove to be important tools for reserve design and conservation decision-making.

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APPENDIX A

Additional database methods (*Ecological Archives* E089-005-A1).

APPENDIX B

Additional methods for spatial and phylogenetic analysis (*Ecological Archives* E089-005-A2).

APPENDIX C

Results of maximum-likelihood models controlling for spatial and phylogenetic autocorrelation (*Ecological Archives* E089-005-A3).

APPENDIX D

Database literature sources (*Ecological Archives* E089-005-A4).

Reports