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PAPER

Are lizards feeling the heat? A tale of ecology and evolution under two temperatures

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ABSTRACT

Aim Temperature influences most components of animal ecology and life history – but what kind of temperature? Physiologists usually examine the influence of body temperatures, while biogeographers and macroecologists tend to focus on environmental temperatures. We aim to examine the relationship between these two measures, to determine the factors that affect lizard body temperatures and to test the effect of both temperature measures on lizard life history.

Location World-wide.

Methods We used a large (861 species) global dataset of lizard body temperatures, and the mean annual temperatures across their geographic ranges to examine the relationships between body and mean annual temperatures. We then examined factors influencing body temperatures, and tested for the influence of both on ecological and life-history traits while accounting for the influence of shared ancestry.

Results Body temperatures and mean annual temperatures are uncorrelated. However, accounting for activity time (nocturnal species have low body temperatures), use of space (fossorial and semi-aquatic species are ‘colder’), insularity (mainland species are ‘hotter’) and phylogeny, the two temperatures are positively correlated. High body temperatures are only associated with larger hatchlings and increased rates of biomass production. Annual temperatures are positively correlated with clutch frequency and annual longevity, and negatively correlated with clutch size, age at first reproduction and longevity.

Main conclusions Lizards with low body temperatures do not seem to have ‘slower’ life-history attributes than species with high body temperatures. The longer seasons prevalent in warm regions, and physiological processes that operate while lizards are inactive (but warm enough), make environmental temperatures better predictors of lizard life-history variation than body temperatures. This surprisingly greater effect of environmental temperatures on lizard life histories hints that global warming may have a profound influence on lizard ecology and evolution.

Keywords

Body temperature, diel cycle, environmental temperature, global warming, life history, lizards, thermal biology.

INTRODUCTION

Animal fitness is greatly influenced by temperature acting on ecological and life-history traits (Angilletta, 2009). Temperature has, therefore, increasingly been recognized as a major factor driving multiple aspects of animal ecology, physiology and evolution (Avery, 1982; Adolph & Porter, 1993). For example, the metabolic theory of ecology stresses that temperature, through its effect on metabolic rates, greatly influences virtually all life-history attributes of organisms (e.g. Brown *et al.*, 2004) and therefore has an enormous impact on ecological and evolutionary dynamics. Temperature affects most components of lizard ecological and reproductive performance, such as sprint speed, metabolic rate, foraging, fecundity and survival (e.g., Van Damme *et al.*, 1989, 1991; Niewiarowski & Waldschmidt, 1992; Pafilis *et al.*, 2007; Angilletta, 2009).

The influence of temperature on ecological and evolutionary processes has traditionally been investigated through two different approaches: while physiologists tend to study body temperatures of active animals, biogeographers and macroecologists mostly focus on environmental temperatures. Thus, for example, ambient temperatures are often closely correlated with lizard species richness (Schall & Pianka, 1978; Currie, 1991, cf. Powney *et al.*, 2010). Indeed, Hawkins *et al.* (2003) identified lizards as the only group of organisms in which measures of ambient energy are usually the strongest correlates of richness. The use of environmental temperatures, such as mean annual temperature, probably partly stems from an assumption (rarely made explicit) that the two measures are strongly and positively correlated. Buckley *et al.* (2008), for example, used environmental temperatures to model lizard densities, assuming that these temperatures reflect body temperatures. They modelled the thermal environment based on environmental temperatures and day length, assuming that 'lizards are active for three-quarters of the daylight period'. Such an inclusive model may, however, be inappropriate for actively thermoregulating lizards, and particularly for nocturnal species.

We use a large-scale, phylogenetic comparative approach to characterize the environmental and body temperatures of lizards and amphisbaenians (henceforth 'lizards'). We examine the relationship between annual temperatures and body temperatures, as well as ecological factors that affect this relationship. Finally, we test which of these two temperature measures better explain lizard life-history attributes.

Factors affecting body temperatures

Herbivorous lizards are thought to maintain high body temperatures to facilitate microbe-assisted fermentation of plant material (Janzen, 1973). Some, therefore, assumed that herbivorous lizards cannot inhabit cold areas because they would be unable to achieve the high body temperatures required for plant digestion (King, 1996). Nevertheless, in some of the coldest areas inhabited by reptiles, *Liolaemus* lizards have repeatedly evolved herbivory by successfully maintaining high body temperatures (Espinoza *et al.*, 2004; Pincheira-Donoso *et al.*, 2008).

Fossorial lizards are thought to have low body temperatures (e.g. Withers, 1981) because they cannot readily increase their body temperature by basking (Avery, 1982). Similarly, because of the high thermal conductance of the aquatic environment, we expect semi-aquatic species to have low body temperatures (Mesquita *et al.*, 2006). Finally, islands often harbour fewer predators. Therefore lizards can spend more time basking without fear of predation, and thus thermoregulate more effectively, and reach higher body temperatures (Case, 1982).

Temperature and lizard life history

High body temperatures are thought to enhance reproduction, because lizard metabolic rates increase with temperature over most of the temperature range at which they are active (Huey *et al.*, 1989; Angilletta *et al.*, 2010). High environmental temperatures are also associated with longer diel and annual periods of activity that facilitate higher energy intake through prolonged foraging (Bueno & López-Urrutia, 2012). Tropical lizards are, therefore, usually active year-round, and can produce multiple clutches each year (Fitch, 1970; Cox *et al.*, 2003; Meiri *et al.*, 2012). In contrast, cold-climate lizards may be active only during summer (as little as 4 months in northern populations of *Zootoca vivipara*, for example; Szczerbak, 2003). They may also be active for relatively short periods of the diel cycle, and can thus usually lay a single annual clutch – or less (Meiri *et al.*, 2012).

The size of a single brood may increase with decreasing environmental temperatures (Ricklefs, 1980; Jetz *et al.*, 2008). Lower temperatures may be associated with a higher productivity pulse (Huston & Wolverton, 2011), enabling high-latitude species to invest more in a single clutch. Furthermore, the lower climatic predictability and high winter mortality associated with low temperatures may select for large clutches (Evans *et al.*, 2005). Increasing clutch size with decreasing temperature can also result from fecundity selection to compensate for reduced opportunities for reproduction (Pincheira-Donoso & Tregenza, 2011).

We therefore test the following predictions: (1) because lizards thermoregulate actively, their body temperatures are less variable than mean annual temperatures – but the two temperature measures are nonetheless positively correlated; (2) diurnal, herbivorous, surface-active and insular lizards have higher body temperatures than nocturnal, carnivorous, semi-aquatic or fossorial and continental species; (3) temperatures greatly affect lizard life history: high body and environmental temperatures are associated with fast growth to maturity, short life span, oviparity, fast brooding rates, relatively few, large hatchlings and overall high rates of biomass production.

METHODS

Data

We collated a dataset of 861 species belonging to 36 of the 42 families of lizards from across the globe (Appendix S1 in

Supporting Information). Lizard body temperatures, life-history and natural-history traits were obtained from published sources and in the field. Taxonomy follows the reptile database (<http://www.reptile-database.org>, accessed 2 May 2012). Body temperatures are mean temperatures of active individuals recorded in the field. The number of individuals observed, when reported, varied between one (e.g. *Ophiomorus latastii*; S.M., unpublished) and 1848 (*Aspidoscelis tigris*; Pianka, 1986). Although these numbers can be small, they are unlikely to be systematically biased, and we therefore used all available data. We excluded preferred temperature data because the correlation between field body temperatures and preferred temperatures is often weak (e.g. Kohlsdorf & Navas, 2006) and biased (i.e. has a non-zero intercept and a slope different from one). We further excluded temperatures of animals known to be inactive when measured (e.g. nocturnal species in their diurnal retreats). If multiple temperature data were available for a species, we averaged the highest and lowest mean values.

We mapped lizard distributions using data in the scientific literature, field guides, IUCN reports, museum databases and our own observations (see <http://www.campusteva.tau.ac.il/campusen/?cmd=workshops.1595>). We then determined the average mean annual temperature within $0.16^\circ \times 0.16^\circ$ grid cells across the range of each species using the climatic data in Hijmans *et al.* (2005). Annual means are more reasonable to use in tropical environments than in temperate ones, because in the latter lizards are not generally active year-round. Furthermore, annual means probably overestimate the temperatures experienced by nocturnal species and underestimate those encountered by diurnal ones. That said, estimating the exact activity period of different species across their geographic ranges throughout the year and across the 24-h cycle (as well as interactions between these factors) is impractical.

We controlled for the effects of body size by using species-specific body mass as a covariate in all analyses. Mass was calculated from maximum snout–vent length (SVL), the most common proxy for body size in lizards (Meiri, 2008), using equations developed by Pincheira-Donoso *et al.* (2011; for Liolaemidae), Novosolov *et al.* (2013; for different gecko families and for *Anolis*) and Meiri (2010; for all other lineages). Weights of legged anguids were calculated using the equation $\log \text{mass} = 3.48 \times \log (\text{SVL}) - 5.765$ (Appendix S2).

For life-history analyses we used mean SVL of adult females, rather than maximum species SVL, as a measure of adult size. In highly dimorphic species males are often larger, but reproductive characteristics such as clutch size and hatchling size are, nonetheless, more likely to be influenced by female rather than by male size. In some cases female and hatchling SVL were unavailable so we used published mass data instead. If neither data type was available we used mean SVL of unsexed adults. Species which we suspected (based, e.g. on maximum SVL) are highly sexually dimorphic were omitted. We classified lizards as carnivores (> 90% animal food by volume), omnivores (50–90% animal food) or herbivores (> 50% plant food). Reproductive mode was classified as ‘viviparous’ or ‘oviparous’. We treated ovoviviparous species as viviparous, because we are interested in

whether gravid females retain their young in the oviduct during pregnancy or whether they lay eggs that are exposed to environmental temperatures. Species that have both oviparous and viviparous populations were classified according to the characteristics of the population for which body temperature was measured. In a preliminary analysis, we found no significant differences between the thermal responses of different categories of surface-active lizards (i.e. terrestrial, arboreal and saxicolous; results not shown), and we therefore examined microhabitat use in three elements: air (the three categories outlined above and their combinations), water (semi-aquatic species) and earth (fossorial species). We find this a particularly appropriate categorization to examine Kleiber’s (1961) ‘fire of life’ (i.e. an animal’s metabolic rate). To examine the effects of activity periods we divided lizards into diurnal, cathemeral (active both day and night) and nocturnal. We did not have sufficient species-specific data to classify diurnal species as heliotherms or shade-loving species. The life-history traits we examined were clutch/litter size, hatchling/neonate size, clutch/litter frequency (per year) and their product (‘productivity’; see Meiri *et al.*, 2012), as well as mean age at sexual maturity and maximum longevity. We used mean values for all continuous variables when available. If more than one mean was available for a species, we averaged the highest and lowest mean values.

Analyses

We \log_{10} -transformed masses, clutch size, brood frequency, productivity, age at first breeding and longevity to comply with the assumptions of parametric tests. We used multiple regression and analyses of covariance to test the various hypotheses, as appropriate. To examine, and correct for, the potential effects of phylogenetic relatedness between species, we assembled a composite species-level phylogeny (Appendix S3) from published phylogenetic trees, following the broad-scale squamate tree of Wiens *et al.* (2010).

Because branch lengths were often lacking, or not always easily comparable, we scaled branches to make the tree ultrametric using the cladogram transformation in FIGTREE (Rambaut, 2010). All analyses were then duplicated to account for phylogenetic non-independence by using phylogenetic generalized least square (PGLS) regression, adjusting the strength of phylogenetic non-independence using the maximum likelihood value of the scaling parameter λ (Pagel, 1999) implemented in the R package caper (Orme *et al.*, 2012). Pagel’s λ is a multiplier of the off-diagonal elements of the variance–covariance matrix, which provides the best fit of the Brownian motion model to the tip data, and ranges between zero (no phylogenetic signal) and one (phylogenetic signal that depends on branch lengths, as in analysis of phylogenetically independent contrasts). All analyses were carried out using R version 2.14.0.

We examined the relationship of life-history characteristics versus body and environmental temperatures. We tested each relationship three times: (1) directly (‘non-phylogenetic’ models); (2) correcting for phylogeny using Pagel’s λ ; and (3)

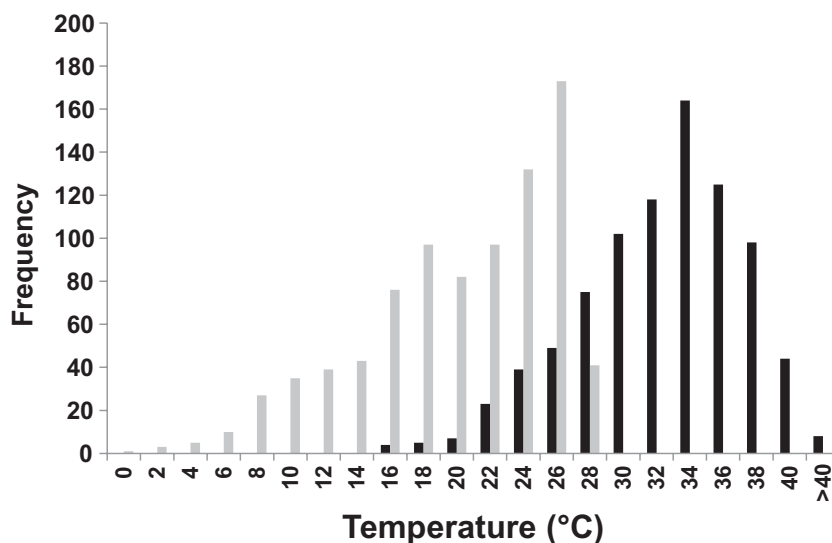


Figure 1 Frequency distribution of mean annual temperatures (light grey) and lizard body temperatures (black).

with family as a fixed effect. The latter analysis serves to highlight the thermal regimes of different clades, rather than treat clade effects as only a factor that needs to be corrected for. We report means ± 1 standard deviation and used a significance level of 5% in all tests.

RESULTS

Our dataset (Appendix S1) covers much of the variation in mean annual environmental temperatures experienced by lizards: in our dataset values range from 0.0 °C for *Zootoca vivipara* to 27.7 °C for *Anolis taylori* (mean = 19.0 ± 5.8 °C). Across all lizards for which we have geographic data (i.e. not only those for which we had body temperature data, $n = 4608$), the corresponding figures are -3.6 °C (*Phrynocephalus lidskii*) to 29.8 °C (*Hemidactylus bavazzanoi*), with a mean of $= 20.9 \pm 5.3$ °C. The body temperatures of lizards we analyse range from 14.95 °C in *Pachydactylus rangei* to 44.3 °C in *Diporiphora bilineata* (mean 31.4 ± 4.9) (Appendix S1).

In general, body temperatures of active lizards are higher than mean annual temperatures in their environment: body temperatures of only 25 of 861 species (2.9%) are lower than their respective mean annual environmental temperatures. Of these species, 18 are tropical, and 11 (including all seven temperate zone species) are nocturnal (Appendix S1). The average lizard body temperature is 12.4 °C higher than the average mean annual temperature. While body temperature range is similar to environmental temperature range (29.4 vs. 27.8 °C), the coefficient of variation for the former (15%) is less than half that of the latter (31%; Fig. 1).

There are differences between lineages in body temperatures: mainly diurnal families such as teiids, phrynosomatids, iguanas, agamas, lacertids and monitors have high body temperatures (all > 33.5 °C), while mainly nocturnal and burrowing families such as amphisbaenians and gecko lineages have low temperatures (≥ 29 °C; Appendix S4).

Modelling lizard body temperatures

By themselves, body and environmental temperatures are uncorrelated (slope = 0.039 ± 0.029 , $t = 1.34$, $P = 0.18$, $n = 861$, Fig. 2). After correcting for the effects of body size, habitat, activity time and insularity (but not diet, $F = 2.24$, $P = 0.11$), however, body and environmental temperatures are significantly and positively correlated (slope: 0.13 ± 0.03 body temperature degree per environmental temperature degree). Body temperatures increase with body mass (slope 1.10 ± 0.19 , $P < 0.0001$); semi-aquatic and fossorial lizards have lower body temperatures than surface-active species (by 4.8 and 1.8 °C, respectively; $n = 861$). In this model omnivorous and herbivorous lizards have higher body temperatures than carnivorous ones (see Appendix S5 for further statistical details).

Diurnal lizards ($n = 718$) have higher body temperatures than nocturnal lizards ($n = 89$; mean 32.5 ± 4.2 vs. 25.1 ± 4.6 °C, $t = 15.3$, $P < 0.0001$; cathemeral species, 27.8 ± 4.2 , $n = 54$), even though they inhabit colder environments (18.8 ± 6.0 vs. 20.5 ± 4.3 °C, $t = 2.6$, $P = 0.009$; cathemeral species, 19.9 ± 3.8 °C; Fig. 3). Insular lizards are 'colder' than mainland species by 2.4 °C ($P < 0.0001$). This model explains 32.6% of the variation in lizard body temperatures, whereas a similar model lacking environmental temperature data explains 30.5% of that variation. Interestingly, in this model, body temperatures of diurnal lizards increase with annual temperatures more gradually (slope = 0.091 ± 0.026), than body temperatures of cathemeral and nocturnal lizards (slopes = 0.549 ± 0.144 and 0.499 ± 0.100 , respectively; $P < 0.001$ in all cases, Fig. 4).

After accounting for phylogenetic relationships, body temperatures are positively, albeit weakly, correlated with mean annual temperatures (slope = 0.15 ± 0.03 , $t = 5.3$, $P < 0.0001$, $n = 861$, $R^2 = 0.03$). Adding the abovementioned factors, mass and diet drop out of the model ($P = 0.89$ and 0.60 , respectively), but the effects of microhabitat (semi-aquatic versus above ground only) and activity time remain. Insularity is marginally non-

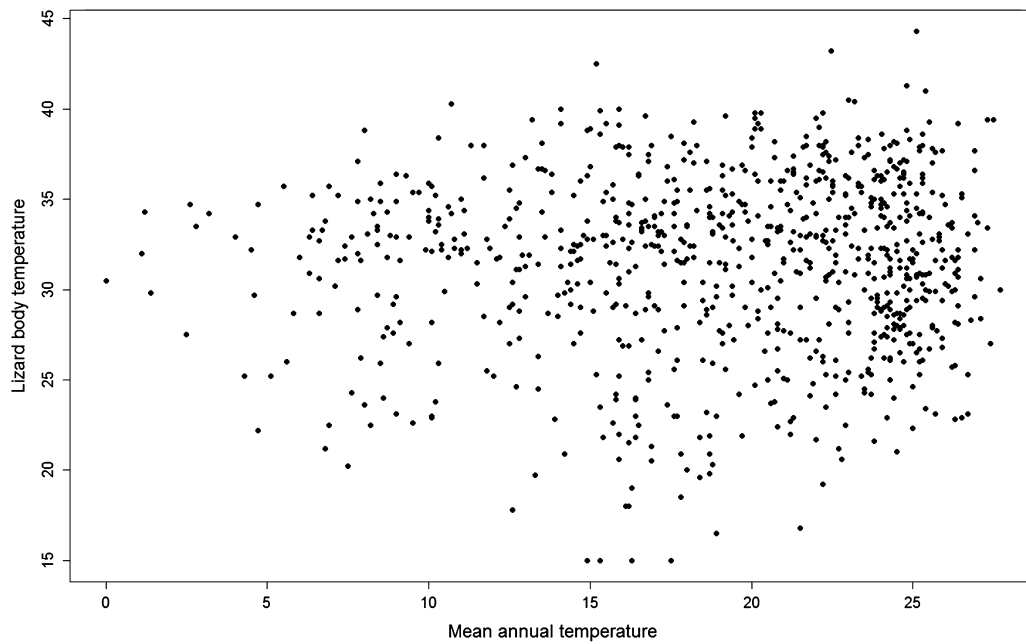


Figure 2 Mean annual environmental temperatures and body temperatures (°C) across lizard species.

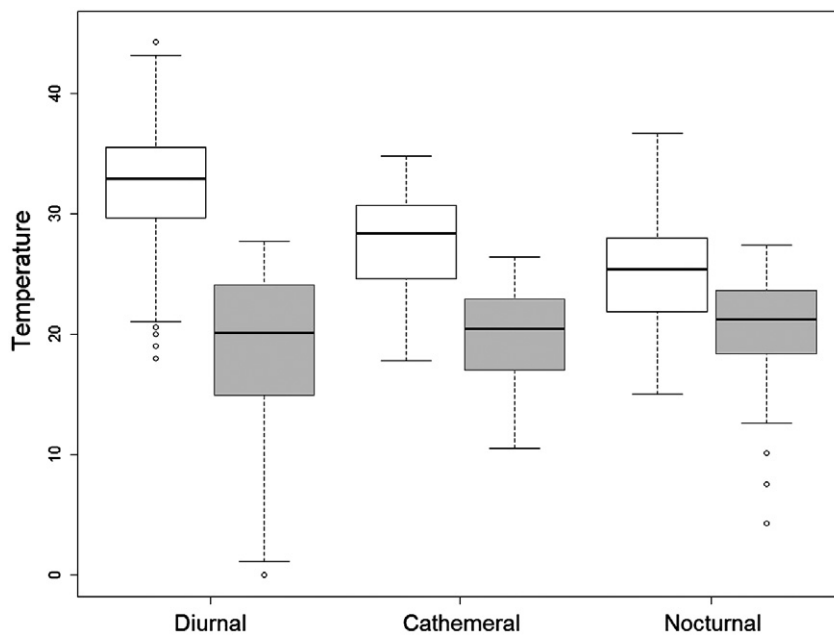


Figure 3 Body (white) and mean annual environmental (grey) temperatures (°C) of diurnal, nocturnal and cathemeral lizards. The box shows the median (horizontal bar) and interquartile range, whiskers are 1.5 times the interquartile range. More extreme values are presented outside of the whiskers.

significant ($P = 0.057$). The best model now explains only 8.4% of the variation in lizard body temperatures.

By partially accounting for phylogeny by using family as a factor, rather than as a nuisance variable as in the PGLS, more variance is explained: familial affiliation alone explains 50.3% of the variance in lizard body temperatures. The minimum adequate model for body temperatures includes family, annual temperature (slope 0.213 ± 0.026), activity time (nocturnal species are 'colder' than diurnal ones by 4.8 ± 0.7 °C) and insularity (insular endemics 'colder' by 1.8 ± 0.3 °C), but neither diet ($F = 0.3$, $P = 0.78$, $n = 861$) nor body size (slope = $-0.06 \pm$

0.22 , $P = 0.80$). This model explains 57.1% of the variation in body temperatures, whereas a similar model without annual temperatures explains 53.9% of that variation.

The effects of temperature on lizard life history

Oviparity and viviparity

Viviparous lizards ($n = 174$) live, on average, at environmental temperatures fully 5.5 °C colder than oviparous species ($n = 678$, 14.6 vs. 20.1 °C, respectively). Their body temperatures,

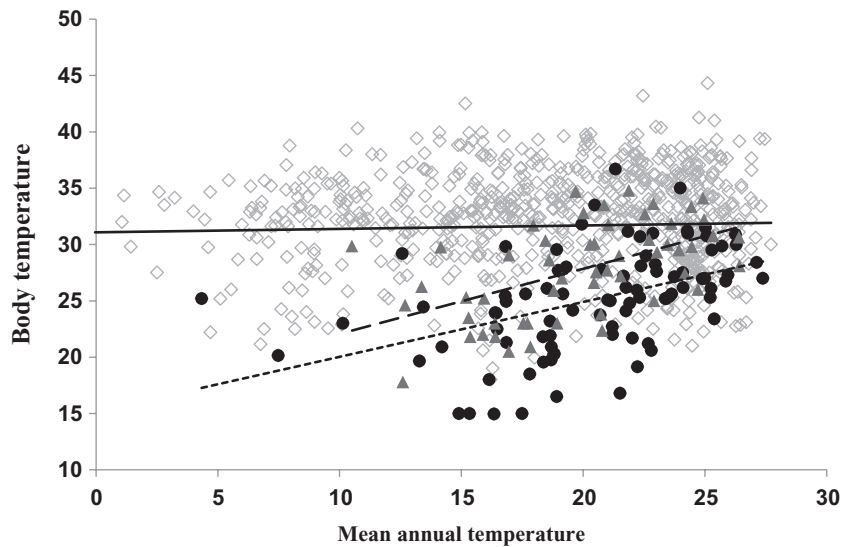


Figure 4 Mean annual environmental temperatures and body temperatures (°C) of diurnal (white diamonds, solid line), nocturnal (black circles, short dash) and cathemeral (grey triangles, long dash) lizards.

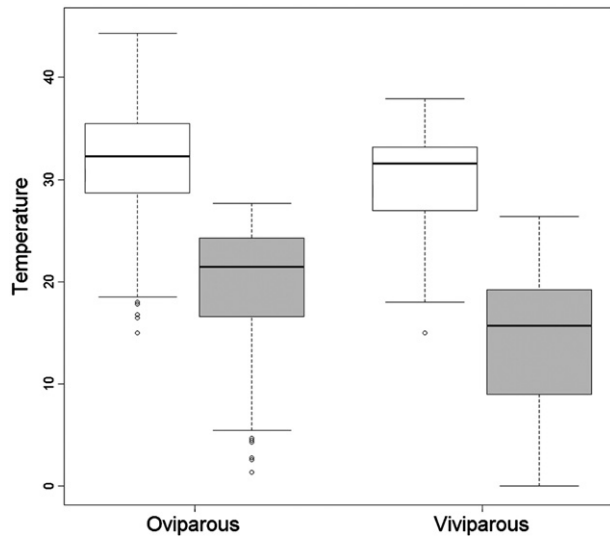


Figure 5 Differences in body (left) and mean annual environmental (right) temperatures (°C) of oviparous and viviparous lizards. The box shows the median (horizontal bar) and interquartile range, whiskers are 1.5 times the interquartile range. More extreme values are presented outside of the whiskers.

however, are only 1.9 °C colder, on average (29.9 vs. 31.8 °C, the median body temperature is only 0.8 °C colder, 31.5 vs. 32.3 °C; Fig. 5; $P < 0.001$ in both tests).

The average differences between mean annual temperatures encountered by egg- and live-bearing species varies among lizard clades. In some taxa (e.g. Scincidae, Phrynosomatidae) the differences are relatively minor, whereas in others (Agamidae, Lacertidae) they are profound (Table 1). This difference is negatively correlated with the (log-transformed) proportion of viviparous species in each family (Fig. 6, $n = 13$ families, $R^2 = 0.58$, $P = 0.003$). In clades where viviparous species

inhabit much colder areas than oviparous species viviparity is rare.

Growth, longevity and reproduction

The relationships between temperature and life-history variables are shown in Table 2. Values of λ ranged from 0.51 for longevity to 0.87 for brood frequency, and were significantly different from both 0 and 1 at the 0.0001 level in all cases. Higher body temperatures are associated with larger offspring, and higher rates of biomass production ('productivity'). The association between high body temperatures and both lower age at first reproduction and large clutch sizes are supported only in non-phylogenetic models. Body temperature is not correlated with either brood frequency or with longevity (Table 2a).

Mean annual temperatures, however, have a much more pervasive effect, and are correlated with all response variables we examined, except with hatchling/neonate size (Table 2b). As expected, clutch frequency and productivity rates increase in hotter environments, whereas clutch size, age at first reproduction and longevity all decrease with increasing temperatures.

DISCUSSION

Body versus environmental temperatures

The body temperatures of active lizards are uncorrelated with the mean annual temperatures across their ranges. Lizards consistently achieve body temperatures that exceed environmental ones by efficiently thermoregulating. Some clades, however, show greater differences between body and environmental temperature than others.

Lizards inhabit regions with a wide range of environmental temperatures, but they hibernate in cold climates and are thus not exposed to the lowest temperatures. We found that nocturnal lizards inhabit warmer environments than diurnal ones. We

Family	<i>n</i>	Temperature: oviparous species	Temperature: viviparous species	% viviparous species
Agamidae*	239	21.1	9.0	2%
Amphisbaenidae	33	22.5	20.9	9%
Anguidae	63	19.8	19.4	60%
Chamaeleonidae*	147	22.0	17.4	22%
Cordylidae*	47	20.4	17.3	72%
Corytophanidae†	9	24.5	21.2	11%
Diplodactylidae*	78	22.3	12.4	9%
Lacertidae*	187	15.3	0.8	2%
Leiosauridae†	24	15.1	8.4	4%
Liolaemidae*	163	12.6	8.1	60%
Phrynosomatidae	111	19.5	19.1	32%
Scincidae*	758	22.4	18.8	30%
Xantusiidae**	16	24.5	19.8	88%

*Significant difference between temperatures of viviparous and oviparous species (*t*-tests, not shown).

***P* = 0.054.

†No significance testing was carried out because the family has just one viviparous species.

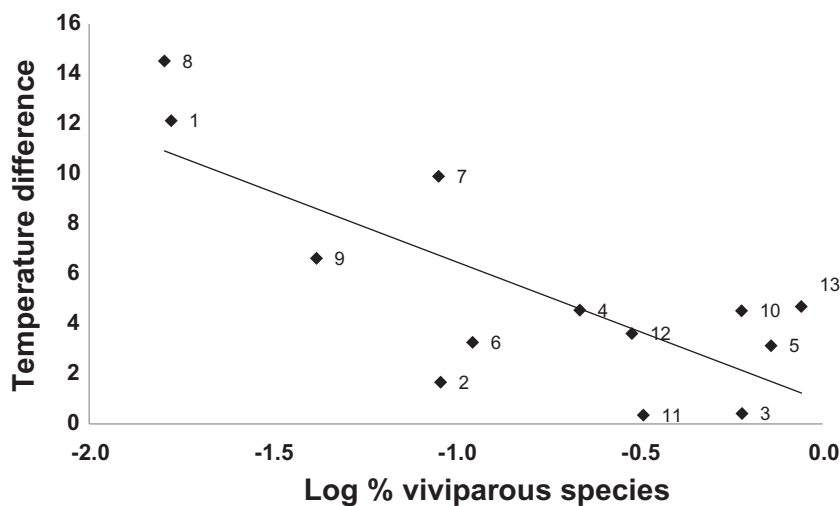


Table 1 Mean annual environmental temperatures (°C) encountered by viviparous and oviparous lizard species, and the percentage of viviparous species within families. The percentage of viviparous species and *n* are the number of species for which we have data on both reproduction and annual temperature in our entire dataset (S.M., unpublished; not in the dataset analysed here).

Figure 6 Relationship between the average difference in mean annual environmental temperatures of oviparous and viviparous members of a family (in °C), and the proportion of viviparous species in this family. Family codes: 1, Agamidae; 2, Amphisbaenidae; 3, Anguidae; 4, Chamaeleonidae; 5, Cordylidae; 6, Corytophanidae; 7, Diplodactylidae; 8, Lacertidae; 9, Leiosauridae; 10, Liolaemidae; 11, Phrynosomatidae; 12, Scincidae; 13, Xantusiidae.

posit that low night-time temperatures act as a biogeographic filter preventing the spread of nocturnal species into high latitudes and elevations that are nonetheless suitable for diurnal species. In keeping with this hypothesis, species of archetypal nocturnal lineages, such as geckos, sometimes evolve diurnal activity in cold regions (e.g. the New Zealand genus *Naultinus* and the High-Atlas Mountains' *Quedenfeldtia*).

The difference between our measure of environmental temperature, mean annual temperatures and the environmental temperatures at which lizards are active is probably greater in colder environments. In cold regions, lizards are almost invariably diurnal, and active only in summer. By taking night temperatures into account, mean annual temperatures probably underestimate the actual thermal preferences of diurnal lizards. The distribution of lizard body temperatures is highly modal, with a mode of approximately 34 °C (Fig. 1, interquartile range 28.4–34.9; 95% of the species have body temperatures between 20.6 and 39.3 °C). Although body temperatures are often corre-

lated with air temperatures in the field, they were uncorrelated with mean annual temperatures – a relationship that is found in mammals (which show an inverse relationship; Lovegrove, 2003).

Activity time

Activity time had the largest effect on lizard body temperatures (a difference of ca. 7.4 °C, on average, between diurnal and nocturnal species). Even among diurnal lineages, families consisting mainly of heliotherms (e.g. Lacertidae, Tropicuridae, Phrynosomatidae, Agamidae) were characterized by species having, on average, higher body temperatures than those with more shade-living species (e.g. Polychrotidae, Anguidae; Appendix S4). Fossorial lizards inhabit a colder medium than air (at least during the day), and have little opportunity to bask. Their thermoregulatory behaviour probably constitutes mainly vertical movement within the ground – towards higher, warmer levels

Table 2 The effects of temperatures on lizard life-history traits: (a) effects of body temperatures; (b) effects of mean annual environmental temperatures.

Trait	Model	<i>n</i>	Slope	SE	<i>R</i> ²	<i>P</i>
(a) Effects of body temperature						
Clutch frequency	Non-phylogenetic		0.004	0.003	0.09	0.120
	Family	490	0.005	0.003	0.60	0.088
	Phylogenetic		0.004	0.003	0.02	0.173
Clutch size	Non-phylogenetic		0.014	0.002	0.39	< 0.001
	Family	798	0.004	0.002	0.72	0.024
	Phylogenetic		0.002	0.002	0.19	0.266
Hatchling size	Non-phylogenetic		0.008	0.002	0.83	< 0.001
	Family	632	0.008	0.002	0.88	< 0.001
	Phylogenetic		0.009	0.002	0.69	< 0.001
Productivity	Non-phylogenetic		0.024	0.003	0.82	< 0.001
	Family	435	0.017	0.004	0.89	< 0.001
	Phylogenetic		0.019	0.004	0.73	< 0.001
Age	Non-phylogenetic		-0.010	0.003	0.37	0.002
	Family	251	-0.005	0.005	0.55	0.349
	Phylogenetic		-0.005	0.005	0.19	0.274
Longevity	Non-phylogenetic		-0.025	0.005	0.37	< 0.001
	Family	185	-0.001	0.006	0.58	0.822
	Phylogenetic		-0.011	0.005	0.24	0.051
(b) Effects of annual temperature						
Clutch frequency	Non-phylogenetic		0.021	0.002	0.23	< 0.001
	Family	490	0.011	0.002	0.63	< 0.001
	Phylogenetic		0.009	0.002	0.05	< 0.001
Clutch size	Non-phylogenetic		-0.016	0.002	0.43	< 0.001
	Family	798	-0.005	0.002	0.72	0.004
	Phylogenetic		-0.003	0.002	0.20	0.039
Hatchling size	Non-phylogenetic		0.0004	0.002	0.83	0.782
	Family	632	0.003	0.002	0.88	0.171
	Phylogenetic		0.003	0.002	0.68	0.201
Productivity	Non-phylogenetic		0.009	0.003	0.80	0.003
	Family	435	0.008	0.003	0.89	0.006
	Phylogenetic		0.008	0.003	0.72	0.007
Age	Non-phylogenetic		-0.018	0.003	0.43	< 0.001
	Family	251	-0.022	0.003	0.63	< 0.001
	Phylogenetic		-0.018	0.003	0.28	< 0.001
Longevity	Non-phylogenetic		-0.015	0.005	0.31	0.002
	Family	185	-0.014	0.004	0.60	0.005
	Phylogenetic		-0.015	0.005	0.26	0.002

Family: non-phylogenetic models with family as a fixed effect. All response variables are log₁₀-transformed. Age is age at first reproduction (in months). Female body mass is used as a covariate in all analyses. Lambda is significantly different from 0 and 1 in all models. Significant associations between temperature and life-history traits are shown in bold.

when they seek to increase their body temperature (Papenfuss, 1982). Semi-aquatic lizards, invariably diurnal, are active in a colder medium than air, which furthermore has a much higher thermal conductivity (Schmidt-Nielsen, 1997). Their low body temperatures are, therefore, in line with our prediction.

Insularity

The low body temperatures of insular lizards are somewhat surprising. Case (1982) hypothesized that they have higher ther-

moregulatory ability and higher body temperatures than mainland species, because vigilance can be reduced in the absence of predators and basking can be enhanced. It may be that lizards can allow themselves to be active at lower than optimal body temperatures where predation pressure is relaxed, because sub-optimal performance is tolerated. We hypothesize that the three parameters of an effective thermoregulation – precision, effectiveness and accuracy (Hertz *et al.*, 1993) – will be lower on predator-free islands. One must bear in mind, however, that islands vary greatly in their biotic and abiotic characteristics,

hence different insular environments select for a plethora of phenotypes rather than for a single optimum (Meiri, 2007; Thomas *et al.*, 2009; Raia *et al.*, 2010; Pafilis *et al.*, 2011). Furthermore, islands usually harbour much denser populations of lizards than do mainland areas (Buckley *et al.*, 2008; Novosolov *et al.*, 2013); although the effects of this on lizard body temperatures remain unclear.

Diet and size

Unexpectedly, we found no relationship between diet and body temperatures. Herbivory was often thought to be possible only in lizards with sufficiently high body temperatures (Pough, 1973; Espinoza *et al.*, 2004). Herbivorous, diurnal species in our dataset do have, on average, higher body temperatures than omnivorous and carnivorous diurnal species (33.9 vs. 32.7 and 32.3 °C, respectively), but the differences are small. No herbivore is active at very low body temperatures (except some South American *Phymaturus*, with a body temperature of 22.5 °C; Ibarquengoytia *et al.*, 2008). Body temperatures of all other diurnal herbivores are higher than 27 °C (those of the four nocturnal and cathemeral herbivores in our dataset range from 25.2 to 33.4 °C; Appendix S1). The modal body temperatures of diurnal lizards are obviously sufficiently high to 'maintain the internal compost heap' (Janzen, 1973) of herbivorous species. The positive relationship between body size and body temperature disappears once phylogenetic affinities are accounted for, but obviously large lizards can easily achieve high body temperatures. Whether they can do so in cold environmental temperatures (i.e. how pervasive is Bergmann's rule in lizards?) remains to be studied.

Life history

The geographic distribution of oviparous species is constrained to regions warm enough for eggs, which cannot thermoregulate, to develop. Viviparous species, in contrast, can inhabit much colder regions (e.g. Shine, 1983, 2005). Here we quantitatively show that viviparous species inhabit colder regions, but body temperatures of egg-laying and live-bearing species are much more alike than the difference in their thermal environment would suggest (Fig. 5).

We hypothesize that these differences reflect, to some extent, the relative difficulty of lizard clades evolving viviparity. The difference between environmental temperatures encountered by viviparous and oviparous species is negatively correlated with the proportion of viviparous species in each family (Table 1, Fig. 6). In skinks, for example, environmental temperatures of oviparous and viviparous taxa are similar, but in agamids and lacertids viviparous species inhabit much colder areas. Viviparity has evolved multiple times in the former, but very few times in the latter (Blackburn, 1999).

Surprisingly, body temperatures are less related to lizard life history than mean annual temperatures. This is despite the former being directly relevant to activity and physiology, and the latter being a gross macroecological measure of temperature

regimes, much of which are not encountered by the individual during activity (e.g. winter temperature for temperate-region species, daily temperatures for nocturnal species). Body temperatures are positively correlated with hatchling/neonate size, and productivity rates. We have data for the age of maturity of only 251 species and about half (115) of them reach sexual maturity in a year or less. We suspect, however, that the true proportion is much higher, because such fast-maturing species are small (mean mass 12.8 g), and species that take longer to mature are much larger (mean 91.2 g, $n = 126$). The mean mass of species for which we have no data for maturation age (17.8 g, $n = 620$) is closer to the mass of the fast-maturing species than to that of the slow-maturing ones. We therefore infer that most lizards mature in a year or less. If most lizards mature quickly, the low growth rates associated with cold temperatures are not compensated by longer growth periods. This can explain the association between low temperatures and small size.

Hatchling size is the sole factor we found not to be correlated with mean annual temperatures. Increased annual temperatures are correlated with 'fast' life-history strategy – the age at first reproduction and life span decrease, while reproductive frequency and overall productivity rates increase. The only shift towards a slower life history associated with increasing temperatures is a trend towards smaller clutches (or broods). Thus, lizards seem to follow the common avian pattern of larger clutches in colder regions (Ashmole's hypothesis; see Andrews & Rand, 1974; Ricklefs, 1980; Jetz *et al.*, 2008).

We suggest that mean annual temperatures reflect the length of lizard activity seasons, which in turn affect life-history traits. We further suggest that substantial metabolic activity related to growth and reproduction in warm regions occurs when animals are asleep. Thus, in warm regions, lizards can forage for a longer part of the year, and of the day (but see Sinervo *et al.*, 2010), and obtain more food. The assimilation of nutrients and the investment of energy into growth and reproduction in warm regions further occur for longer parts of the diel cycle. These translate to faster growth and enhanced reproduction. The patterns we observed can therefore result from lizards in warm environments being able to reproduce several times per year, whereas species inhabiting cold climates can only reproduce annually or less (Fitch, 1970; Pincheira-Donoso & Tregenza, 2011; Meiri *et al.*, 2012). This acceleration of life-history traits comes at a cost of reduced longevity, though whether 'effective longevity' (the total amount of time spent active over the lifetime) is reduced remains to be studied. The two avenues open for lizards inhabiting cold regions are to increase their clutch or litter size, or increase their life span. Both strategies have been adopted. Clutch sizes are larger in cold regions (Andrews & Rand, 1974; this study). Few taxa retain small clutches in cold areas. Nocturnal *Homonota* geckos inhabiting cold regions of the Andes can take 9 years to mature and are limited to one egg per clutch, and one clutch every 1 or 2 years (Ibarquengoytia, 2008). The increased longevity that we found to be associated with life in cold regions may enable such species to achieve lifetime reproductive success on a par with warm-region taxa.

Overall, we found that high temperatures accelerate lizard life history, as we predicted; especially it seems that, for lizards at least, hotter sex also means more (frequent) sex. The fact that environmental temperatures seem more important in shaping life history than do body temperatures, however, is surprising. These findings suggest that the increase in global temperature is likely to profoundly affect lizard life histories.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Data and references for lizard body temperatures, natural history and life-history traits.

Appendix S2 Data used to derive mass–length allometry for legged anguid lizards.

Appendix S3 Phylogenetic relationships of lizard in the dataset: tree in Newick format and references.

Appendix S4 Mean body temperatures and mean annual temperatures in different lizard families.

Appendix S5 Models of factors correlated with lizard body temperatures.

BIOSKETCH

Shai Meiri studies the biogeography of animal traits in different vertebrate clades, the evolutionary responses to insularity and the patterns, drivers and consequences of the global distribution of animals, especially reptiles.

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