

## Article (refereed) - postprint

---

Meiri, Shai; Bauer, Aaron M.; Chirio, Laurent; Colli, Guarino R.; Das, Indraneil; Doan, Tiffany M.; Feldman, Anat; Herrera, Fernando-Castro; Novosolov, Maria; Pafilis, Panayiotis; Pincheira-Donoso, Daniel; Powney, Gary; Torres-Carvajal, Omar; Uetz, Peter; Van Damme, Raoul. 2013. **Are lizards feeling the heat?: a tale of ecology and evolution under two temperatures.** *Global Ecology and Biogeography*, 22 (7). 834-845. [10.1111/geb.12053](https://doi.org/10.1111/geb.12053)

© 2013 John Wiley & Sons Ltd

This version available <http://nora.nerc.ac.uk/504711/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

**This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. Some differences between this and the publisher's version remain. You are advised to consult the publisher's version if you wish to cite from this article.**

The definitive version is available at <http://onlinelibrary.wiley.com>

Contact CEH NORA team at  
[noraceh@ceh.ac.uk](mailto:noraceh@ceh.ac.uk)

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

2 Shai Meiri<sup>1,\*</sup>, Aaron M. Bauer<sup>2</sup>, Laurent Chirio<sup>3</sup>, Guarino R. Colli<sup>4</sup>, Indraneil Das<sup>5</sup>, Tiffany M.  
3 Doan<sup>6</sup>, Anat Feldman<sup>1,15</sup>, Fernando-Castro Herrera<sup>7</sup>, Maria Novosolov<sup>1,16</sup>, Panayiotis Pafilis<sup>8</sup>,  
4 Daniel Pincheira-Donoso<sup>9</sup>, Gary Powney<sup>10,11</sup>, Omar Torres-Carvajal<sup>12</sup>, Peter Uetz<sup>13</sup>, & Raoul Van  
5 Damme<sup>14</sup>

## 6 **Research Paper**

7

8 1. Department of Zoology, Tel Aviv University, 69978, Tel Aviv, Israel

9 2. Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova,  
10 Pennsylvania 19085, USA. aaron.bauer@villanova.edu

11 3. Département de Systématique et Evolution, Muséum National d'Histoire Naturelle, 25 rue  
12 Cuvier, 75231 Paris, France. lchirio@hotmail.com

13 4. Departamento de Zoologia, Universidade de Brasilia, 70910-900 Brasilia, DF, Brasil.  
14 grcolli@unb.br

15 5. Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak,  
16 94300, Kota Samarahan, Sarawak, Malaysia. idas@ibec.unimas.my

17 6. Department of Biology, Central Connecticut State University, New Britain, Connecticut,  
18 USA. tiffperu@yahoo.com

19 7. Departamento de Biología Facultad de Ciencias Naturales y Exactas, Universidad del Valle,  
20 Cali, Colombia. fcastro11@hotmail.com

21 8. School of Biology, Department of Zoology and Marine Biology, University of Athens, 157-  
22 84, Panepistimioupolis, Ilissia, Greece. ppafil@biol.uoa.gr

23 9. Laboratory of Evolutionary Ecology of Adaptations, School of Life Sciences, University of  
24 Lincoln, Riseholme Campus, Lincoln, LN2 2LG, Lincolnshire, UK.

25 DPincheiraDonoso@lincoln.ac.uk

- 26 10. NERC Centre for Ecology & Hydrology, Maclean Building, Benson Lane, Crowmarsh  
27 Gifford, Wallingford, Oxfordshire, OX10 8BB, UK. g.powney@googlemail.com
- 28 11. Department of Life Sciences, Imperial College London, Silwood Park, Ascot, SL5 7PY, UK
- 29 12. Pontificia Universidad Católica del Ecuador, Escuela de Biología. Avenida 12 de Octubre y  
30 Roca, Apartado 17-01-2184, Quito, Ecuador. omartorcar@gmail.com
- 31 13. Center for the Study of Biological Complexity, Virginia Commonwealth University,  
32 Richmond, VA 23284, USA. peter@uetz.us
- 33 14. Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610, Wilrijk,  
34 Belgium. raoul.vandamme@ua.ac.be
- 35 15. anatfeld@post.tau.ac.il
- 36 16. marianovosolov@gmail.com
- 37 \* Corresponding author, uneshai@post.tau.ac.il

38 Running title: lizard body & environmental temperatures

39 Keywords

40 Body temperature, diel cycle, environmental temperature, global warming, life history, lizards,  
41 Thermal biology

42

43 **ABSTRACT**44 **Aim**

45 Temperature influences most components of animal ecology and life history – but what kind of  
46 temperature? Physiologists usually examine the influence of body temperatures, while  
47 biogeographers and macroecologists mostly focus on environmental temperatures. We used a large  
48 (861 species) global dataset of lizard body temperatures, and the mean annual temperatures across  
49 their geographic ranges to examine the relationships between these two measures.

50 **Location:** Worldwide

51 **Methods:** We examined factors influencing body temperatures, and tested for the influence of both  
52 body and mean annual temperatures on ecological and life history traits, while accounting for the  
53 influence of shared ancestry.

54 **Results:** Body temperatures and mean annual temperatures are uncorrelated. However, accounting  
55 for activity time (nocturnal species have low body temperatures), use of space (fossorial and semi-  
56 aquatic species were “colder”), insularity (mainland species are “hotter”) and phylogeny, the two  
57 temperatures are positively correlated. High body temperatures are only associated with larger  
58 hatchlings (contra the temperature size rule) and with increased rates of biomass production. Annual  
59 temperatures are positively correlated with clutch frequency and annual longevity, and negatively  
60 correlated with clutch size, age at first reproduction and longevity. High annual temperatures are  
61 positively correlated with productivity and brood frequency, but negatively correlated with clutch  
62 size, age at first reproduction, and longevity.

63 **Main conclusions:** Cold-bodied lizards do not seem to have ‘slower’ life history attributes  
64 than species with high body temperatures. The longer seasons prevalent in warm regions, and the  
65 ability to carry on physiological processes while inactive (but warm enough), make environmental  
66 temperatures better predictors of lizard life history variation than body temperatures. This

67 surprisingly greater effect of environmental temperatures on lizard life histories hints that global  
68 warming may have a profound influence on lizards.

69

70

## 71 INTRODUCTION

72 Animal fitness is heavily influenced by temperature acting on ecological and life history traits  
73 (Angilletta 2009). Temperature has therefore increasingly been recognized as a major factor driving  
74 multiple aspects of animal ecology, physiology and evolution (Avery et al. 1982; Adolph and Porter  
75 1993). For example, the metabolic theory of ecology stresses that temperature, through its effect on  
76 metabolic rates, greatly influences virtually all life history attributes of organisms (e.g., Brown et al.  
77 2004) , hence, having enormous impact of ecological and evolutionary dynamics. Temperature has  
78 been found to affect most components of lizard ecological and reproductive performance, such as  
79 sprint speed, metabolic rate, foraging, fecundity, and survival (e.g., Van Damme et al. 1989, 1991;  
80 Niewiarowski and Waldschmidt 1992; Pafilis et al. 2007; Angilletta 2009).

81 The influence of temperature on ecological and evolutionary processes has traditionally been  
82 investigated through two different approaches: while physiologists tend to study body temperatures  
83 of active animals, most biogeographic and macroecological studies focus on environmental  
84 temperatures. Thus, for example, ambient temperatures are often closely correlated with lizard  
85 species richness (Schall and Pianka 1978; Currie 1991, cf. Powney et al. 2010). Indeed, Hawkins et  
86 al. (2003) identified lizards as the only group in which measures of ambient energy are usually the  
87 strongest correlate of richness. The use of environmental temperatures, such as mean annual  
88 temperature, probably partly stems from an assumption (rarely made explicit) that the two measures  
89 are strongly and positively correlated. Buckley et al. (2008), for example, used environmental  
90 temperatures to model lizard densities, assuming that these temperatures reflect body temperatures.  
91 They modeled the thermal environment based on environmental temperatures and day length,  
92 assuming that “lizards are active for three-quarters of the daylight period”. Such an inclusive model  
93 may, however, be inappropriate for actively thermoregulating lizards, particularly for nocturnal  
94 species.

95 We use a large-scale, phylogenetic comparative approach to characterize the environmental and  
96 body temperatures saurians and amphisbaenians (henceforth ‘lizards’) live in. We examine the  
97 relationship between annual temperatures and body temperatures, and ecological factors that affect  
98 it. Finally, we test which of these two temperature measures better explains lizard life history  
99 attributes.

#### 100 *Factors affecting body temperatures*

101 Herbivorous lizards are thought to maintain high body temperatures to facilitate microbe-  
102 assisted fermentation of plant material (Janzen 1973). It was therefore assumed that herbivorous  
103 lizards cannot inhabit cold areas because they would be unable to achieve the high body  
104 temperatures required for plant digestion (King 1996). Nevertheless, in some of the coldest areas  
105 inhabited by reptiles, *Liolaemus* lizards have repeatedly evolved herbivory, by successfully  
106 maintaining high body temperatures in association with a tendency for small body mass to  
107 accelerate heating rates (Espinoza et al. 2004; Pincheira-Donoso et al. 2008).

108 Fossorial lizards are thought to have low body temperatures (e.g., Withers 1981) because they  
109 cannot readily increase their body temperature by basking (Avery et al. 1982). Similarly, because of  
110 the high thermal conductance of the aquatic environment, we expect semi-aquatic species to have  
111 low body temperatures (Mesquita et al. 2006). Finally, islands often harbor fewer predators,  
112 enabling lizards to thermoregulate more effectively (Case 1982).

#### 113 *Temperature and lizard life history*

114 High body temperatures are thought to enhance reproduction, because lizard metabolic rates  
115 increase with temperatures over most of the temperature range at which they are active (Huey et al.  
116 1989; Angilletta et al. 2010). High environmental temperatures are also associated with longer diel  
117 and annual periods of activity that facilitate higher energy intake through prolonged foraging  
118 (Bueno and Lopez-Urrutia 2012). Tropical lizards are therefore usually active year-round, and can

119 produce multiple clutches each year (Fitch, 1970; Cox et al., 2003; Meiri et al., 2012). In contrast,  
120 cold climate lizards may be active only during summer (as little as four months in northern  
121 populations of *Zootoca vivipara*, Szczerbak 2003). They may also be active for relatively short  
122 periods of the diel cycle, and can thus usually lay a single annual clutch – or less (Meiri et al.,  
123 2012).

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

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

138

## 139 **METHODS**

### 140 **Data**

141 We collated a dataset of 861 species belonging to 36 of the 42 families of saurians and  
142 amphisbaenians from across the globe (Appendix S1). Lizard body temperatures, life history and



143 natural history traits were obtained from published sources, and in the field. Taxonomy follows the  
144 reptile database (<http://reptile-database.reptarium.cz>, accessed May 02, 2012). Body temperatures  
145 are mean temperatures of active individuals recorded in the field. The number of individuals  
146 observed is not always reported, and when it does it vary greatly between species (e.g., with our  
147 own data it can vary between one [*Ophiomorus latastii*, Meiri, unpublished] and hundreds of  
148 observation [e.g., *Podarcis* spp., Pafilis, unpublished]). Although the numbers can be small they are  
149 unlikely to be systematically biased, and we therefore use all available data. We excluded preferred  
150 temperature data because the correlation between field body temperatures and preferred  
151 temperatures is often weak (e.g., Kohlsdorf and Navas 2006) and biased (i.e., has a non-zero  
152 intercept and a slope different from one). We further excluded temperatures of animals known to  
153 be inactive when measured (e.g., nocturnal species in their diurnal retreats). If multiple temperature  
154 data were available for a species, we averaged the highest and lowest mean values.

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

165 We controlled for the effects of body size by using species-specific body mass as a covariate in  
166 all analyses. Masses were calculated from maximum snout-vent lengths (SVL), the most common  
167 proxy for body size in lizards (Meiri 2008), using equations developed by Pincheira-Donoso et al.

168 (2011; for Liolaemidae), Novosolov et al. (In Press, for different gecko families and for *Anolis*) and  
169 Meiri (2010, for all other lineages). Weights of legged anguids were calculated using the equation  
170  $\log \text{ mass} = 3.48 * \log (\text{SVL}) - 5.765$  (Appendix S2).

171 For life history analyses we used mean SVL of adult females rather than maximum species SVL  
172 as a measure of adult size, because the maxima are often of males of highly sexually dimorphic  
173 species, but the reproductive characteristics (e.g., clutch size and hatchling size) in these species are  
174 more likely to be influenced by female, rather than by male size. We then converted female and  
175 hatchling SVLs to masses using the same equations described above. In some cases female and  
176 hatchling SVL were unavailable, and we used published mass data instead. If neither data were  
177 available, we used mean SVL of unsexed adults, unless we had indication (e.g., from maximum  
178 SVL) that a species is sexually dimorphic – in which case they were omitted from further analyses.  
179 We classified lizards as either carnivores (>90% animal food by volume), omnivores (50-90 %  
180 animal food) or herbivores (>50% plant food). Reproductive mode was classified as viviparous or  
181 oviparous. We treated ovoviviparous species as viviparous, because we are interested in whether  
182 gravid females retain their young in the oviduct during pregnancy or whether they lay eggs that are  
183 exposed to environmental temperatures. Species that have both oviparous and viviparous  
184 populations were classified according to the characteristics of the population for which body  
185 temperature was measured. In a preliminary analysis, we found no significant differences between  
186 the thermal responses of different categories of surface-active lizards (i.e., terrestrial, arboreal and  
187 saxicolous, results not shown), and we therefore examined microhabitat use in three elements: air  
188 (the three categories outlined above and their combinations), water (semi-aquatic species), and earth  
189 (fossorial species). We find this particularly appropriate a categorization to examine Kleiber's  
190 (1961) "fire of life" (i.e., an animal's metabolic rate). To examine the effects of activity periods we  
191 divided lizards into diurnal, cathemeral (active both day and night) and nocturnal. We did not have  
192 sufficient species-specific data to classify diurnal species as heliotherms or shade-loving species.  
193 The life history traits we examined are clutch/litter size, hatchling/neonate size, clutch/litter

194 frequency (per year), and their product (“productivity”, see Meiri et al. 2012), as well as mean age  
195 at sexual maturity and maximum longevity. We used mean values for all continuous variables when  
196 available. If more than one mean was available for a species, we averaged the highest and lowest  
197 mean values.

## 198 *Analyses*

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

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

215 We examined the relationship of life history characteristics versus body and environmental  
216 temperatures. We tested each relationship three times, directly (“non-phylogenetic” models), using  
217 family as a fixed effect, and correcting for phylogeny using Pagel’s lambda. We report means  $\pm$  1  
218 standard deviation and used a significance level of 5% in all tests.

219

220 **RESULTS**

221 Our dataset (Appendix S1) covers much of the variation in mean annual environmental  
222 temperatures experienced by lizards: in our dataset values range from 0.0°C for *Zootoca vivipara* to  
223 27.7°C for *Anolis taylori* (mean =  $19.0 \pm 5.8$  °C). Across all lizards for which we have geographic  
224 data (i.e., not only those we had body temperature data for,  $n = 4608$ ), the corresponding figures are  
225  $-3.6$  °C (*Phrynocephalus lidskii*) to 29.8°C (*Hemidactylus bavazzanoi*), mean =  $20.9 \pm 5.3_{SD}$ . The  
226 body temperatures of lizards we analyze range from 14.95°C in *Pachydactylus rangei* to 44.3 °C in  
227 *Diporiphora bilineata*, mean  $31.4 \pm 4.9$  (Appendix S1).

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

235 Body and environmental temperatures are uncorrelated (slope =  $0.039 \pm 0.029$ ,  $t = 1.34$ ,  $p =$   
236  $0.18$ ,  $n = 861$ , Figure 2).

237 There are differences between lineages in body temperatures: mainly diurnal families (e.g.,  
238 teiids, phrynosomatids, iguanas, agamas, lacertids, monitors, all with mean body temperatures  
239 higher than 33.5°C) show high body temperatures, while mainly nocturnal and burrowing families  
240 (e.g., amphisbaenians and gecko lineages, all with mean body temperatures  $\geq 29$ °C, Appendix S4)  
241 show low temperatures.

242 **Modeling lizard body temperatures**

243 We retrieved a significant relationship between body and mean annual temperatures (slope 0.13  
244  $\pm 0.03$  degree of body temperature for every degree of environmental temperature), once we  
245 accounted for several ecologically relevant factors. Correcting for the effects of body size, habitat,  
246 activity time, and insularity (but not diet,  $F = 2.24$ ,  $p = 0.11$ ), body and environmental temperatures  
247 are significantly and positively correlated. Body temperatures increase with body mass (slope  $1.10$   
248  $\pm 0.19$ ,  $p < 0.0001$ ), semi aquatic and fossorial lizards have lower body temperatures than surface-  
249 active species (by  $4.8$  and  $1.8$  °C, respectively,  $n = 861$ . In this model omnivorous and herbivorous  
250 lizards have higher body temperatures than carnivorous ones (see Appendix S5 for further statistical  
251 details).

252 Diurnal lizards ( $n = 718$ ) have higher body temperatures than nocturnal lizards ( $n = 89$ , mean  
253  $32.5 \pm 4.2$  vs.  $25.1 \pm 4.6$  °C,  $t = 15.3$ ,  $p < 0.0001$ ; cathemeral species:  $27.8 \pm 4.2$ ,  $n = 54$ ), even  
254 though they inhabit colder environments ( $18.8 \pm 6.0$  vs.  $20.5 \pm 4.3$  °C,  $t = 2.6$ ,  $p = 0.009$ , cathemeral  
255 species:  $19.9 \pm 3.8$  °C, Figure 3). Insular lizards are “colder” than mainland species by  $2.4$  °C ( $p <$   
256  $0.0001$ ). This model explains 32.6% of the variation in lizard body temperatures, whereas a similar  
257 model lacking environmental temperature explains 30.5%. Interestingly, in this model, body  
258 temperatures of diurnal lizards increase with annual temperatures more gradually (slope =  $0.091 \pm$   
259  $0.026$ ), than body temperatures of cathemeral and nocturnal lizards (slopes =  $0.549 \pm 0.144$  and  
260  $0.499 \pm 0.100$ , respectively,  $p < 0.001$  in all cases, Figure 4).

261 Accounting for phylogenetic relationships, body temperatures are positively, albeit weakly,  
262 correlated with mean annual temperatures (slope =  $0.15 \pm 0.03$ ,  $t = 5.3$ ,  $p < 0.0001$ ,  $n = 861$ ,  $R^2 =$   
263  $0.03$ ). Adding the abovementioned factors, mass and diet drop out of the model ( $p = 0.89$  and  $0.60$ ,  
264 respectively), but the effects of microhabitat (semi aquatic, vs. above ground only), and activity  
265 time remain. Insularity is marginally non-significant ( $p = 0.057$ ). The best model now explains only  
266 8.4% of the variation in lizard body temperatures.

267 Partially accounting for phylogeny by using family as a factor, rather than as a nuisance variable  
 268 as in the PGLS, more variance is explained: familial affiliation alone explains 50.3% of the variance  
 269 in lizard body temperatures. The minimum adequate model for body temperatures includes Family,  
 270 annual temperature (slope  $0.213 \pm 0.026$ ), activity time (nocturnal species “colder” than diurnal ones  
 271 by  $4.8 \pm 0.7$  °C), and insularity (insular endemics “colder” by  $1.8 \pm 0.3$  °C), but neither diet ( $F = 0.3$ ,  
 272  $p = 0.78$ ,  $n = 861$ ) nor body size (slope =  $-0.06 \pm 0.22$ ,  $p = 0.80$ ). This model explains 57.1% of the  
 273 variation in life history, whereas a similar model without annual temperatures explains 53.9%.

274

## 275 **The effects of temperature on lizard life history**

### 276 *Oviparity and viviparity*

277 Viviparous lizards ( $n = 174$ ) live, on average, at environmental temperatures fully 5.5 degrees  
 278 colder than oviparous species ( $n = 678$ , 14.6 vs. 20.1 °C, respectively). Their body temperatures,  
 279 however, are only 1.9 degrees colder, on average (29.9 vs. 31.8 °C, the median body temperature is  
 280 only 0.8 degree colder, 31.5 vs. 32.3 °C, Figure 5).

281 The average differences between mean annual temperatures encountered by egg- and live  
 282 bearing species varies among lizard clades. In some taxa (e.g., Scincidae, Phrynosomatidae) the  
 283 differences are relatively minor, whereas in others (Agamidae, Lacertidae) they are profound  
 284 (Table 1). This difference is negatively correlated with the (log-transformed) proportion of  
 285 viviparous species in each family (Figure 6,  $n = 13$  families,  $R^2 = 0.58$ ,  $p = 0.003$ ). In clades where  
 286 viviparous species inhabit much colder areas than oviparous species viviparity is rare.

### 287 *Growth, longevity & reproduction*

288 The relationships between temperature and life history variables are shown in Table 2. Values  
 289 of lambda ranged from 0.51 for longevity to 0.87 for brood frequency, and were significantly  
 290 different from both 0 and 1 at the 0.0001 level in all cases. Higher body temperatures are associated  
 291 with larger offspring (contra the temperature size rule), and higher rates of biomass production

292 (“productivity”). The association between high body temperatures and both lower age at first  
293 reproduction and large clutch sizes are supported only in non-phylogenetic models. Body  
294 temperature is correlated with neither clutch frequency, nor with longevity (Table 2a).

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

299

## 300 **DISCUSSION**

### 301 *Body versus environmental temperatures*

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

306 Lizards inhabit regions with a wide range of environmental temperatures, but they hibernate in  
307 cold climates and are thus not exposed to the lowest temperatures. We found that nocturnal lizards  
308 inhabit warmer environments than diurnal ones. We posit that low night-time temperatures act as a  
309 biogeographic filter preventing the spread of nocturnal species to high latitudes and elevations that  
310 are nonetheless suitable to diurnal species. In keeping with this, species of archetypal nocturnal  
311 lineages, such as geckos, sometimes evolve diurnal activity in cold regions (e.g., the New Zealand  
312 genus *Naultinus* and the High-Atlas Mountains *Quedenfeltia*).

313 The difference between our measure of environmental temperature, mean annual temperatures,  
314 and the environmental temperatures that lizards are active at is likely greater the colder the  
315 environment is. In cold regions, lizards are almost invariably diurnal, and active only in summer.  
316 By taking night temperatures into account, mean annual temperatures, probably underestimate the  
317 actual thermal preferences of diurnal lizards. The distribution of lizard body temperatures is highly

318 modal, with a mode of approximately 34°C (Figure 1, interquartile range 28.4-34.9; 95% of the  
319 species have body temperatures between 20.6 and 39.3°C). Although body temperatures are often  
320 correlated with air temperatures in the field, they were uncorrelated with mean annual temperatures  
321 – a relationship that is found in mammals (which show an inverse relationship, Lovegrove 2003).  
322 These findings falsify our first hypothesis.

### 323 *Activity time*

324 Activity time had the largest effect on lizard body temperatures (a difference of ~7.4 °C, on  
325 average, between diurnal and nocturnal species). Even among diurnal lineages, families consisting  
326 mainly of heliotherms (e.g., Lacertidae, Tropiduridae, Phrynosomatidae, Agamidae) were  
327 characterized by species having, on average, higher body temperatures than those with more shade-  
328 living species (e.g., Polychrotidae, Anguidae, Appendix S4). Fossorial lizards inhabit a colder  
329 medium than air (at least during the day), and have little opportunity to bask. Their  
330 thermoregulatory behavior probably constitutes mainly vertical movement within the ground –  
331 towards higher, warmer levels when they seek to increase their body temperature (Papenfuss 1982).  
332 Semi aquatic lizards, invariably diurnal, are active in a colder medium than air, which furthermore  
333 has a much higher thermal conductivity (Schmidt-Nielsen 1997). Thus their low body temperatures  
334 are in line with our prediction.

### 335 *Insularity*

336 The low body temperatures of insular lizards are somewhat surprising. Case (1982)  
337 hypothesized that they have higher thermoregulatory ability and higher body temperatures than  
338 mainland species, because vigilance can be reduced in the absence of predators and basking can be  
339 enhanced. It may be that lizards can allow themselves to be active at lower than optimal body  
340 temperatures where predation pressure is relaxed, because sub-optimal performance is tolerated. We  
341 hypothesize that the three parameters of an effective thermoregulation: precision, effectiveness, and  
342 accuracy (Hertz et al. 1993), will be lower on predator-free islands. One must bear in mind,  
343 however, that islands vary greatly in their biotic and abiotic characteristics, hence different insular



344 environments select for a plethora of phenotypes rather than for a single optimum (Meiri 2007;  
345 Thomas et al. 2009; Raia et al. 2010; Pafilis et al. 2011). Furthermore, islands usually harbor much  
346 denser populations of lizards than do mainland areas (Buckley *et al.*, 2008; Novosolov et al., 2012),  
347 although the effects of this on lizard body temperatures remain unclear.

#### 348 *Diet & size*

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

#### 362 *Life history*

363 The geographic distribution of oviparous species has long been known to be constrained to  
364 regions warm enough for eggs, which cannot thermoregulate, to develop. Viviparous species, in  
365 contrast, can inhabit much colder regions (e.g. Shine 1983; 2005). Here we quantitatively show that  
366 viviparous species inhabit colder regions, but body temperatures of egg-laying and live-bearing  
367 species are much more alike than the difference in their thermal environment would suggest (Figure  
368 5).

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

376 Surprisingly, body temperatures are less related to lizard life history than mean annual  
377 temperatures. This is despite the former being directly relevant to activity and physiology, and the  
378 latter being a gross macroecological measure of temperature regimes, much of which are not  
379 encountered by the individual during activity (e.g., winter temperature for temperate-region species,  
380 daily temperatures for nocturnal species). Body temperatures are positively correlated with  
381 hatchling/neonate size, and productivity rates. Interestingly, this runs contra the temperature size  
382 rule. We have data for the age of maturity of only 241 species and about half (115) of them reach  
383 sexual maturity in a year or less. We suspect, however, that the true proportion is much higher,  
384 because such fast-maturing species are small (mean mass 12.8 g), and species that take longer to  
385 mature are much larger (mean 91.2 g,  $n = 126$ ). The mean mass of species we have no maturation-  
386 age our dataset (17.8 g,  $n = 620$ ) is closer to the mass of the fast-maturing species than to that of the  
387 slow maturing ones. We therefore infer that most lizards mature in a year or less. If most lizards  
388 mature quickly, the low growth rates associated with cold temperatures are not compensated by  
389 longer growth periods. This can explain the association between low temperatures and small size.

390 Hatchling size is the sole factor we found not to be correlated with mean annual temperatures.  
391 Increased annual temperatures are correlated with 'fast' life history strategy – the age at first  
392 reproduction and lifespan decrease, while reproductive frequency and overall productivity rates  
393 increase. The only shift towards a slower life history associated with increasing temperatures is a  
394 trend towards smaller clutches (or broods). Thus, lizards seem to follow the common avian pattern

395 of larger clutches in colder regions (Ashmole's hypothesis, see Andrews and Rand 1974; Ricklefs  
396 1980).

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

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

**421 Acknowledgements**

422 We thank members of the Global Assessment of Reptile Distribution Working Group, Barry  
423 Sinervo and an anonymous referee for valuable discussion. We thank Uri Roll for enlightening  
424 comments on a previous draft of this manuscript. Erez Maza and Meirion Hopkins have been  
425 indispensable in mapping lizard geographic ranges. Shai Meiri is supported by an Alon Fellowship.  
426 A.M. Bauer is supported by Grant DEB 0844523 from the National Science Foundation (USA).  
427 Guarino Colli is supported by CAPES, CNPq and FAPDF. D. Pincheira-Donoso is supported by the  
428 Leverhulme Trust.

429

**430 Supplementary material**

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

432

433 Appendix S1: Data and references for lizard body temperatures, natural & life history traits

434 Appendix S2: data used to derive mass-length allometry for legged anguid lizards

435 Appendix S3: Phylogenetic relationships of lizard in the dataset: newick code and references

436 Appendix S4: mean body temperatures and mean annual temperatures in different lizard families

437 Appendix S5 – models of factors correlated with lizard body temperatures

438

**439 REFERENCES**

440

- 441 Adolph, S. C. & Porter, W. P. (1993) Temperature, activity, and lizard life histories. *American*  
442 *Naturalist*, **142**, 273-295.
- 443 Andrews, R. M. & Rand, A. S. (1974) Reproductive effort in anoline lizards. *Ecology*, **55**, 1317-  
444 1327.
- 445 Angilletta, M. J. (2009) *Thermal adaptation. A theoretical and empirical synthesis*. Oxford  
446 University Press, Oxford.
- 447 Angilletta, M. J., Huey, R. B. & Frazier, M. R. (2010) Thermodynamic effects on organismal  
448 performance: is hotter better? *Physiological and Biochemical Zoology*, **83**, 197-206.
- 449 Avery, R. A. (1982) Field studies of body temperatures and thermoregulation. *Biology of the*  
450 *Reptilia*, **12**, 93-166.
- 451 Bickford, D., Howard, S. D., Ng, D. J. J. & Sheridan, J. A. (2010) Impacts of climate change on the  
452 amphibians and reptiles of Southeast Asia. *Biodiversity and Conservation*, **19**, 1043-1062.
- 453 Blackburn, D. G. (1999) Are viviparity and egg-guarding evolutionarily labile in squamates?  
454 *Herpetologica*, **55**, 556-573.
- 455 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. (2004) Toward a metabolic  
456 theory of ecology. *Ecology*, **85**, 1771-1789.
- 457 Buckley, L. B., Rodda, G. H. & Jetz, W. (2008) Thermal and energetic constraints on ectotherm  
458 abundance: a global test using lizards. *Ecology*, **89**, 48-55.
- 459 Bueno, J. & Lopez-Urrutia, A. (2012) The offspring-development-time/offspring-number trade-off.  
460 *American Naturalist*, **179**, E196-E203.
- 461 Case, T. J. (1982) Ecology and evolution of the insular giant chuckawallas, *Sauromalus hispidus*  
462 and *Sauromalus varius*. *Iguanas of the world: their behavior, ecology and conservation* (ed by G.  
463 M. Burghardt & A. S. Rand) pp. 184-212. Noyes Publications, Park Ridge, New Jersey.
- 464 Cox, R. M., Skelly, S. L. and John-Alder, H. B. (2003) A comparative test of adaptive hypotheses  
465 for sexual size dimorphism in lizards. *Evolution*, **57**, 1653-1669.

- 466 Currie, D. J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *American*  
467 *Naturalist*, **137**, 27-49.
- 468 Espinoza, R. E., Wiens, J. J. & Tracy, C. R. (2004) Recurrent evolution of herbivory in small, cold-  
469 climate lizards: breaking the ecophysiological rules of reptilian herbivory. *Proceedings of the*  
470 *National Academy of Sciences, USA*, **101**, 1681916824.
- 471 Evans, K. L., Duncan, R. P., Blackburn, T. M. & Crick, H. Q. P. (2005) Investigating geographic  
472 variation in clutch size using a natural experiment. *Functional Ecology*, **19**, 616-624.
- 473 Fitch, H. S. (1970) Reproductive cycles of lizards and snakes. *University of Kansas Museum of*  
474 *Natural History Miscellaneous Publications*, **52**, 1-247.
- 475 Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guegan, J. F., Kaufman, D. M., Kerr, J. T.,  
476 Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E. & Turner, J. R. G. (2003) Energy,  
477 water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105-3117.
- 478 Hertz, P. E., Huey, R. B. & Stevenson, R. D. (1993) Evaluating temperature regulation by field-  
479 active ectotherms: the fallacy of the inappropriate question. *American Naturalist*, **142**, 796-818.
- 480 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. (2005) Very high resolution  
481 interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**,  
482 1965-1978.
- 483 Huey, R. B., Niewiarowski, P. H., Kaufmann, J. & Herron, J. C. (1989) Thermal biology of  
484 nocturnal ectotherms: is sprint performance of geckos maximal at low body temperatures?  
485 *Physiological Zoology*, **62**, 488-504.
- 486 Huston, M. A. & Wolverton, S. (2011) Regulation of animal size by eNPP, Bergmann's rule, and  
487 related phenomena. *Ecological Monographs*, **81**, 349-405.
- 488 Ibarquengoytia, N. R. (2008) Estrategias reproductivas en reptiles. *Herpetología de Chile* (ed. By  
489 M. A. Vidal & A. Labra), pp 391-425. Science Verlag Ediciones. Santiago, Chile.

- 490 Ibarquengoytia, N. R., Ascota, J. C., Boretto, J. M., Villavicencio, H. J., Marinero, J. A. & Krenz, J.  
491 D. (2008) Field thermal biology in *Phymaturus* lizards: comparisons from the Andes to the  
492 Patagonian steppe in Argentina. *Journal of Arid Environments*, **72**, 1620-1630.
- 493 Janzen, D. H. (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types,  
494 elevation, time of day, and insularity. *Ecology*, **54**, 687-701.
- 495 Jetz, W., Sekercioglu, C. H. & Bohning-Gaese, K. (2008) The worldwide variation in avian clutch  
496 size across species and space. *PLoS Biology*, **6**, e303.
- 497 King, G. M. (1996) *Reptiles and herbivory*. Chapman and Hall, London.
- 498 Kleiber, M. (1961) *The fire of life. An introduction to animal energetics*. John Wiley, New York.
- 499 Kohlsdorf, T. & Navas, C. A. (2006) Ecological constraints on the evolutionary association between  
500 field and preferred temperatures in Tropidurinae lizards. *Evolutionary Ecology*, **20**, 549-564.
- 501 Lovegrove, B. G. (2003) The influence of climate on the basal metabolic rate of small mammals: a  
502 slow-fast metabolic continuum. *Journal of Comparative Physiology B.*, **173**, 87-112.
- 503 Meiri, S. (2007) Size evolution in island lizards. *Global Ecology and Biogeography*, **16**, 702-708.
- 504 Meiri, S. (2008) Evolution and ecology of lizard body sizes. *Global Ecology and Biogeography*, **17**,  
505 724-734.
- 506 Meiri, S. (2010) Length–weight allometries in lizards. *Journal of Zoology*, **281**, 218-226.
- 507 Meiri, S., Brown, J. H. & Sibly, R. M. (2012) The ecology of lizard reproductive output. *Global*  
508 *Ecology and Biogeography*, **21**, 592-602.
- 509 Mesquita, D. O., Colli, G. R., Costa, G. C., Franca, F. G. R., Garda, A. A. & Peres, A. K. (2006) At  
510 the water's edge: ecology of semiaquatic teiids in Brazilian Amazon. *Journal of Herpetology*, **40**,  
511 221-229.
- 512 Niewiarowski, P. H., & Waldschmidt, S. R. (1992) Variation in metabolic rates of a lizard; use of  
513 SMR in ecological contexts. *Functional Ecology*, **6**, 15-22.
- 514 Novosolov, M., Raia, P. & Meiri, S. (2012) The island syndrome in lizards. *Global Ecology and*  
515 *Biogeography*, DOI: 10.1111/j.1466-8238.2012.00791.x,

- 516 Orme, C. D. L., Freckleton, R. P., Thomas, G. H., Petzoldt, T., Fritz, S. A. & Isaac, N. J. B. (2012)  
517 CAPER: Comparative Analyses of Phylogenetics and Evolution in R. *Methods in Ecology and*  
518 *Evolution, In press*
- 519 Pafilis, P., Foufopoulos, J., Poulakakis, N., Lymberakis, P. & Valakos, E. (2007) Digestive  
520 performance in five Mediterranean lizard species: effects of temperature and insularity. *Journal*  
521 *of Comparative Physiology B.*, **177**, 49-60.
- 522 Pafilis, P., Foufopoulos, J., Sagonas, K., Runemark, A., Svensson, E., & Valakos, E. D. (2011)  
523 Reproductive biology of insular reptiles: marine subsidies modulate expression of the ‘‘Island  
524 Syndrome’’. *Copeia*, **2011**, 545-552.
- 525 Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877-884.
- 526 Papenfuss, T. J. (1982) The ecology and systematics of the amphisbaenian genus *Bipes*.  
527 *Occasional Papers of the California Academy of Sciences*, **136**, 1-42.
- 528 Pincheira-Donoso, D. & Tregenza, T. (2011) Fecundity selection and the evolution of reproductive  
529 output and sex-specific body size in the *Liolaemus* lizard adaptive radiation. *Evolutionary*  
530 *Biology*, **38**, 197-207.
- 531 Pincheira-Donoso, D., Fox, S. F., Scolaro, J. A., Iburgüengoytia, N. Acosta, J. C., Corbalan, V.,  
532 Medina, M., Boretto, J., Villavicencio, H. J. & Hodgson, D. J. (2011) Body size dimensions in  
533 lizard ecological and evolutionary research: exploring the predictive power of mass estimation  
534 equations in two *Liolaemidae* radiations. *Herpetological Journal*, **21**, 35-42.
- 535 Pincheira-Donoso, D., Hodgson, D. J. & Tregenza, T. (2008) The evolution of body size under  
536 environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? *BMC*  
537 *Evolutionary Biology*, **8**, 68.
- 538 Pough, F. H. (1973) Lizard energetics and diet. *Ecology*, **54**, 837-844.
- 539 Powney, G. D., Grenyer, R., Orme, C. D. L., Owens, I. P. F. & Meiri, S. (2010) Hot, dry and  
540 different: Australian lizard richness is unlike that of mammals, amphibians, and birds. *Global*  
541 *Ecology and Biogeography*, **19**, 386-396.



- 542 Raia, P., Carotenuto, F. & Meiri, S. (2010) One size does not fit all: No evidence for an optimal  
543 body size on islands. *Global Ecology and Biogeography*, **19**, 475-484.
- 544 Rambaut, A. (2010) FigTree, version 1.3.1. Institute of Evolutionary Biology, University of  
545 Edinburgh.
- 546 Reading, C. J., Luiselli, L. M., Akani, G. C., Bonnet, X., Amori, G., Ballouard, J. M., Filippi, E.,  
547 Naulleau, G., Pearson, D. & Rugiero, L. (2010) Are snake populations in widespread decline?  
548 *Biology Letters*, **6**, 777-780.
- 549 Ricklefs, R. E. (1980) Geographical variation in clutch size among passerine birds: Ashmole's  
550 hypothesis. *Auk*, **97**, 38-49.
- 551 Schall, J. J. & Pianka, E. R. (1978) Geographical trends in numbers of species. *Science*, **201**, 679-  
552 686.
- 553 Schmidt-Nielsen, K. (1997) Animal physiology. Book, NA, NA
- 554 Shine, R. (1983) Reptilian viviparity in cold climates: testing the assumptions of an evolutionary  
555 hypothesis. *Oecologia*, **57**, 397-405.
- 556 Shine, R. (2005) Life-history evolution in reptiles. *Annual Review of Ecology and Systematics*, **36**,  
557 23-46.
- 558 Sinervo, B., Mendez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz,  
559 M., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M. L., Meza-Lazaro, R. N.,  
560 Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Rocha, C. F. D.,  
561 Ibarguengoytia, N., Puntriano, C. A., Massot, M., Lepetz, V., Oksanen, T. A., Chapple, D. G.,  
562 Bauer, A. M., Branch, W. R., Clobert, J. & Sites, J. W. (2010) Erosion of lizard diversity by  
563 climate change and altered thermal niches. *Science*, **328**, 894-899.
- 564 Szczerbak, N. (2003) *Guide to the reptiles of the Eastern Palearctic*. Krieger Publishing Company,  
565 Malabar.
- 566 Thomas, G. H., Meiri, S. & Phillimore, A. B. (2009) Body size diversification in Anolis: Novel  
567 environment and island effects. *Evolution*, **63**, 2017-2030.

- 568 Van Damme, R., Bauwens, D. & Verheyen, R. F. (1991) The thermal dependence of feeding  
569 behavior, food consumption and gut-passage time in the lizard *Lacerta vivipara*. *Functional*  
570 *Ecology*, **5**, 507-517.
- 571 Van Damme, R., Bauwens, D., Castilla, A. & Verheyen, R. F. (1989) Altitudinal variation of the  
572 thermal biology and running performance in the lizard *Podarcis tiliguerta*. *Oecologia*, **80**, 516-  
573 524.
- 574 Wiens, J. J., Kuczynski, C. A., Townsend, T., Reeder, T. W., Mulcahy, D. G. & Sites, J. W. (2010)  
575 Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular  
576 data change the placement of fossil taxa. *Systematic Biology*, **59**, 674-688.
- 577 Withers, P. C. (1981) Physiological correlates of limblessness and fossoriality in scincid lizards.  
578 *Copeia*, **1981**, 197-204.

579

580

581 **Biosketch:**

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

585

586 **Table 1** – mean annual temperatures (°C) encountered by viviparous and oviparous lizard species,  
 587 and the percentage of viviparous species within families. ), The % of viviparous species and n are  
 588 the number of species for which we have data on both reproduction and annual temperature in our  
 589 entire dataset (Meiri, unpublished, not in the dataset analyzed here). \*: significant difference  
 590 between temperatures of viviparous and oviparous species (t tests, not shown). \*\*:  $p = 0.054$ . †: na  
 591 (1 viviparous species).

Family	n	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%

592

593

594

595 **Table 2** – the effects of body and environmental temperatures on lizard life history traits596 **a. body temperature**

trait	model	n	slope	se	model R <sup>2</sup>	p
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	<b>&lt;0.001</b>
	Family	798	0.004	0.002	0.72	<b>0.024</b>
	phylogenetic		0.002	0.002	0.19	0.266
hatchling size	non-phylogenetic		0.008	0.002	0.83	<b>&lt;0.001</b>
	Family	632	0.008	0.002	0.88	<b>&lt;0.001</b>
	phylogenetic		0.009	0.002	0.69	<b>&lt;0.001</b>
productivity	non-phylogenetic		0.024	0.003	0.82	<b>&lt;0.001</b>
	Family	435	0.017	0.004	0.89	<b>&lt;0.001</b>
	phylogenetic		0.019	0.004	0.73	<b>&lt;0.001</b>
age	non-phylogenetic		-0.010	0.003	0.37	<b>0.002</b>
	Family	251	-0.005	0.005	0.55	<b>0.349</b>
	phylogenetic		-0.005	0.005	0.19	0.274
longevity	non-phylogenetic		-0.025	0.005	0.37	<b>&lt;0.001</b>
	Family	185	-0.001	0.006	0.58	0.822
	phylogenetic		-0.011	0.005	0.24	0.051

597

598

599 **b. annual temperature**

trait	model	n	slope	se	model R <sup>2</sup>	p
clutch frequency	non-phylogenetic	490	0.021	0.002	0.23	<b>&lt;0.001</b>
	Family		0.011	0.002	0.63	<b>&lt;0.001</b>
	phylogenetic		0.009	0.002	0.05	<b>&lt;0.001</b>
clutch size	non-phylogenetic	798	-0.016	0.002	0.43	<b>&lt;0.001</b>
	Family		-0.005	0.002	0.72	<b>0.004</b>
	phylogenetic		-0.003	0.002	0.20	<b>0.039</b>
hatchling size	non-phylogenetic	632	0.0004	0.002	0.83	0.782
	Family		0.003	0.002	0.88	0.171
	phylogenetic		0.003	0.002	0.68	0.201
productivity	non-phylogenetic	435	0.009	0.003	0.80	<b>0.003</b>
	Family		0.008	0.003	0.89	<b>0.006</b>
	phylogenetic		0.008	0.003	0.72	<b>0.007</b>
age	non-phylogenetic	251	-0.018	0.003	0.43	<b>&lt;0.001</b>
	Family		-0.022	0.003	0.63	<b>&lt;0.001</b>
	phylogenetic		-0.018	0.003	0.28	<b>&lt;0.001</b>
longevity	non-phylogenetic	185	-0.015	0.005	0.31	<b>0.002</b>
	Family		-0.014	0.004	0.60	<b>0.005</b>
	Phylogenetic		-0.015	0.005	0.26	<b>0.002</b>

600

601 Life history traits as functions of a. body temperatures; b. mean annual temperatures; Family:  
602 non phylogenetic models with family as a fixed effect. All response variables are log<sub>10</sub>  
603 transformed. Age is age at first reproduction (in months). Female body mass is used as a covariate  
604 in all analyses. Lambda is significantly different from 0 and 1 in all models. Significant associations  
605 between temperature and life history traits are shown in bold.

606

607 **Figure Legend:**

608 **Figure 1:** Frequency distribution of mean annual temperatures (light gray) and lizard body  
609 temperatures (black).

610 **Figure 2:** Mean annual environmental temperatures and body temperatures across lizard species.

611 **Figure 3:** Body (white) and mean annual temperatures (gray) of diurnal, nocturnal and cathemeral  
612 lizards. The box shows the median (horizontal bar) and interquartile range, whiskers are 1.5 times  
613 the interquartile range, More extreme values are presented outside of the whiskers.

614 **Figure 4:** Mean annual environmental temperatures and body temperatures of diurnal (white  
615 diamonds), nocturnal (black circles) and cathemeral (gray triangles) lizards

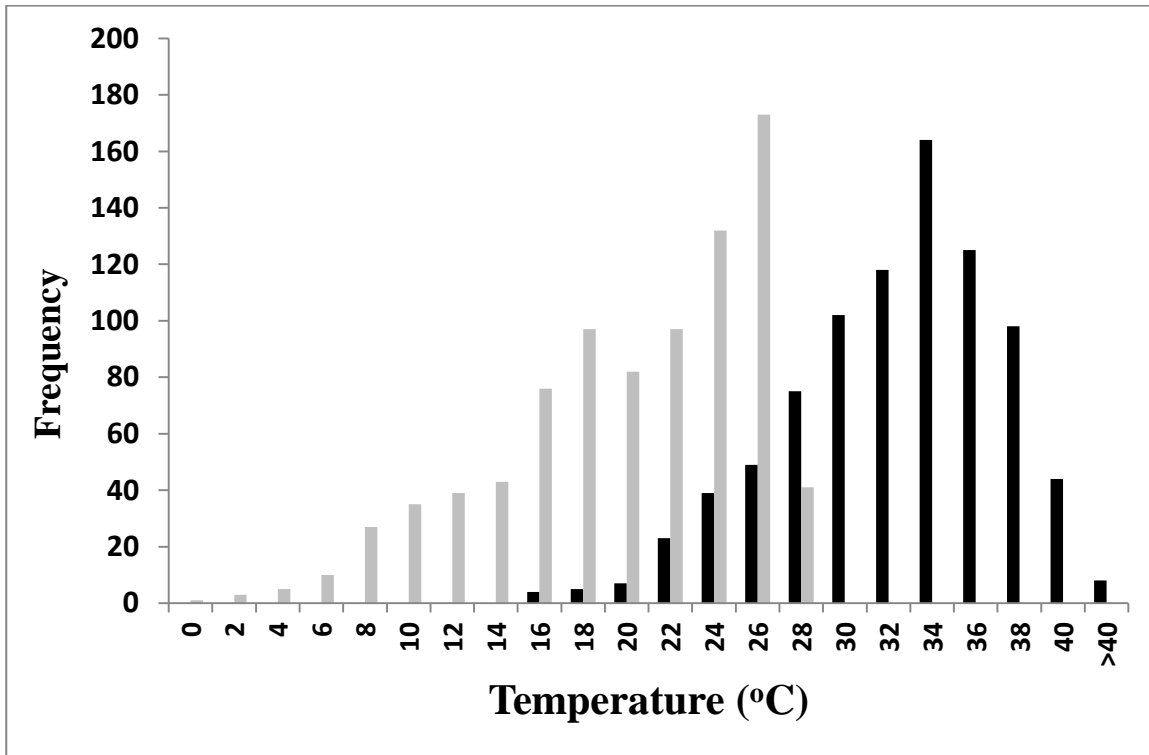
616 **Figure 5:** Differences in body (left) and environmental temperatures (right) of oviparous and  
617 viviparous lizards. The box shows the median (horizontal bar) and interquartile range, whiskers are  
618 1.5 times the interquartile range, More extreme values are presented outside of the whiskers.

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

624

625

626 **Figure 1:** Frequency distribution of mean annual temperatures (light gray) and lizard body  
627 temperatures (dark gray).



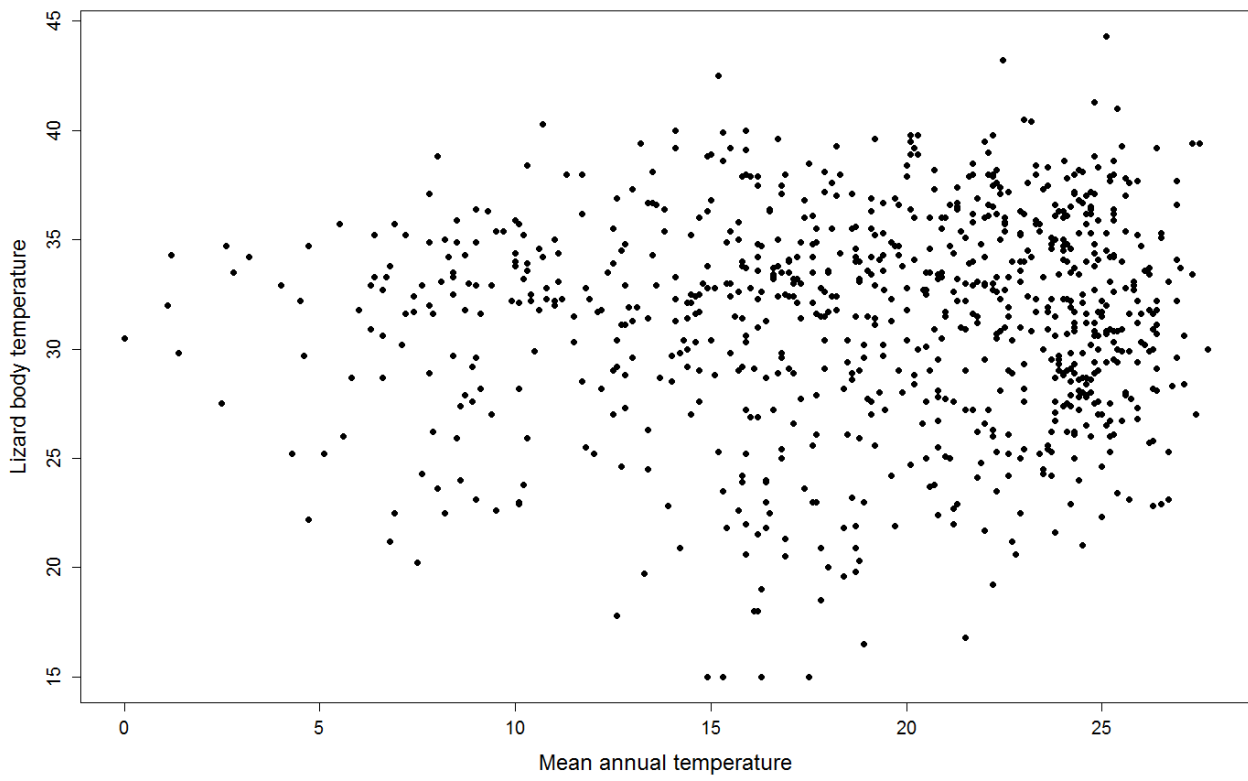
628

629

630

631

632 **Figure 2** – Mean annual environmental temperatures and body temperatures across lizard  
633 species.

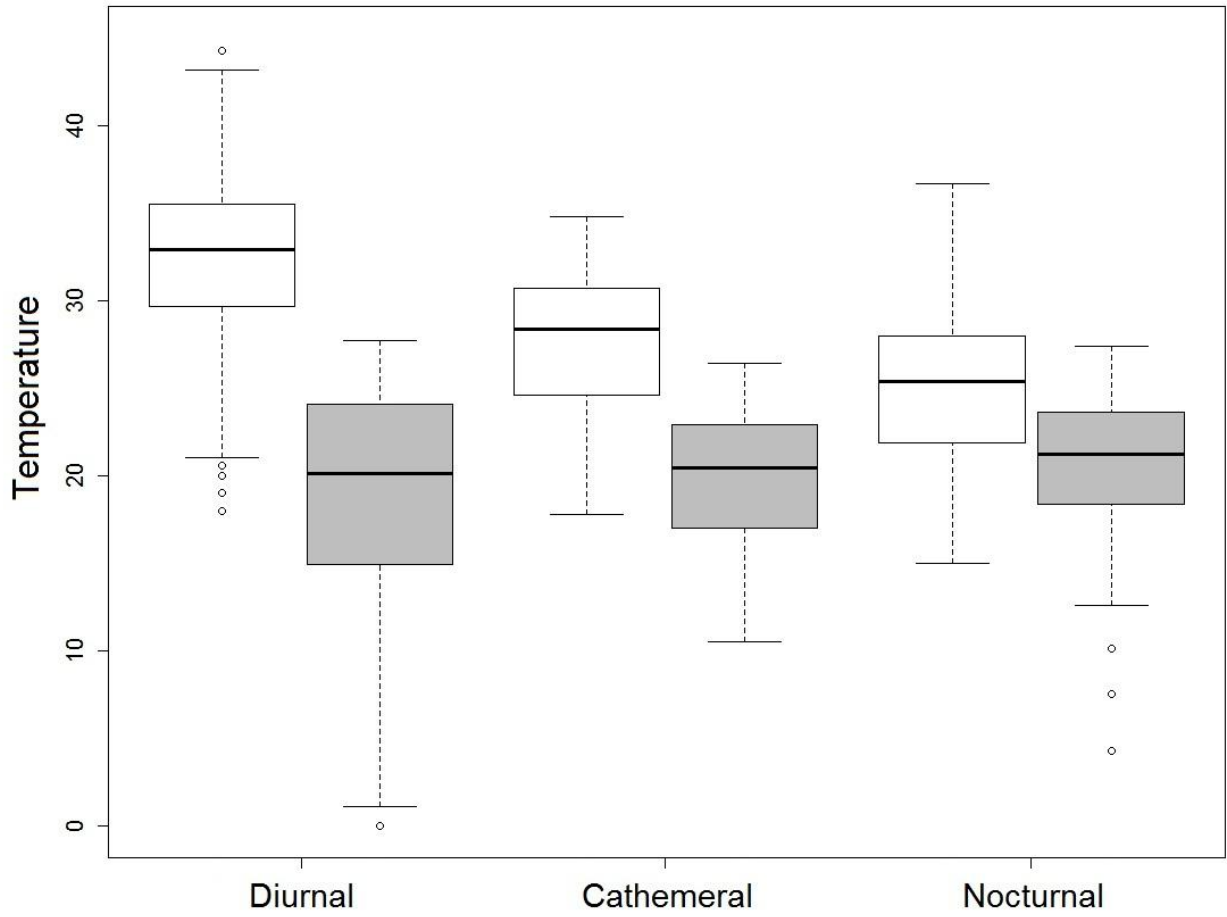


634



635 **Figure 3**

636



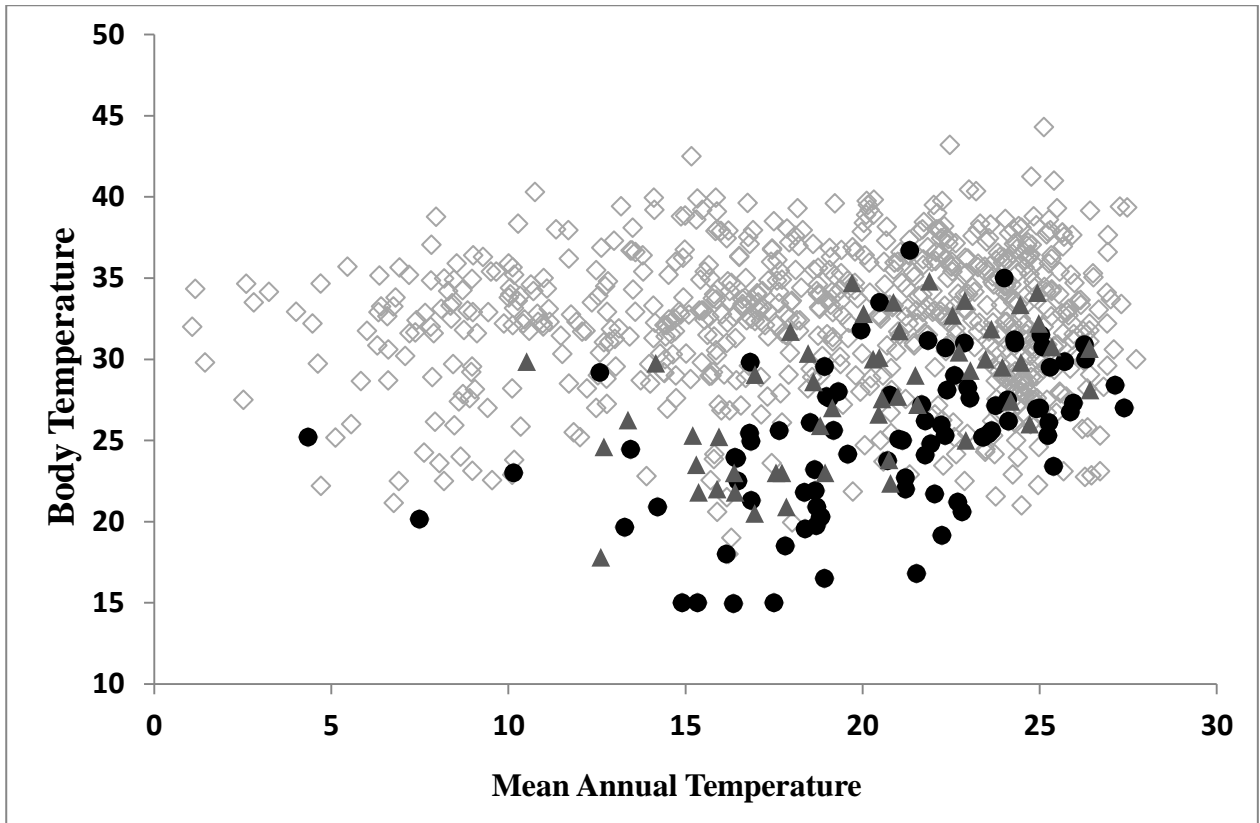
637

638

639

640 **Figure 4**

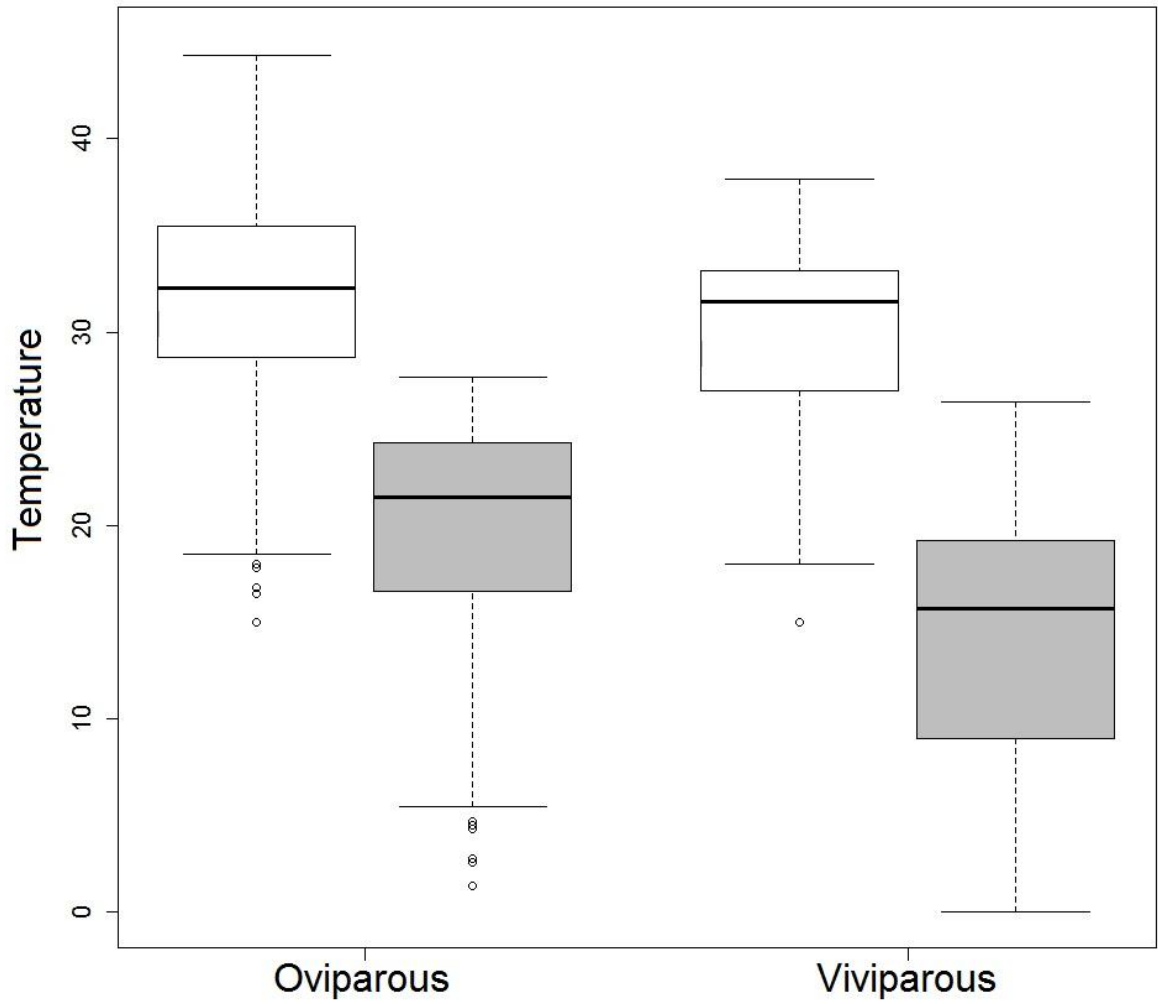
641



642

643

644 **Figure 5** - body temperatures (left, white) and mean annual temperatures (right, gray) of  
645 oviparous and viviparous lizards.



646

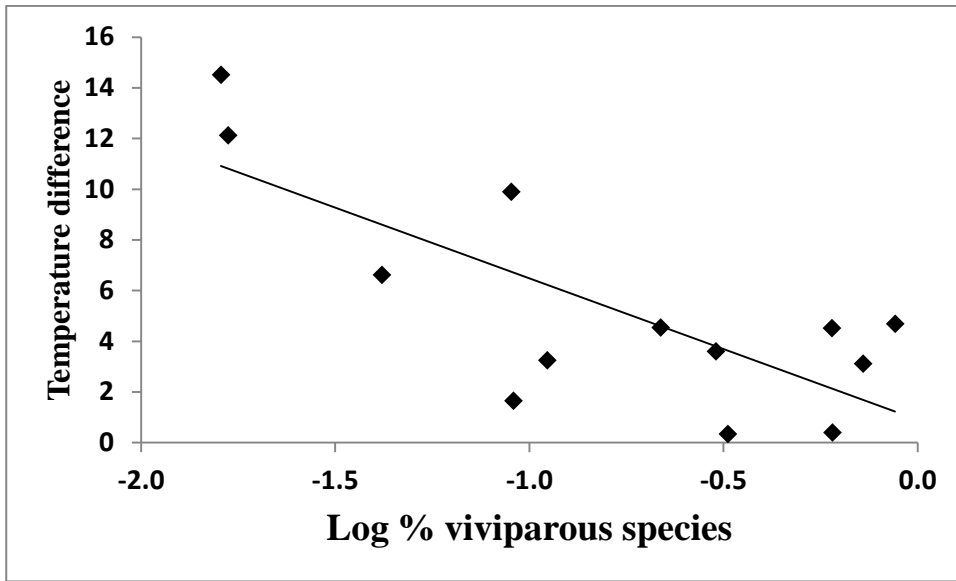
647

648

649

650 **Figure 6**

651



652

653

654

655