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

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Research Paper

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38 Running title: lizard body & environmental temperatures

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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 thanspecies 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). 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 mass = 3.48 * log (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 λ (Pagel 1999)

210   implemented in the R package caper (Orme et al. 2012). Pagel's λ 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

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 = $19.0 \pm 5.8^{\circ}$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 ± 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 ± 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 $\geq 29^{\circ}$C, Appendix S4)

241   show low temperatures.

Modeling lizard body temperatures

243   We retrieved a significant relationship between body and mean annual temperatures (slope 0.13

244   ± 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   ± 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 ± 4.2 vs. 25.1 ± 4.6°C, t = 15.3, p < 0.0001; cathemeral species: 27.8 ± 4.2, n = 54), even

254   though they inhabit colder environments (18.8 ± 6.0 vs. 20.5 ± 4.3 °C, t = 2.6, p = 0.009, cathemeral

255   species: 19.9 ± 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 ±

259   0.026), than body temperatures of cathemeral and nocturnal lizards (slopes = 0.549 ± 0.144 and

260   0.499 ± 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 ± 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±0.026), activity time (nocturnal species "colder" than diurnal ones

271   by $4.8 \pm 0.7\,^{\circ}$C), and insularity (insular endemics "colder" by $1.8 \pm 0.3^{\circ}$C), but neither diet (F = 0.3,

272   p = 0.78, n = 861) nor body size (slope = -0.06 ± 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. $31.8\,^{\circ}$C, the median body temperature is

280   only 0.8 degree colder, 31.5 vs. $32.3\,^{\circ}$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 (Agamididae, 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, Ibargüengoytía 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.

19

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

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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

Table 1 – mean annual temperatures (^{o}C) encountered by viviparous and oviparous lizard species, and the percentage of viviparous species within families.), The % 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 (Meiri, unpublished, not in the dataset analyzed here). *: significant difference between temperatures of viviparous and oviparous species (t tests, not shown). **: p = 0.054. †: na (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%

595 **Table 2 –** the effects of body and environmental temperatures on lizard life history traits

596   **a. body temperature**

trait	model	n	slope	se	model R^2	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	**<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

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598

599   **b. annual temperature**

trait	model	n	slope	se	model R^2	p
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**

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 log10

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

Figure Legend:

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

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

Figure 3: Body (white) and mean annual temperatures (gray) 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.

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

Figure 5: Differences in body (left) and environmental temperatures (right) 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.

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

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

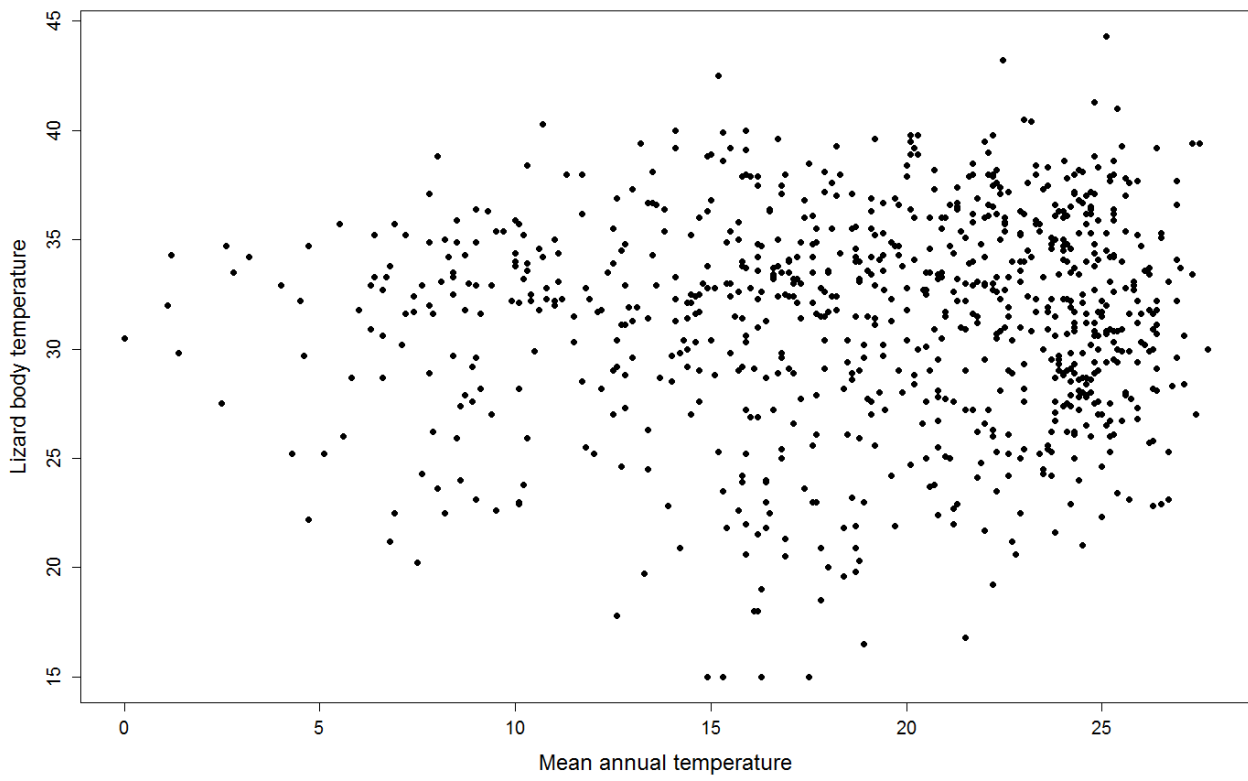627   temperatures (dark gray).

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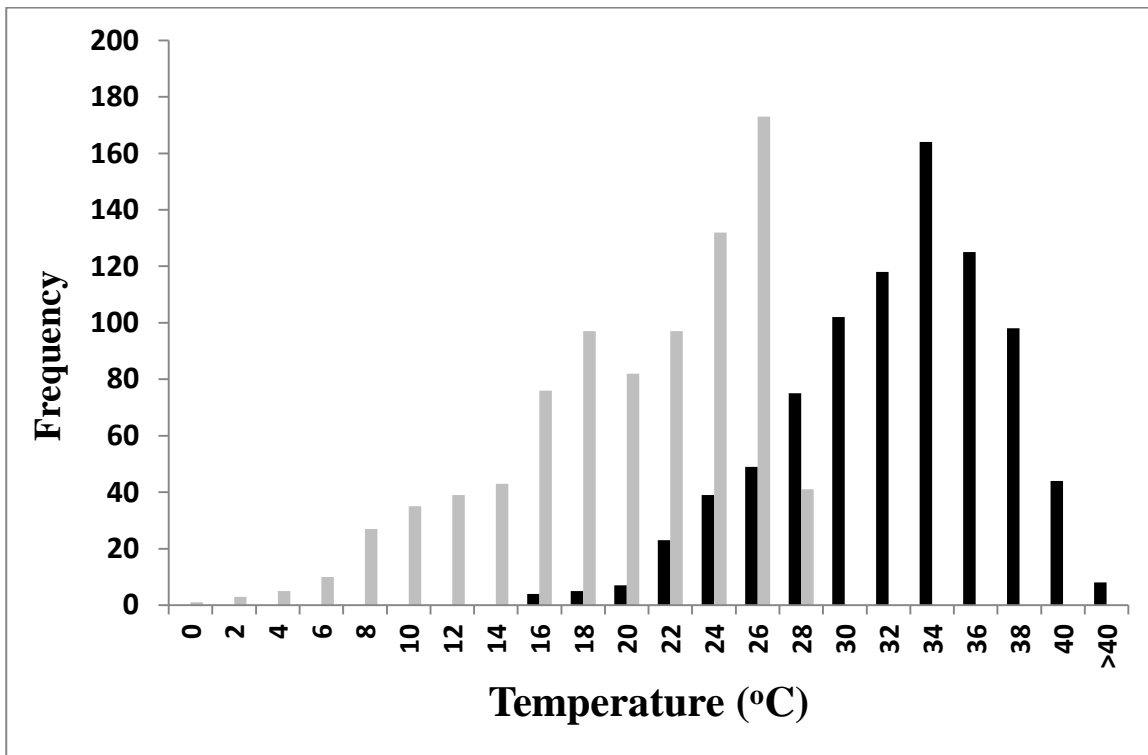
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632   **Figure 2** – Mean annual environmental temperatures and body temperatures across lizard
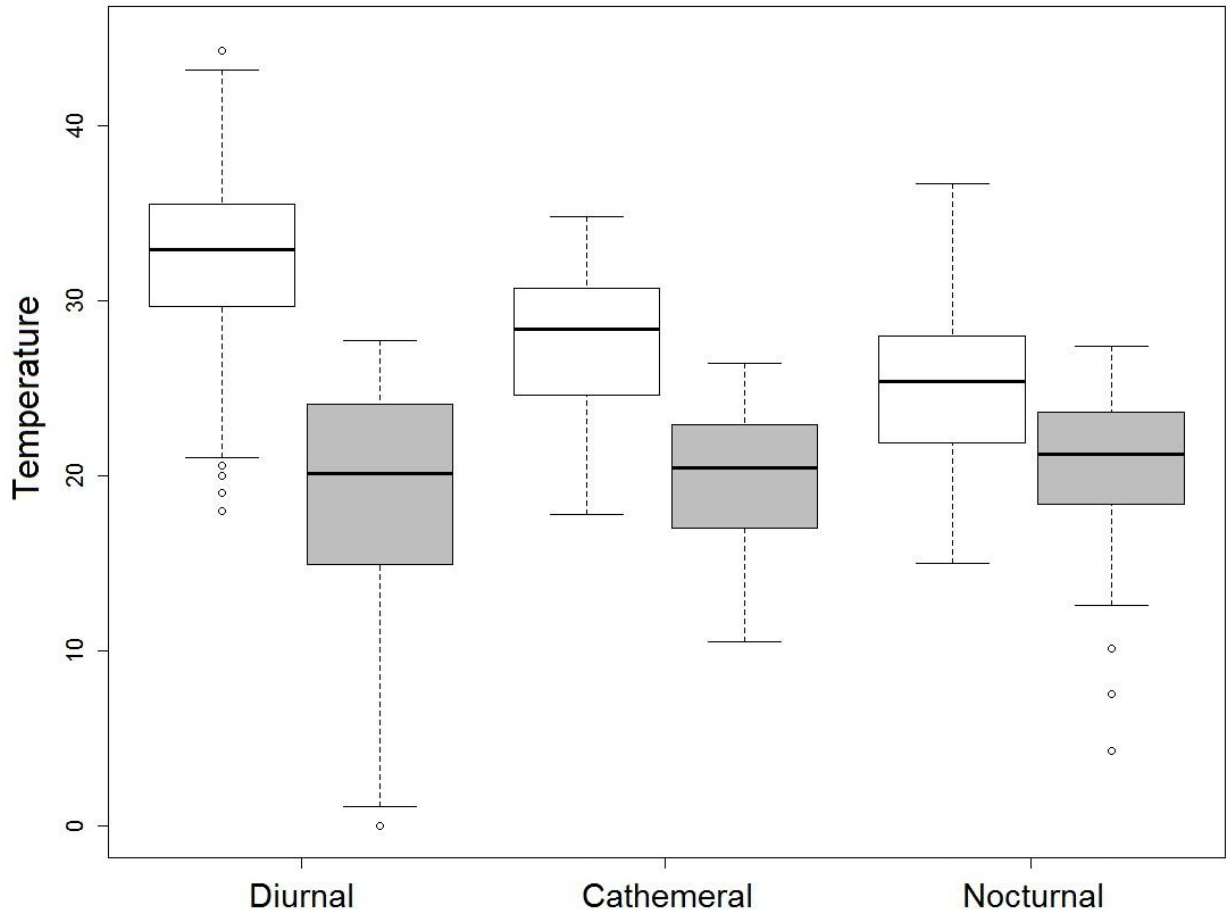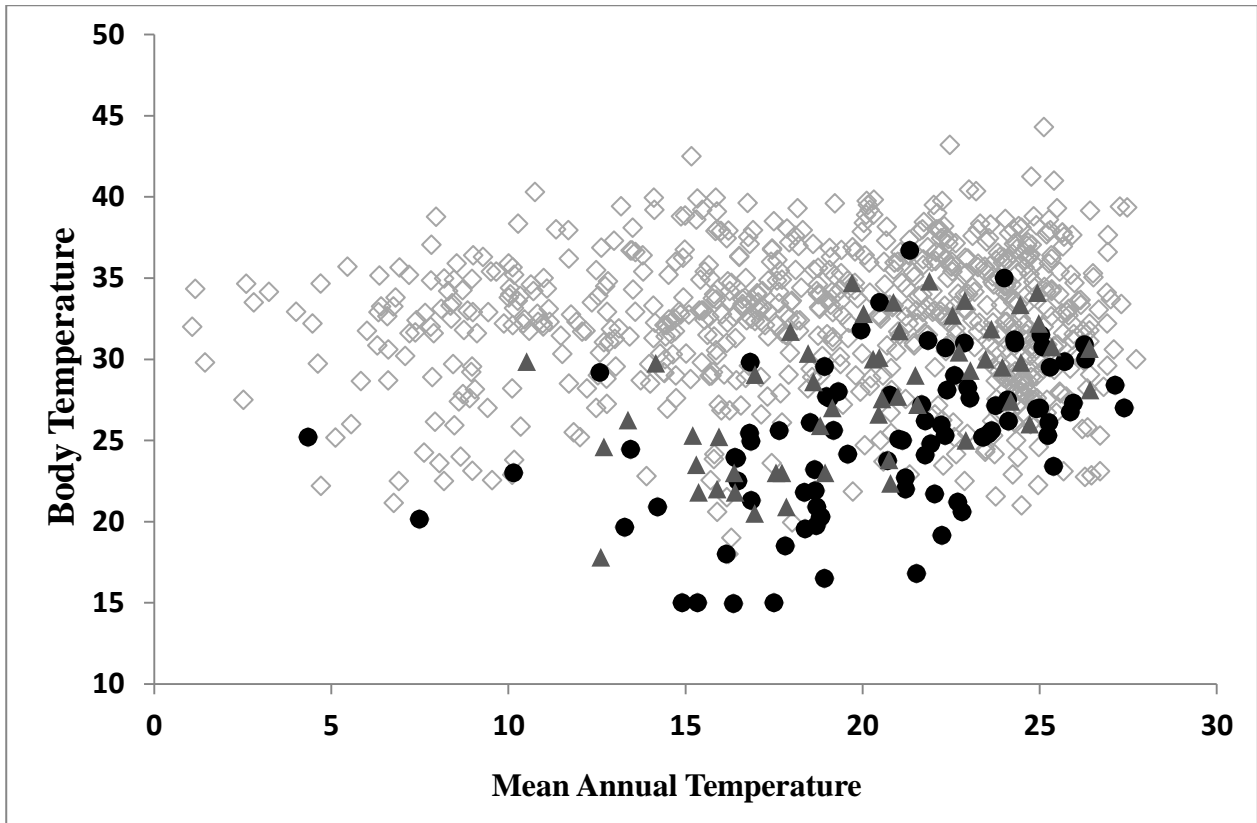
633   species.

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635   **Figure 3**
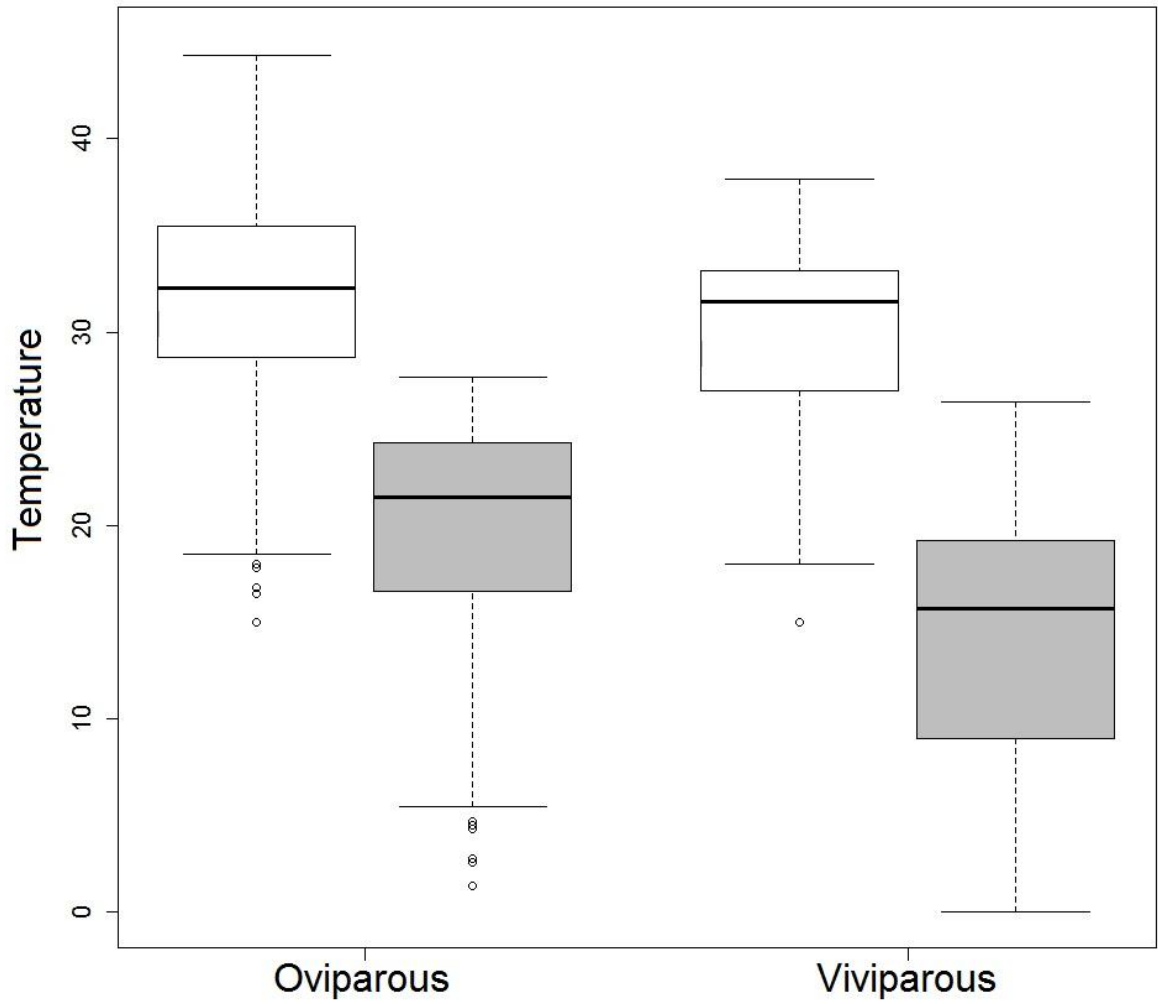
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640   **Figure 4**

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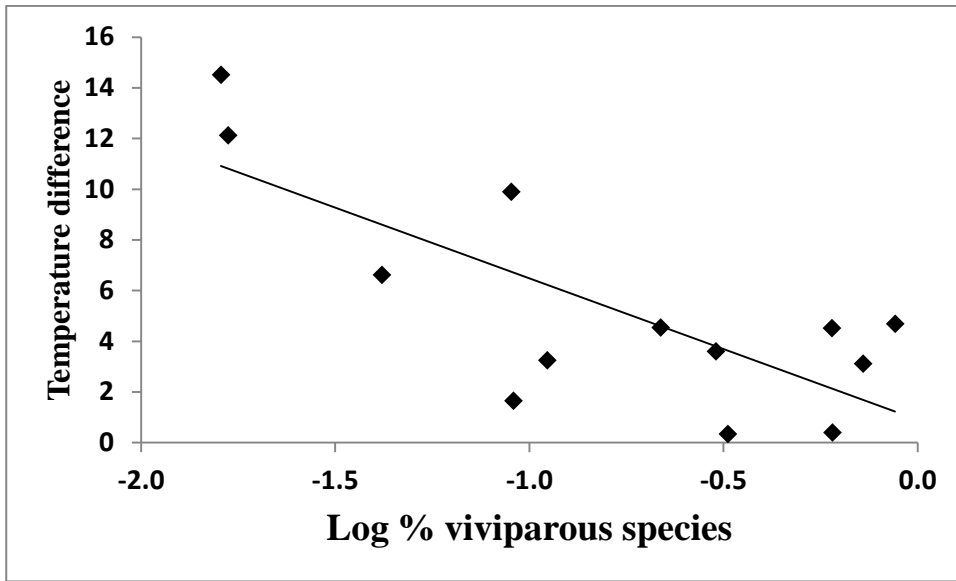
645 oviparous and viviparous lizards.

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650   **Figure 6**

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