

**Eco-physiological Predictors of Ectothermic Species Response  
to Climate Change in a Global Biodiversity Hotspot**

by

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## **ABSTRACT**

As ecological conditions are transformed by a changing global climate, it is becoming increasingly essential to understand the vulnerability and response of organisms to these altered environmental circumstances. Whereas some strides have been made in understanding the effects of global climate change on endotherms, woefully little is known about ectotherms, which constitute the bulk of the diversity of species in natural ecosystems. Though ectothermic organisms can compensate for fluctuations in the thermal environment by modifying their behavior and physiology, these adjustments likely represent a tradeoff between maintaining an optimal body temperature and allocating energy to other important life history processes (i.e. foraging, anti-predator behaviors and mate-finding). While global climate change is likely to affect many aspects of a species' life history and ecology (e.g. susceptibility to disease, food availability, etc.) some of the most direct impacts are likely to come from a possible mismatch between newly prevailing thermal conditions and the species' thermal preferences.

We investigated the thermal biology of four ecologically important reptile species in the Central Aegean Sea (Greece): *Podarcis erhardii* (Linnaeus 1756, *Lacertidae*), *Laudakia stellio* (Linnaeus 1758, *Agamidae*), *Mediodactylus kotschy* (Steindachner 1870, *Gekkonidae*), and *Hemidactylus turcicus* (Linnaeus 1758, *Gekkonidae*). We determined the preferred body temperature for each species using a controlled thermal gradient in the lab. Combining these average thermal preferences with morphological measurements, field body temperatures, and microhabitat characteristics, our work sheds light on the thermal ecology of each species.

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## INTRODUCTION

Global climate change is known to affect a broad range of ecosystems and ecological processes (Sala *et al.* 2000). By the end of the 21st century, mean global temperatures are predicted to increase by 2°C (IPCC 2014). To manage and ameliorate the impacts of these changes on earth's biodiversity, it is essential for scientists to understand the processes through which climate change affects free-ranging organisms (Hughes 2000). Ectotherms are species that cannot control their temperature metabolically, but rather depend on external sources for heating and cooling. They are the most common group of organisms on the planet, and are particularly susceptible to changes in the ambient thermal environment. Yet most of the research to date has focused on endothermic organisms, i.e. mammals and birds, which constitute a relatively small part of the planet's biodiversity.

To evaluate the vulnerability of ectothermic species to changing environmental conditions, i.e. their ability to survive under altered thermal environments, it is critical to have accurate ecological (e.g. habitat preferences, prevailing environmental conditions), as well as physiological (e.g. thermal preferences) data (Huey *et al.* 2012; Williams *et al.* 2008). This information is particularly useful if it can be combined with data on species performance under altered thermal regimes; measuring a direct response to increased temperatures, like performance, allows us to quantify the potential adaptability to climate change.

To address this question I focused on 4 common species of reptiles to survey and to measure their thermal preferences. Research took place in a region that is likely to

experience particularly important climate shifts in the future: the Mediterranean Basin. This region is not only a global biodiversity hotspot, but has also been identified as an area likely to experience severe climate change as ambient temperatures are expected to increase by 4-5°C in the warm season (Giorgi 2006; Giorgi & Lionello 2008).

## **Reptile Thermal Biology**

### ***Thermoregulation in Ectotherms***

Unlike endotherms, ectothermic organisms cannot use metabolic heat for thermoregulation and thus must deal with variable temperature by regulating their body temperature through behavioral, physiological, and morphological modifications. The interaction between prevailing climatic conditions and a species' ability to thermoregulate ultimately determines where a species is found. If prevailing temperatures shift outside a species' thermal preference, the population may decline or even be driven to extinction (Huey & Kingsolver 1989; Foufopoulos *et al.* 2011). Environmental factors like wind speed and air temperature have an impact on the prevailing environmental temperature; the variations of these factors over time and space create patterns of thermal heterogeneity in an environment. Altitude, aspect, and slope also impact these patterns by altering the conditions that an organism might experience on a microhabitat scale (Angilletta 2009).

Ectotherms weigh the costs and benefits of each thermoregulatory tactic to maximize their fitness and survival. For instance, energy expended for thermoregulation cannot be used in growth or reproduction. Similarly, reptiles basking on an exposed rock

may expose themselves to predators. Reptiles may also utilize evaporative cooling to shed heat, but this may be at a cost to the organism, because water loss affects performance (Angilletta 2009). On a finer scale, the body's biochemical and physiological reactions have a thermal dependence, and these constraints affect organismal function and performance (Huey *et al.* 2012). Although organisms can skirt their thermal limits through careful choice of appropriate activity and thermal microhabitat, these changes can be of limited use depending on the characteristics of the habitat and predation risk (Deutsch *et al.* 2008).

Ectothermic individuals perform at their best if they are close to their thermal optimum (Angilletta 2009). Additionally, organisms with a higher thermal optimum have a higher peak performance than organisms with a lower thermal optimum; this is because enzymes catalyze chemical reactions faster and more efficiently at hotter temperatures (Angilletta *et al.* 2009). One study examined the correlation between thermal optimum and maximal locomotion performance of 13 European lizard species (Bauwens *et al.* 1995). The results indicated that higher preferred temperatures were related to higher maximal performance (below the critical thermal maximum): species at optimal temperatures reached the highest speeds and were able to run at near-maximum levels (Bauwens *et al.* 1995).

### ***Using Laboratory Thermal Preference Data to Draw Population Inferences***

Measuring thermal preferences of an ectotherm organism involves recording its body temperature under standardized conditions as it selects its preferred temperature



from a monotonic heat gradient. This method allows us to avoid other variables that may be interacting with thermal preference like the presence of water, food, and threat of predators. Measuring thermal preferences in a setting where only temperature is variable is a standard and repeatable methodology in reptile thermal biology (Licht *et al.* 1966; Osojnik *et al.* 2013; Angilletta 2009).

Thermal preferences can be compared with measures of temperature in the field to see how organisms are thermoregulating in their natural environments and thus, how organisms are utilizing behavioral and physiological strategies. To measure thermal heterogeneity on small scales, it is standard to use mathematical, statistical, or physical models (Angilletta 2009). Data loggers inside physical models of an individual lizard, can be deployed at research sites, and are convenient in that they measure the properties of living organisms in the absence of physiological function; they can be particularly useful on small scales like in an island microhabitat.

Morphological characteristics of an ectothermic individual, like body size, may also have an impact on body temperature. Thermal inertia represents the body's ability to conduct and store heat: in general, larger individuals will heat up more slowly but also retain heat longer than smaller individuals. Larger ectothermic reptiles raise their temperature more slowly and thus often have lower thermal preferences than smaller species, which generally heat up more rapidly (Cowles & Bogert 2006; Garrick 2008).

Comparing thermal preference measurements with morphological and thermal environment data allows for species-specific connections in a survey of common Mediterranean reptiles located in different microhabitats.

### **Sensitivity of Mediterranean Reptiles to Climate Change**

Current research suggests that the Mediterranean is exceptionally vulnerable to climate change. Giorgi (2006) used data from the most recent climate assessment to identify climate change 'Hot-Spots' around the world using a Regional Climate Change Index (RCCI), which is based on comparisons between current and predicted surface air temperatures and precipitation. This index represents how much each region will be subject to climate change, relative to other regions included in the analysis. Second only to Northeastern Europe, the Mediterranean region is one of the top most prominent climate change Hot-Spots emerging from the RCCI analysis (Giorgi 2006). The Mediterranean ranked high because of the potential for a greater than average decrease in mean precipitation in the dry season coupled with an increase in precipitation variability (Giorgi *et al.* 2001; Giorgi & Lionello 2008).

Being taxa of low vagility, most reptile species are restricted to the thermal conditions provided by their immediate thermal environment. Mediterranean island reptiles are restricted both by location and by prevailing regional thermal conditions; this may make them further vulnerable as climate change is expected to force species distributions toward higher elevations and latitudes (Araujo *et al.* 2006; Walther *et al.* 2002).

## METHODS

### Study System

Research was conducted during summer 2015 on the Mediterranean island of Naxos in the Aegean Sea (Greece). This region is located between arid North Africa and rainy, temperate central Europe (Giorgi & Lionello 2008) and is characterized by a maritime climate with long dry summers and mild rainy winters. The specific island was chosen because it harbors particularly diverse species communities; visiting them permits sampling a significant portion of the reptile species found in the NE Mediterranean Basin (Ioannides *et al.* 1994).

We measured field body temperature at the time of capture ( $T_b$ ), laboratory thermal preferences ( $T_p$ ), and environmental characteristics of each individual lizard's microhabitat. We sampled 4 species from 7 sites that represent a variety of typical Mediterranean habitats (Fig. 1).

### Study Organisms

For this study I focused on *Laudakia stellio* (rough-tailed agama, *Agamidae*), *Mediodactylus kotschy* (Kotschy's gecko, *Gekkonidae*), *Hemidactylus turcicus* (Turkish gecko, *Gekkonidae*), and *Podarcis erhardii* (Aegean wall lizard, *Lacertidae*). These species are among the most common reptiles on the Aegean Islands and inhabit a broad swath of habitats across the Cycladic archipelago.

The rough-tailed agama is distributed through a portion of the Middle East and reaches its western limit of its geographic range in Greece. It can grow to an adult snout-

to-vent (SVL) length of 12 cm and occurs in all Mediterranean habitats that provide enough vertical structure to be used as climbing refugia (Foufopoulos *et al.* 2011). Individual agamas can change their dorsal coloration, often showing displays of blue or yellow, but are primarily a dark grey background color with plate-like scales (Valakos *et al.* 2008).

Kotschy's gecko is a small gecko with an average SVL of 4 cm and is common throughout mainland Greece, and on the islands of the Aegean and Ionian Seas (Valakos *et al.* 2008). It is generally encountered low to the ground on stony structures or rocks. This species is also present on very small islets and at high altitudes, indicating its ability to persist in unproductive environments (Valakos *et al.* 2008).

The Turkish gecko (~4 cm SVL) also inhabits stony structures and rocks but has adhesive pads and a pinkish-white translucent color, distinguishing it from Kotschy's gecko (Valakos *et al.* 2008). This organism is typically nocturnal but can be found active during the day in spring and summer (Valakos *et al.* 2008). In addition to utilizing the cool underside of rocks for refuge from overheating and predators, the Turkish gecko is found particularly often on urban structures like light posts and the walls of buildings (V. Tamez, personal obs.), reflecting its superb climbing abilities.

Lastly, the Aegean wall lizard (*Podarcis erhardii*) is a Balkan endemic that is the most common species encountered on the Aegean islands (Valakos *et al.* 2008). There are many differences in coloration and patterning across the species' populations, with females tending to have a brown dorsum and males ranging from brown juveniles to green as adults. Reaching an SVL of about 7.5 cm, the Aegean wall lizard occurs in all

habitats on Naxos except in closed-canopy forest. It is particularly common along rock walls that provide thermoregulatory opportunities and refugia from predation, but island populations can also occur in more open areas like sand dunes (Valakos *et al.* 2008).

### **Field Measurements**

*Assessment of organism's environment-* We captured individuals using a string noose attached to a telescopic fishing pole, or by hand. Sampling took place during known active hours each day (morning to mid-afternoon), and both during the day and at night for the nocturnal Turkish gecko. Body temperature was measured within 3s of capture by inserting a quick-read glass cloacal thermometer (Miller & Weber Model T-6000) approximately 5mm into the cloaca. Immediately following the body temperature measurement, substrate temperature was determined by pointing an infrared thermometer (Fluke 62 MAX 2012) at the exact location that the lizard was captured from – the type of substrate the individual was found on was also recorded. To identify each species' environmental preferences, microhabitat type and the location of each individual in the microhabitat were recorded. Lastly, we noted the activity of the individual when found (basking, sprinting, or hiding) as well as any associated behaviors.

*Habitat data* – Information on the local thermal environment was obtained by deploying 7 long-term data loggers in a variety of reptile microhabitats (Huey *et al.* 2012) – the collected temperature data were then calibrated using available long-term meteorological datasets from the Naxos weather stations. Each data logger probe was inserted into a white PVC tube closed on both ends with cork and silicone (Bakken 1992; Dzialowski

2005). Data loggers were placed in olive grove, forest, phrygana, farm field, riparian, rock field, and beach habitats to capture conditions in typical reptile habitats. Temperature was recorded at 10 min intervals over 4-12 sampling days at each of the study sites; daily mean, maximum, and minimum site temperatures were then calculated from these data. Any daily temperature measurement that was deemed implausible was removed from the analysis; this included days where less than 24 h of data were collected, days where the data logger was not functioning (due wildlife interference rendering the probe damaged), and days where the data logger was in the possession of the field team and not actively collecting habitat data. The following number of days were removed from each site prior to analysis: olive grove – 2, forest – 11, phrygana – 1, farm field – 2, riparian – 0, rock field – 0, beach – 0.

### **Laboratory Measurements**

*Housing* – After collection, all animals were transported to a lab and housed individually in 32 x 17 x 9 cm terrariums with screen lids. A 40W incandescent light bulb was hung 20 cm above one end of the terrarium to provide a thermal gradient; rocks were placed at each end of the terrarium to allow for basking or refuge. The timed light bulbs remained on between 6:00 and 18:00, then switched off, to maintain 12h-12h day/night cycles. Water was supplied *ad libitum*, and animals were fed unlimited mealworms post-testing. Following data collection, all animals were immediately released back into their original territories.

*Morphology* – Mass and snout-vent length (SVL) measurements were collected upon capture, and sex of all individuals and reproductive condition of females was noted.

*Assessment of thermal preferences* – Individuals were acclimated to laboratory conditions for at least 8h before testing, and were tested within 12h of capture. Each animal was moved to a 150cm x 20cm x 42cm fiberboard corridor with 1-2 cm of sand on the corridor floor to represent a typical substrate. A broad thermal gradient (~20-43 °C) was created by securing a 100W heating lamp 40 cm above the corridor floor on one end and a bag of ice at the other, which allowed the animal to select its preferred  $T_b$ . To measure reptile body temperatures, a 0.8mm thermocouple covered in epoxy was taped to the cloaca (B. Sinervo, *pers. comm.*), and the other end of the thermocouple was plugged into a digital thermometer (Omega Engineering Model HH506A), which allowed for constant body temperature readings throughout each trial without restricting the organism's movement. Once placed in the corridor, each individual was allowed to acclimatize for 10 min before  $T_b$  was measured for 60 min at 2-min intervals. Temperature measurements collected over the 60 min trial were averaged to produce the individual's  $T_p$ ; individual values were then averaged across each species to estimate that taxon's  $T_p$ .

All work was carried out in accordance with the Hellenic National Law (Presidential Decree 67/81) on the humane use of animals, and the University of Michigan Committee on Care and Use of Animals (UCUCA permit #PRO00005585).

## **Statistical Analysis**

Data were analyzed using IBM SPSS Statistics Ver. 20 (IBM Corporation, 2011). If behavioral notes indicated that an individual was stressed or not compliant at the time of  $T_p$  measurements, we excluded all relevant data from the analyses. We tested all variables for violations of test assumptions regarding linearity, homoscedasticity, normality and independence of residuals, and confirmed that all assumptions were satisfied.

To compare the thermal properties of different habitats on Naxos we constructed general linear models using mean, maximum, or minimum site temperatures from data loggers as the dependent variables, and included site as a fixed factor, as well as the corresponding Naxos weather station statistics (mean, maximum, or minimum daily temperatures respectively) as covariates.

We used a general linear model (GLM) to determine differences in field body temperatures across sites; body temperature was the dependent variable and site was the fixed effect. We used a one-way ANOVA to compare species thermal preferences between the 4 study species. Pearson's Correlation Coefficient was used to determine relationships between species thermal preference and measurements of SVL, mass, substrate temperature, and field body temperature. We also used Pearson's Correlation Coefficient to determine relationships between species field temperature and SVL, mass, and substrate temperature. Independent samples t-tests were used to test the differences between male and female thermal preferences, and a t-test allowing for unequal variances was used when necessary.



## **RESULTS**

### **Environmental Conditions**

The GLM analyzing daily temperature by site revealed significant differences between mean ( $F = 92.865$ ,  $df1 = 6$ ,  $df2 = 76$ ,  $p < 0.01$ ), maximum ( $F = 86.343$ ,  $df1 = 6$ ,  $df2 = 76$ ,  $p < 0.01$ ), and minimum ( $F = 6.931$ ,  $df1 = 6$ ,  $df2 = 76$ ,  $p < 0.01$ ) temperature across the seven habitat types: beach, forest, riparian, phrygana, olive grove, farm field, and rock field (Appendix A, Table 1). This result indicates that thermal conditions differ by site, with sparsely vegetated sites being the warmest in maximum and mean temperature, and the coolest sites represented by those habitats with more dense vegetation and spaces for refuge (Fig. 2).

A one-way ANOVA found a significant difference in field body temperature of the four species across the sites ( $F = 7.207$ ,  $df1 = 3$ ,  $df2 = 82$ ,  $p < 0.01$ ,  $n = 87$ ). Field body temperature and substrate temperature were significantly positively correlated (Pearson's  $r = 0.690$ ,  $p < 0.01$ ,  $n = 87$ ).

### **Interspecific Comparisons**

Mean thermal preferences by species are reported in Fig. 3. A one-way ANOVA was conducted to determine if thermal preferences differed by species ( $F = 4.306$ ,  $df1 = 3$ ,  $df2 = 84$ ,  $p = 0.007$ ). Tukey post-hoc test revealed that the Turkish gecko ( $n = 17$ ) had

a significantly different thermal preference than the other 3 species, but no other differences were statistically significant.

In the next stage of the analysis, we conduct intraspecific analyses on the effects of field body temperature, substrate temperature, SVL, mass, and sex on thermal preferences.

### **Intraspecific Comparisons**

In Kotschy's gecko ( $n = 27$ ), substrate temperature was significantly correlated with field body temperature ( $r = 0.770$ ,  $p < 0.001$ ), but not with thermal preference ( $r = -0.032$ ,  $p = 0.865$ ). Mass and thermal preference were also significantly correlated ( $r = 0.398$ ,  $p = 0.040$ , Fig. 4). There was a marginal correlation between mass and Kotschy's gecko field body temperature ( $r = -0.376$ ,  $p = 0.053$ ). In contrast, neither SVL ( $r = 0.067$ ,  $p = 0.742$ ), nor field body temperature ( $r = 0.050$ ,  $p = 0.805$ ) were significantly correlated with Kotschy's gecko thermal preference. Kotschy's gecko SVL and field body temperature were also not correlated ( $r = -0.101$ ,  $p = 0.617$ ).

Field body temperature was higher in male Kotschy's geckos ( $29.350 \pm 1.775$  °C,  $n = 14$ ) than female Kotschy's geckos ( $25.954 \pm 3.643$  °C,  $n = 13$ ) according to an independent samples t-test with unequal variances assumed ( $t = 3.042$ ,  $p = 0.007$ ). Thermal preferences differed significantly between Kotschy's gecko sexes and were higher for males ( $34.708 \pm 4.185$  °C) than for females ( $34.369 \pm 3.524$  °C) once we adjusted for the effects of mass and SVL in an ANCOVA ( $F = 5.334$ ,  $df1 = 1$ ,  $df2 = 26$ ,  $p = 0.030$ ).

In the agama ( $n = 21$ ), substrate temperature was significantly correlated with field body temperature ( $r = 0.655$ ,  $p = 0.001$ ), but not with thermal preference ( $r = -0.058$ ,  $p = 0.803$ ). Mass had a marginally significant correlation with thermal preference ( $r = -0.370$ ,  $p = 0.099$ ), but no correlation with field body temperature ( $r = -0.195$ ,  $p = 0.397$ ). Neither SVL ( $r = -0.285$ ,  $p = 0.210$ ) nor field body temperature ( $r = -0.177$ ,  $p = 0.442$ ) were correlated with agama thermal preference. Agama SVL was also not correlated with field body temperature ( $r = -0.324$ ,  $p = 0.152$ ). An independent samples t-test revealed that there were no significant differences between agama male ( $n = 10$ ) and female ( $n = 11$ ) thermal preferences ( $t = -0.009$ ,  $p = 0.993$ ). There were also no sex differences in agama field body temperature according to an independent samples t-test ( $t = -0.171$ ,  $p = 0.866$ ).

Turkish gecko ( $n = 17$ ) field body temperature was not correlated with substrate temperature ( $r = 0.454$ ,  $p = 0.067$ ), and thermal preference was also not correlated with substrate temperature ( $r = -0.123$ ,  $p = 0.639$ ). SVL was correlated with field body temperature ( $r = -0.492$ ,  $p = 0.045$ ) but not with thermal preference ( $r = 0.048$ ,  $p = 0.856$ ). Turkish gecko mass was neither correlated with thermal preference ( $r = 0.222$ ,  $p = 0.391$ ) nor with field body temperature ( $r = -0.404$ ,  $p = 0.107$ ). Field body temperature was also not correlated with Turkish gecko thermal preference ( $r = 0.093$ ,  $p = 0.724$ ). An independent samples t-test with unequal variances assumed indicated that thermal preferences did not differ between male ( $n = 3$ ) and female ( $n = 14$ ) Turkish geckos ( $t = 1.925$ ,  $p = 0.101$ ). Field body temperatures were higher in male Turkish geckos ( $28.200 \pm$

0.721 °C, n = 3) than females ( $25.843 \pm 3.213$  °C, n = 14) according to an independent samples t-test with unequal variances assumed ( $t = 2.470$ ,  $p = 0.026$ ).

For Aegean wall lizard (n = 22) substrate temperature was correlated with field body temperature ( $r = 0.479$ ,  $p = 0.024$ ) but not with thermal preference ( $r = -0.015$ ,  $p = 0.946$ ). Aegean wall lizard SVL was not correlated with field body temperature ( $r = 0.078$ ,  $p = 0.728$ ) or thermal preference ( $r = -0.308$ ,  $p = 0.164$ ). Mass was not correlated with thermal preference ( $r = -0.226$ ,  $p = 0.311$ ) or field body temperature ( $r = 0.073$ ,  $p = 0.747$ ). Aegean wall lizard field body temperature was also not correlated with thermal preference ( $r = -0.047$ ,  $p = 0.836$ ). Due to imbalance of sexes in the Aegean wall lizard sample size, we did not analyze sex differences in field body temperature or thermal preference.

## **DISCUSSION**

The use of thermoregulation to achieve and maintain optimum body temperature allows reptiles to persist in a variety of thermally diverse habitats. This project explores the variation in temperature across several distinct Mediterranean habitats, as well as the thermal preferences of the most important resident species of reptiles.

Our survey of common Mediterranean reptile habitats revealed significant differences in mean, maximum, and minimum temperature across the different habitats (Appendix A, Table 3). Beach was most exposed habitat to direct sunlight, and correspondingly had the highest maximum temperature (52.1°). In contrast, the habitats

with greater proportions of dense vegetation – forest (21.9°), riparian (22.5°), and olive grove (19.9°) habitats – had low mean temperatures (Appendix A, Table 3).

The presence of the agama, Kotschy's gecko, and the Aegean wall lizard at each site (excluding the nocturnal gecko, which was encountered infrequently), coupled with the similarity in thermal preferences among these species, suggests that these 3 species employ a variety of thermoregulatory approaches to achieve their optimal activity temperatures. All species are widespread across a range of sites and habitats on the islands underscoring their abilities as effective thermoregulators. Predicted increases in air temperature and dryness in the Mediterranean Basin could disrupt this balance if thermal environments are altered beyond the ability of reptile thermoregulatory capabilities (Giorgi & Lionello 2008).

Our analyses indicated that only 1 of our 4 study taxa, the Turkish gecko, differed significantly in thermal preference from the other species. This was the only nocturnal species of the group and its  $T_p$  was significantly lower than the rest (Fig. 3). Night provides limited opportunities for thermoregulation, and thus, nocturnal lizards are often active at a lower and more variable temperature than diurnal species (Autumn *et al.* 1994). A study comparing the thermal biology of 5 nocturnal gecko species (including *H. turcicus*) with diurnal lizard thermal preferences revealed that the nocturnal geckos had a lower preferred temperature and a greater body temperature variability than the diurnal taxa (Huey *et al.* 1989). Lower thermal preferences and body temperatures in geckos have additional implications for sprint performance, predation avoidance, and foraging,

all of which are all directly affected by body temperature. Our results fit these conclusions that lower activity temperatures in the field are correlated with a lower  $T_p$ .

Sex-specific differences were also analyzed within all species except the Aegean wall lizard. Male and female lizards have differing reproductive schedules, which are likely to affect the thermal biology of each sex. Male lizards are generally more active as they are more likely to engage in territorial activities than females (Stamps 1977; Tokarz 1995); because of this higher rate of activity which is facilitated by high metabolic rates, one would expect male lizards to select for both higher field body temperatures and have higher thermal preferences in the lab. In contrast, we predicted that females would select for lower body temperatures because they don't need to engage in similarly intense interactions. Furthermore, there is evidence that female lizards are required to maintain lower temperatures while gravid for proper egg development (Mathies & Andrews 1997). We found significant differences between male and female Kotschy's gecko thermal preferences and field body temperatures, with males preferring a higher temperature than females in both cases as predicted (Appendix A, Table 2). There were no sex-related differences in thermal preference or field body temperature for the other species.

This research explored the variety of thermal environments in which these model ectotherms have acclimated to, and reveals that that these 4 species are able to thermoregulate effectively in order to persist in several distinct habitats. Our data and conclusions lend support to how these important Mediterranean ectothermic species acclimate to environmental variability, and will hopefully influence further studies

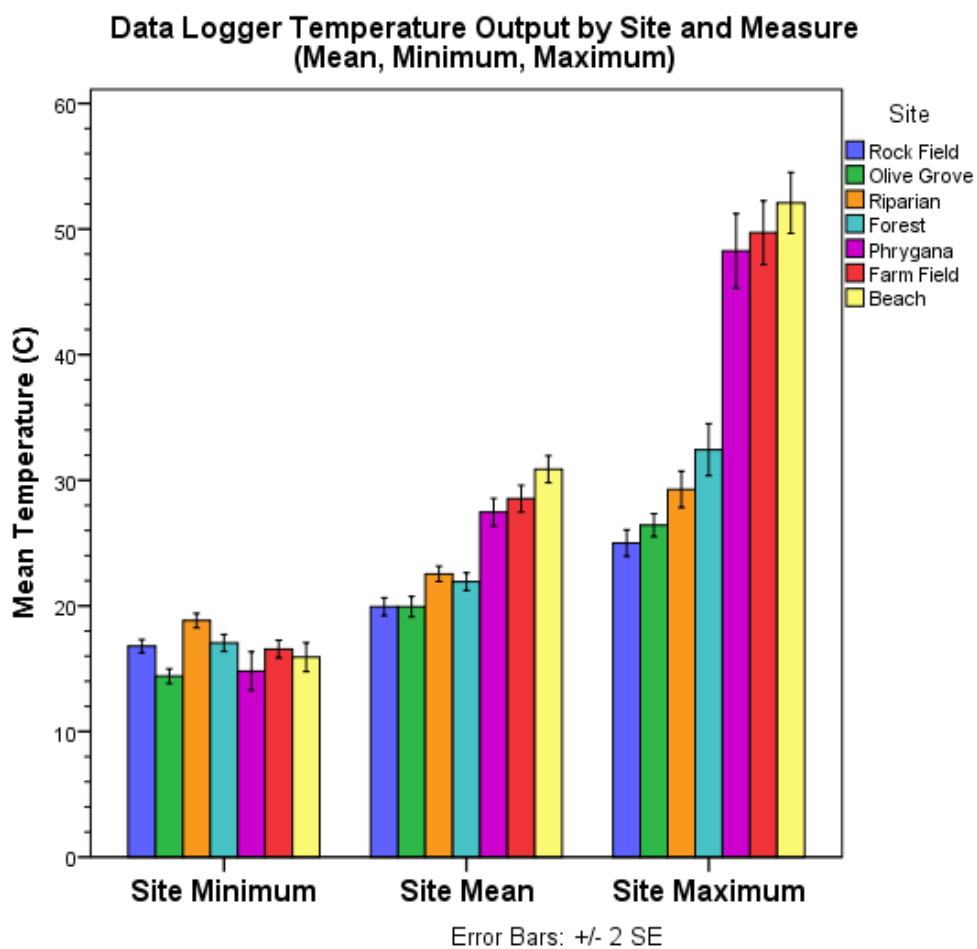
examining Mediterranean ectotherm adaptability and survival in the context of climate change.

## FIGURES

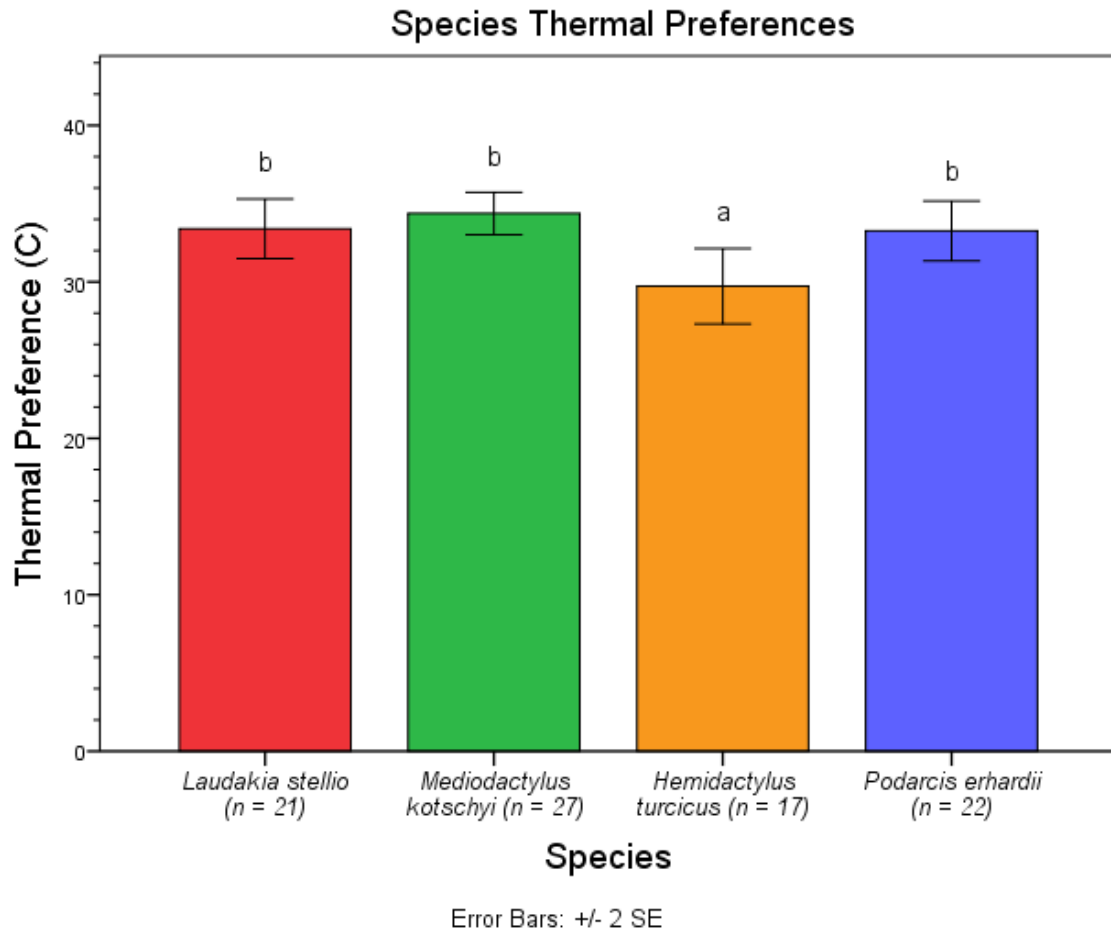


**Fig. 1:** Study sites on the island of Naxos, (Cyclades, C. Aegean Sea, Greece).

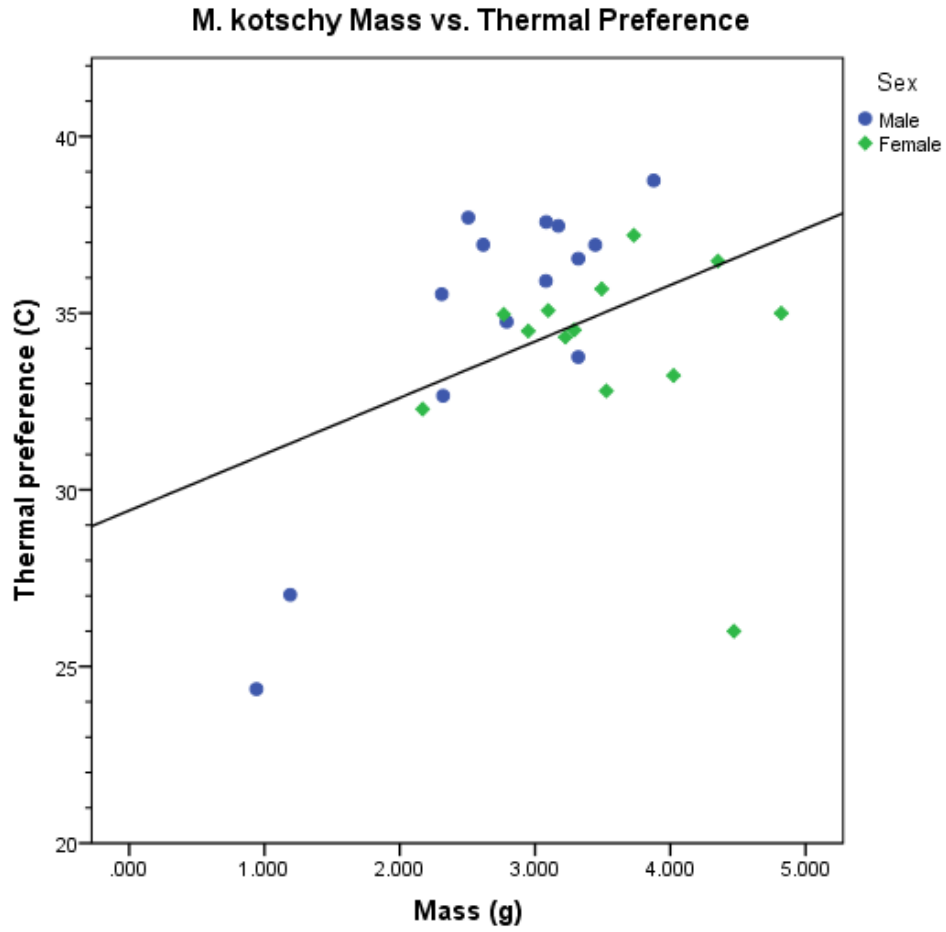




**Fig. 2:** Microhabitat temperature data (daily mean, maximum, and minimum) from 7 common habitat types in the study area.



**Fig 3:** Lab thermal preferences of the species studied



**Fig. 4:** Plot of male and female Kotschy's gecko mass measurements vs. thermal preference

## APPENDIX A

Species	n	SVL (cm)		Mass (g)		Field body temperature (°C)		Thermal preference (°C)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
<i>Laudakia stellio</i>	21	10.20	0.20	57.31	4.03	32.0	0.80	33.4	0.96
<i>Mediodactylus kotschy</i>	27	4.38	0.10	3.11	0.17	27.7	0.60	34.4	0.68
<i>Hemidactylus turcicus</i>	17	4.78	0.10	2.93	0.18	26.3	0.70	29.7	1.21
<i>Podarcis erhardii</i>	22	6.12	0.10	6.65	0.33	31.2	0.70	33.3	0.96

**Table 1:** Species sample sizes, average field body temperatures, thermal preferences, and morphological measures

Sex	<i>Laudakia stellio</i>		<i>Mediodactylus kotschy</i>		<i>Hemidactylus turcicus</i>		<i>Podarcis erhardii</i>	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Male	33.4	1.53	34.7	1.12	32.9	1.48	33.1	1.00
Female	33.4	1.26	34.0	0.77	29.0	1.38	35.9	0.00
Sample size	M = 10, F = 11		M = 14, F = 13		M = 3, F = 14		M = 21, F = 1	

**Table 2:** Sex differences in thermal preference by species

Habitat Type	Average Minimum Temperature (°C)		Average Mean Temperature (°C)		Average Maximum Temperature (°C)	
	Mean	SE	Mean	SE	Mean	SE
Rock Field	16.8	0.26	19.9	0.35	25.0	0.532
Olive Grove	14.4	0.29	19.9	0.41	26.4	0.46
Riparian	18.8	0.29	22.6	0.30	29.3	0.73
Forest	17.1	0.34	21.9	0.35	32.4	1.04
Phrygana	14.8	0.77	27.5	0.55	48.3	1.48
Farm Field	16.6	0.36	28.5	0.53	49.7	1.27
Beach	15.9	0.30	30.9	0.54	52.1	1.22

**Table 3:** Common Mediterranean reptile habitats and their average daily mean, minimum, and maximum temperatures collected by data loggers

**BIBLIOGRAPHY**

Andrews, R.M. 1998. Geographic variation in field body temperature of *Sceloporus* lizards. *Journal of Thermal Biology* 23:329-334.

Angilletta, M.J. 2009. *Thermal Adaptation: a theoretical and empirical synthesis*. Oxford University Press, Oxford.

Angilletta, M.J., Huey, R.B., & Frazier, M.R. 2009. Thermodynamic effects on organismal performance: is hotter better? *Physiological and Biochemical Zoology* 83(2): 197-206.

Araujo, M.B., Thuiller, W., & Pearson, R.G. 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33(10): 1712-1728.

Autumn, K., Weinstein, R.B., & Full, R.J. 1994. Low cost of locomotion increases performance at low temperature in a nocturnal lizard. *Physiological Zoology* 67(1): 238-262.

Bakken, G.S. 1992. Measurement and application of operative and standard operative temperatures in ecology. *American Zoologist* 32(2): 194-216.

Bauwens, D., Garland, T., Castilla, A.M., & Van Damme, R. 1995. Evolution of sprint speed in Lacertid lizards: Morphological, physiological and behavioral covariation. *Evolution* 49(5): 848-863.

Byers, J., Hebets, E., & Podos, J. 2010. Female mate choice based on male motor performance. *Animal Behaviour* 79(2010) 771-778.

Calsbeek, R. & Cox, R.M. 2010. Experimentally assessing the relative importance of predation and competition as agents of selection. *Nature* 465: 613-616.

Cowles, R.B. & Bogert, C.M. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History* 83: 261-296.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., & Martin, P.M. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* 105: 6,668-6,672.

Donihue, C. 2016. Micrographic variation in locomotor traits among lizards in a human-built environment. *PeerJ* 4:1776.

- Du, W., Yan, S., & Ji, Xiang. 2000. Selected body temperature, thermal tolerance and thermal dependence of food assimilation and locomotor performance in adult blue-tailed skinks, *Eumeces elegans*. *Journal of Thermal Biology* 25(3): 197-202.
- Dzialowski, E.M. 2005. Use of operative and standard operative temperature models in thermal biology. *Journal of Thermal Biology* 30: 317-334.
- Foufopoulos, J. & Ives, A.R. 1999. Reptile extinctions on land-bridge islands: Life-history attributes and vulnerability to extinction. *The American Naturalist* 153: 1-25.
- Foufopoulos, J., Kilpatrick, A.M., & Ives, A.R. 2011. Climate change and elevated extinction rates of reptiles from Mediterranean islands. *The American Naturalist* 177: 119-129.
- Gabroit, M., Balleri, A., Lopez, P., & Martin, J. 2013. Differences in thermal biology between two morphologically distinct populations of Iberian wall lizards inhabiting different environments. *Annales Zoologici Fennici* 50(4): 225-236.
- Garland, T., Hankins, E., & Huey, R.B. 1990. Locomotor capacity and social dominance in male lizards. *Functional Ecology* 4: 243-250.
- Garrick, D. 2008. Body surface temperature and length in relation to the thermal biology of lizards. *Bioscience Horizons* 1(2): 136-142.
- Giorgi, H. 2006. Climate change hot-spots. *Geophysical Research Letters* 33: 1-4.
- Giorgi, F. & Lionello, P. 2008. Climate change projections for the Mediterranean region. *Global and Planetary Change* 63: 90-104.
- Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A., Jess, M., & Williams, S.E. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B* 370: 1665-1679.
- Huey, R.B. & Kingsolver, J.G. 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution* 4: 131-135.
- Huey, R.B., Niewiarowski, P.H., Kaufmann, J., & Herron, J.C. 1989. Thermal biology of nocturnal ectotherms: is sprint performance of geckos maximal at low body temperatures? *Physiological Zoology* 62(2): 488-504.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution* 15: 56-61.



- Husak, J.F. 2006. Does speed help you survive? A test with Collard Lizards of different ages. *Functional Ecology* 20: 174-179.
- Husak, J.F., Fox, S.F., Lovern, M.B., & Van Den Bussche, R.A. 2006. Faster lizards sire more offspring: sexual selection on whole-animal performance. *Evolution* 60(10): 2122-2130.
- Ioannides, Y., & Dimitropoulos, A. 1994. The herpetofauna of Samos (Eastern Aegean, Greece). *Ann. Musei Goulandris* 9: 445-456.
- IPCC 2014: Climate Change 2014: Synthesis Report. Core Writing Team, Pachauri, R.K and Meyer, L. (eds.]. IPCC, Geneva, Switzerland, 130 pp.
- Irschick, D.J. & Garland, T. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annu. Rev. Ecol. Syst.* 32: 367-396.
- Irschick, D.J. & Meyers, J.J. 2007. An analysis of the relative roles of plasticity and natural selection in the morphology and performance of a lizard (*Urosaurus ornatus*). *Oecologia* 153: 489-499.
- Lailvaux, S.P. & Irschick, D.J. 2007. Effects of temperature and sex on jump performance and biomechanics in the lizard *Anolis carolinensis*. *Functional Ecology* 21: 534-543.
- Licht, P., Dawson, W.R., Vaughan, H.S., & Main, A.R. 1966. Observations on the thermal relations of Western Australian lizards. *Copeia* 1966(1): 97-110.
- Lima, S.L. & Dill, L.M. 1990. Behavioral decisions under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.
- Lima, S.L. 2002. Putting predators back into behavioral predator-prey interactions. *Trends in Ecology & Evolution* 17(2): 70-75.
- Mathies, T., & Andrews, R. M. 1997. Influence of pregnancy on the thermal biology of the lizard, *Sceloporus jarrovi*: Why do pregnant females exhibit low body temperatures? *Functional Ecology* 11: 498-507.
- Osojnik, N., Zagar, A., Carretero, M.A., García-Muñoz, E. & Vrezec, A. 2013. Ecophysiological dissimilarities of two sympatric lizards. *Herpetologica* 69: 445-454.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M.,

Mooney, H.A., Oesterheld, M., Poff, N., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. 2000. Global Biodiversity Scenarios for the Year 2100. *Science* 287: 1770-1774.

Stamps, J.A. 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. *Ecology* 58: 349-358.

Strobbe, F., McPeck, M.A., De Block, M., De Meester, L., & Stoks, R. 2009. Survival selection on escape performance and its underlying phenotypic traits: a case of many-to-one mapping. *Journal of Evolutionary Biology* 22: 1172–1182.

Sunday, J.M., Bates, A.E., & Dulvy, N.K. 2010. Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society of London B*. 278: 1823-1830.

Tokarz, R. R. 1995. Mate choice in lizards: A review. *Herpetological Monographs* 9: 17-40.

Valakos, E.D., Pafilis, P., Sotiropoulos, K., Lymberakis, P., Maragou, P., & Foufopoulos, J. 2008. *The Amphibians and Reptiles of Greece*. Chimera Editions, Frankfurt am Main.

Van Damme, R., Bauwens, D., Castilla, A.M., & Verheyen, R.F. 1989. Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta*. *Oecologia* 80(4): 516-524.

Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O., & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., & Langham, G. 2008. Towards an Integrated Framework for Assessing the Vulnerability of Species to Climate Change. *Public Library of Science (Biology)* 6: 2621-2626.

Xiang, J., Weiguo, D., & Pingyue, S. 1996. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, *Takydromus septentrionalis*. *Journal of Thermal Biology* 21(3): 155-151.

Zamora-Camacho, F.J., Reguera, S., & Moreno-Rueda, G. 2014. Effects of limb length, body mass, gender, gravidity, and elevation on escape speed in the lizard *Psammmodromus algirus*. *Evolutionary Biology* 41(4): 509-517.