

THERMAL ECOLOGY IN ISLAND POPULATIONS
OF ERHARD'S WALL LIZARD, *PODARCIS ERHARDII*

by

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ABSTRACT

Global climate change has already impacted the majority of natural ecosystems and is expected to lead to numerous extinctions. The effects will be particularly severe for populations that have been reduced and isolated through habitat fragmentation, an important mechanism of human-caused biodiversity loss. Despite the worldwide occurrence of both processes, we have a poor understanding of how habitat fragmentation (and the associated loss in genetic diversity) renders species increasingly susceptible to climate change. Elucidating this relationship is important if we are to conserve global biodiversity. In this study, we examined thermal ecology and physiology across Cycladic land bridge island populations of Erhard's Wall Lizard (*Podarcis erhardii*). Populations on land bridge islands have been isolated from the mainland by rising sea levels, a process that is similar to anthropogenic habitat fragmentation. Previous research has shown that *P. erhardii* populations in the Cyclades show a predictable gradient of genetic diversity according to island size and age, and this species is considered a model ectotherm for studies of thermal ecology. We quantified environmental conditions (T_e), field body temperatures (T_b), preferred temperatures (T_{pref}), critical thermal maxima and minima (CT_{max} and CT_{min}) and evaporative water loss (EWL) across five populations that differed in either genetic structure (low vs. high genetic diversity) or site environmental characteristics (elevation and aspect). Our findings suggest that: 1) genetic diversity does not appear to underlie differences in physiology or variability in thermal ecology; and 2) while environmental differences do not affect thermal biology, they do shape the water retention ability of individuals in a population. These results have implications for the management of fragmented species under shifting climate conditions.

INTRODUCTION

Biodiversity continues to be threatened by human activity, with global climate change and habitat fragmentation cited as two of the most severe anthropogenic stressors faced by wildlife (Pereira et al., 2010). Significant changes in species occurrences worldwide have already been documented as a result of these two processes, with impacts notably including shifts in geographic ranges (Walther et al., 2002) and inbreeding depression due to genetic impoverishment (Frankham et al., 2002), respectively. Climate change and fragmentation are not only ubiquitous across the globe, but also are continuing to increase as a result of natural resource exploitation by humans. While the impacts of each process on species and ecosystems has been widely studied and quantified, very little is known regarding their interactions or potential synergistic effects (Stork et al., 1999).

Direct effects of global climate change in extreme cases may include mortality as temperatures approach or exceed the Critical Thermal Maximum (CT_{max}), the highest tolerable temperature of a species, as this is more rigid than other aspects of thermal biology (Leal and Gunderson, 2012; Sinervo et al., 2010). This may be especially true for taxa with low vagility and high dependence on environmental conditions, both of which characterize many ectothermic species. However, it is predicted that climate change impacts on animals may more commonly be experienced via indirect effects, for example, mediated through biotic interactions. These can include spatiotemporal mismatches between interacting species (Parmesan, 2006; Schweiger et al., 2008). Associated species may also shift their geographic ranges (Schweiger et al., 2008), niche use (Lavorel, 1999), or phenologies to differing extents in response to changes in climate, while tolerant species may not necessarily shift at all

(Parmesan, 2006). Indirect effects may also be mediated through changes in habitat structure or composition which decrease niche quality (Parmesan, 2006), and may result in increased constriction of the activity period due to warmer temperatures, especially for behaviorally thermoregulating ectotherms which retreat to thermal refugia to avoid experiencing their CT_{max} (Sinervo et al., 2010). In some reptile species that are live-bearing or viviparous, gravid females may require cooler temperatures for proper gestation (Sinervo and Adolph, 1989; Mathies and Andrews, 1997), which has obvious implications for recruitment and population stability in the face of climate warming.

Increased habitat dryness resulting from climate change may further impact ectotherms, because activity levels can be affected not only by temperature but also humidity (Gunderson and Leal, 2012; Lorenzon et al., 1999). Habitat moisture can affect water balance or flux in ectotherms (Dmi'el et al., 1997; Grenot et al., 1987). Water availability may be a factor in time-energy budget determination for lizards, a group which may contribute significantly to ecosystem energy flow in systems such as small islands where lizards attain high population densities (Brown et al., 1992), and serve as the primary food source for either island endemic birds or endemic snakes. Although a species may evolve increased tolerance of hotter and drier habitats, the predicted rate of global climate change is likely too fast for phenotypic evolution to keep pace (Gienapp et al., 2008). Indeed, the high mortality fraction necessary to allow species to evolutionarily respond to rapid increases in temperature and aridity has already been shown to result in local extinctions (Sinervo et al., 2010).

Likewise, habitat fragmentation presents numerous challenges for wildlife populations. Nearly all continents and ecosystems on earth have been fragmented (Perfecto and Vandermeer, 2010). Increased edge habitat can, among other things, change the outcome

of competition, predation, and disease, and thereby alter community structure when natural landscapes are fragmented (Ewers and Didham, 2006). Moreover, as the quality of habitat between patches decreases because of human activity, migration within metapopulations declines, leading to vulnerable, isolated subpopulations (Cushman, 2006). For species that are able to survive fragmentation, genetic impoverishment resulting from isolation can lead to inbreeding depression that decreases fitness and population stability or resilience (Eldridge et al., 1999; Frankham et al., 2002). Moreover, habitat heterogeneity can result in some fragments inevitably containing suboptimal habitat, resulting in population fitness decreases beyond those resulting solely from genetic impoverishment or environmental stochasticity (Remon et al., 2011). For example, sub-optimal habitat for ectotherms may not contain appropriate thermoregulatory sites, which can cause declines in overall performance (Kearney et al., 2009). In the long term, edge effects and non-point stressors can result in degradation of even high quality habitat patches created by anthropogenic fragmentation (Harrison and Bruna, 1999). In time, we may therefore expect fragmented populations to decline or even become extirpated (Tilman et al., 1994), especially as isolated populations become increasingly vulnerable to sudden or random changes in the environment (Barrows and Allen, 2007). This vulnerability can conceivably be due to genetic impoverishment, geographic limitations on dispersal to refugia (Le Galliard et al., 2005), or both.

Despite knowledge of the individual impacts of global climate change and habitat fragmentation on ecosystems, little is known about how these two processes may interact to impact wildlife populations. Niche-based and deterministic models have been used to evaluate the relative contribution of each process to species extinction (Pereira et al., 2010). It has been acknowledged that depending on the severity of fragmentation, the impacts of

climate change may be exacerbated due to geographic limitations on range shifts (Opdam and Wascher, 2003; Davis and Shaw, 2001). Fine-scale information on potential synergies of these two processes is lacking, as disentangling the impacts of environmental conditions, habitat changes, and biotic factors can be highly complicated (Stork et al., 2009). Making predictions about potential interactions of multiple anthropogenic impacts can be particularly problematic where spatial heterogeneity of climate or land-use change is high (Hay et al., 2002).

The land bridge islands that compose the Cyclades archipelago (NE Aegean Sea, Greece) provide a model system for studies of long-term effects of habitat fragmentation (Foufopoulos and Ives, 1999), as these islands have been formed over the past several tens of thousands of years by rising sea levels, isolating populations of Erhard's Wall Lizards (Lacertidae: *Podarcis erhardii*) that once constituted a continuous population. The lizards are poor over-water dispersers and their genetic diversity varies predictably according to island size and age (Hurston et al., 1999), indicating that isolation of these populations is highly likely. The lizards are also widespread among diverse habitats on the islands, allowing for comparison of environmentally induced adaptations across localities. These population characteristics make this system ideal for examining long-term intraspecific impacts of habitat fragmentation.

To quantify the effects of climate change on a species, it is imperative to integrate behavior and fine-scale measurements of thermal ecology, and ectotherms can serve as important study models (Deutsch et al., 2008; Gunderson and Leal, 2012). Because of their close reliance on ambient temperatures for regulation of physiological and metabolic processes, these animals are also likely to be among the first species impacted by changes in

climate (Porter and Gates, 1969). The effects of climate change are likely to be especially severe for ectotherms living in arid environments, because these species are already living close to their CT_{max} , reducing the margin or “buffer zone” between environmental temperature and the upper temperature threshold for survival (Gunderson and Leal, 2012). Unfortunately, a large proportion of ectotherm biodiversity is found in the warmest ecosystems on Earth, which also are likely to experience extremely rapid changes in community structure due to climate warming (Archer and Predick, 2008). For example, in the Mediterranean region, a hotspot of reptile diversity, changes in climate are altering vegetation structure, which in turn impacts these sensitive animals in part due to their reliance on vegetation cover for appropriate thermoregulatory opportunities (Sarris et al., 2006; 2010). Indeed, loss of suitable habitat due to climate change has been implicated as a critical driver behind historic reptile extinctions across this region (Foufopoulos et al., 2011).

Given the implications of both current and past changes in climate and habitat in the Mediterranean region, Cycladic lizard populations can serve as an ideal system for studying the potential effects of long-term intraspecific fragmentation on thermal ecology. Such impacts could include differences due to loss of genetic diversity resulting in reduced variability or evolutionary potential on smaller islands (Willi et al., 2006; Remon et al., 2011), or relegation to sub-optimal habitats resulting in ecological differences across populations. In this study, we examined thermal ecology in *P. erhardii* on one large, genetically diverse baseline island and two small, genetically impoverished satellite islet populations. Populations were evaluated both in terms of average physiological characteristics (i.e., in the form of mean values for the measured parameters) and the magnitude of variance in these characteristics within populations. We attempted to isolate the

effects of genetic impoverishment to evaluate whether inbred populations exhibited lower variability in thermal ecology and hydric physiology. We also tested for the effects of environmental differences across populations with similar genetic diversity to evaluate differences that may be due to the abiotic environment. In light of the rapidity and ubiquity of global climate change across increasingly fragmented landscapes, our results have important conservation implications.

METHODS

Study organism

Our study organism, Erhard's Wall Lizard (or the Aegean Wall Lizard), *Podarcis erhardii*, (Lacertidae, Reptilia) occurs across a broad range of habitats on the Aegean Sea islands. Because it has a very wide distribution in the region, including many very small islets in the Cyclades, it is an ideal organism for this type of study. In the anthropogenically modified landscapes of the Aegean Sea, *P. erhardii* is strongly dependent on refugia, such as man-made dry stone walls. The species is relatively small-bodied with a mean snout-vent length (SVL) of approximately 75 mm (Valakos et al. 2008). These diurnal lizards have a bimodal activity pattern, and exhibit a mid-day rest period which increases in length with increasingly warmer conditions as the summer progresses.

P. erhardii is an active forager, making it easy to obtain estimates of relative density during periods of activity. Mating usually occurs in late spring/early summer. Oviposition timing varies depending on ecological conditions, with populations in warmer areas laying eggs sooner than those in cooler regions. Females generally lay up to two clutches in one breeding season, with clutches typically varying from one to four eggs (Valakos, 1990).

Study sites

We conducted this study on the large island of Naxos and its satellite islets, all located within the Cyclades island cluster (Central Aegean Sea, Greece). Three study sites were located on Naxos proper and one each on two islets in the immediate vicinity (Fig. 1). The three Naxos sites were chosen to span a broad range of ecological conditions. To sample the full range of climatic conditions on the island, two sites were selected in the same, relatively high elevation region but on locations with different aspects. The Naxos South-Facing site (NSF, 37°6.5' N, 25°32.0' E) is located at 642 m asl whereas the nearby (~0.8 km distant) Naxos North-Facing site (NNF, 37°6.2' N, 25°31.6' E; 631m asl) is situated on the opposing side of the same valley. The south-facing site encompasses a terraced landscape of largely abandoned fields, lined with man-made stone walls; it is largely devoid of trees and characterized by rather dry *phrygana* (dwarf bush steppe) vegetation cover. The north-facing site is also covered by a mosaic of abandoned terraces, covered by a diverse community of forbs, ferns and grasses and patches of relict Kermes oak (*Quercus coccifera*) forest. Due to the northern aspect, the relative steepness of the slope (~35%), and the shade provided by the trees, this site is both noticeably cooler and more wet than the neighboring south-facing site. Portions of these sites are heavily grazed by goats and sheep.

To investigate the role of islet effects while controlling for ecological similarity, the remaining Naxos Low Elevation site (NLE) was located at a low elevation on the west coast of the island. This site is situated just inland from the coastal community of Plaka (37°3' N, 25°23' E). The ecological conditions and habitat at this low elevation site (25m asl) are very similar to those on the islets, described below. This site is characterized by dry thermo-

Mediterranean vegetation, and borders small, extensively used grain fields. Man-made dry stone walls are abundant at this site, which comprise important thermoregulatory sites for lizards by providing both basking areas (flat surfaces on top of stones) and refugia (hiding places between stones).

Aspronissi islet (or Glaronissi, henceforth referred to as “ASP”) is located off the western coast of Naxos, approximately 2km S-SW from the coastal village of Agia Anna (37°2.8' N, 25°21.1' E). The small island (0.0102 km², 6m elevation), consisting of eroded granodiorite boulders, has very shallow soil profiles and is partially covered with nitrophilous vegetation. The island harbors a significant number of breeding birds, including yellow-legged gulls (*Larus michahellis*) and shags (*Phalacrocorax aristotelis*), which provide substantial marine subsidies and therefore increased productivity. The island is inhabited by a population of a few hundred *P. erhardii*.

The second islet, Ovriokastro (OVR), is located ca. 8 km W-NW of Naxos and just 400m off the NE tip of the large island of Paros (37°9.07' N, 25°17.75' E.). The islet (0.22 km², 23m elevation) is comprised of a flat-topped slab of limestone covered by open *Juniperus phoenicea* chaparral interspersed with low, open *phrygana* scrub. The island harbors a substantial colony of Yellow-legged gulls (*Larus michahellis*) and Manx shearwaters (*P. puffinus*). On Ovriokastro we also documented rats (*Rattus* sp.) and sand boas (*Eryx jaculus*). Goats are introduced seasonally and graze sections of the island each year. Ovriokastro is inhabited by a population of a few thousand *P. erhardii*.

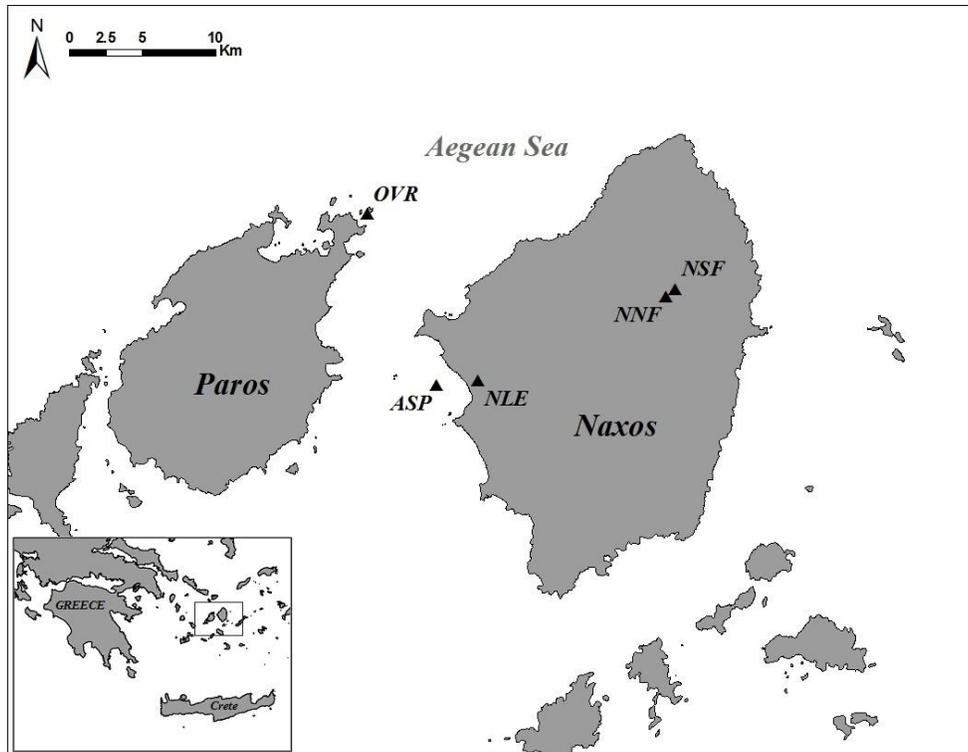


Figure 1. Map depicting the location of study sites within the study area. Study sites are indicated with dark triangles. Codes correspond to sites as follows: ASP – Aspronissi; OVR – Oviokastro; NLE – Naxos low elevation; NSF – Naxos high elevation, South-facing; NNF – Naxos high elevation, North-facing.

Capture and housing

The five study sites were sampled in summer 2011 (5-15 through 7-15). Sampling varied depending on prevailing conditions but in general took place in the mid-morning hours (8:00-11:00) and late afternoon hours (15:00-19:00) coinciding with periods of peak lizard activity. When in the field, we recorded prevailing environmental conditions, including wind speed, weather, and air temperature in both sun and shade.

Individual lizards were captured using either nooses or mealworms (*Tenebrio sp.* larvae) attached to a telescopic fishing pole. Individuals kept for laboratory studies were marked and transferred to plastic terraria with screen lids. Lizards were provided with water

and food (mealworms) *ad libitum*, as well as access to sunlight and shade during the daytime to allow for appropriate thermoregulation. Sex, reproductive status for females (gravid or non-gravid), weight, snout-vent length, tail length, and tail condition (autotomized or complete) were recorded for each lizard. Prior to all laboratory experiments (discussed below), lizards were acclimated at constant conditions for at least 24h.

Environmental conditions

HOBO data loggers (Onset, Model U23-003) were used to record microsite temperature profiles at each of the five study sites. The end of each logger probe was inserted into a hollow lizard model composed of a 1.5 cm diameter PVC pipe cut to approximately 8 cm in length roughly corresponding to the body size of an adult *P. erhardii* (Dzialowski, 2005). Thus the metal end of the probe was located entirely inside the model, and was positioned so that it would not touch the sides of the model. The models were painted to emulate the color pattern of a *P. erhardii* lizard.

Six data loggers were deployed at each site, each with two probes for a total of twelve models. Two of the loggers were placed in shade (either within a stone wall or within a bush), two were placed in mixed sun and shade (e.g., at the edge of a wall or vegetation cover) and two were placed in the sun (on typical basking surfaces, such as on top of a stone wall or on a rock). The loggers recorded the temperature at 5 *min* intervals for a period of approximately 24 hours. This was repeated over five sampling days for each site on Naxos, and over two sampling days for each of the small island sites.

Field body temperature

Lizard body temperature was taken in the field within 20 s of capture, and care was taken to avoid touching the lizard's abdomen to avoid affecting the measurement. Internal body temperature was measured with a glass rapid-read cloacal thermometer (Miller & Weber Model T-6000). Substrate temperature was measured by touching the tip of the thermometer to the substrate on the spot where the lizard was captured, and air temperature was also measured 5 cm above the substrate. Each lizard's activity prior to capture was also recorded, and categorized as follows: a lizard was deemed 'basking' if it was observed still in a sunny, exposed area; 'hiding' if the lizard was found in a concealed position (e.g., between stones in a wall, within a bush) and not moving; and 'foraging' if captured while actively moving across the substrate.

Laboratory thermal preferences

Thermal preference was determined experimentally for 10-12 males, non-gravid females, and gravid females from each of the five study sites. For females that were gravid upon capture, the measurements were repeated after oviposition; this paired design allowed us to evaluate how reproductive status might affect temperature preferences. For approximately eight hours prior to the beginning of the experiment, lizards were kept cool and were not fed to avoid possible effects on selected temperatures. A 0.8mm thermocouple (Omega Engineering Model 5SC-TT-T-40-36) was inserted 5mm into the cloaca and secured with a small piece of tape. The other end of the thermocouple was then plugged into a digital thermometer (Omega Engineering Model HH506A) that displayed constant readings of the lizard's internal body temperature. Lizards were then placed in a long polyurethane-coated

fiberboard corridor (L x W x H \approx 1m x 5cm x 30cm). At one end of the corridor a heat lamp was used to increase the temperature to approximately 45°C, while at the other end ice packs were stacked on the outside of the corridor to reduce temperature to approximately 15°C. Lizards were placed on the warm side of the corridor and allowed to acclimate for ten minutes. Following this period, lizard temperature was recorded for 60 minutes at two minute intervals, and these measurements were averaged to obtain an estimate of each individual's T_{pref} .

Critical thermal maximum experiment

This experiment was conducted on at least ten spent (post-partum) females from each of the five study populations, in order to provide a baseline against which to compare hatchling lizards from each study population in the future. Females were not fed for at least 4 hours prior to the experiment. Lizard body temperatures were monitored continuously through the trials using the same digital thermometer setup as the laboratory thermal preference study. The lizard was placed in a tall plastic container, and a 100W incandescent lamp was used to apply heat. The lizard was then heated progressively from its resting temperature (generally 30-35°C) to 40°C, and then flipped onto the back inside the container. After the lizard righted itself, heat was applied again, until the lizard's internal body temperature reached 40.5°C, at which point it was flipped again. This was repeated at 0.5 degree intervals until 42.5°C was reached, at which point the lizard was flipped at 42.8°C, and then at 0.2 degree intervals. The temperature at which the lizard could no longer right itself within a reasonable amount of time (approximately ten seconds) was taken as the critical thermal maximum (CT_{max}) for that lizard. At this point, the lizard was transferred to a

container of cool water for several seconds to assist in quickly lowering its body temperature. Individuals were closely observed throughout the experiment for tremors or other signs of deterioration in function, and if these became apparent, the experiment was terminated and the lizard was immediately cooled down.

Critical thermal minimum experiment

Just as in the critical thermal maximum test, this experiment was conducted on at least ten post-reproductive females from each of the five study populations. Each female was placed in an individual small plastic terrarium and left in a standard refrigerator freezer (set to approximately -15°C) for six minutes. At this point, the lizard was removed from the freezer and rapidly flipped onto its back with care to minimize contact with the abdomen. If the lizard could right itself, it was returned to the terrarium and left in the freezer for an additional two minutes, and then the test was repeated. If the lizard's activity level appeared to be decreasing rapidly, it was left in the freezer for a shorter period of time. When a lizard could no longer right itself, its internal body temperature was measured using a glass cloacal thermometer (Miller & Weber Model T-6000), and recorded as the critical thermal minimum (CT_{\min}). Duration of the trial was also recorded for each individual for use as a possible analysis covariate.

Evaporative water loss experiment

We measured the ability of lizards from four different populations to conserve water when challenged in a standard dry environment. This experiment was only conducted on males in 2011, and was repeated on post-reproductive females and their lab-reared offspring

in 2012. Data were only compared within years (i.e., males were only compared with males, females and offspring were only compared with one another) to avoid potential effects resulting from performing this experiment in separate field seasons. To reduce confounding weight changes due to defecation, we did not feed the lizards for eight hours prior to the beginning of the experiment. Lizards were initially weighed with a digital scale (1mg accuracy, American Weigh Gemini-20 Digital), then placed individually in small, mesh-lid plastic terraria with a single sheet of newspaper lining the bottom (Dmi'el, Perry, and Lazell, 1999). For the duration of the experiment, the boxes were kept in a dark and quiet though well-ventilated area in the lab.

The experiment was run for approximately seven hours, and box positions were rotated twice during each trial to eliminate any potential order or air humidity/temperature gradient effects. Temperature and humidity were recorded at the beginning, at the halfway point, and at the end of each trial using a wall-mounted thermometer/hygrometer to determine whether these explain any variation in our results. At the end of the trial, each lizard was weighed again, and the difference in weight was taken as the evaporative water loss. However if a lizard defecated during the trial, it was reweighed and the experiment was restarted. Water loss was then corrected for the duration of the trial by dividing weight difference by length of trial. Body surface area was estimated for each lizard by making the simplifying assumption that the trunk was cylinder-shaped and the tail was cone-shaped. Surface area was calculated with SVL as the height and mid-body girth as the circumference of the cylinder, with tail length as the height of the cone and girth just above the cloaca as the base circumference of the cone. Water loss per unit time was then divided by total lizard surface area estimates in order to obtain size independent water loss rate.

Because initial analyses revealed a potential pattern related to differences in habitat moisture, soil samples were collected from Naxos sites in the following year (Summer 2012). Three samples were randomly selected within a 3m radius of one another at each of the three Naxos sites using 10 x 10 cm quadrats. As soil profiles are very shallow throughout the study sites, soil was collected from within a quadrat until bedrock was encountered, which was generally approximately 5 cm below the surface of the soil. Soil samples were weighed, air dried, and then weighed again. In order to ensure accurate measurements, samples were repeatedly weighed for several days after the final weight was recorded to verify that no additional loss of weight occurred, which would indicate incomplete drying. All samples were classified as the same soil type (sandy loam); as such, weight difference, used as a proxy for soil moisture content, was directly compared across samples.

Data analysis

Data were analyzed and test assumptions verified using IBM SPSS Statistics Ver. 20. Unless otherwise noted, Tukey's HSD was used for post-hoc pairwise comparisons.

RESULTS

Environmental conditions

To assess differences in environmental conditions across sites, General Linear Models were created for mean, maximum, and minimum temperatures across the study sites ($n = 5$ sampling day for each site for a total of $N = 25$ samples), with the corresponding statistic (mean, maximum or minimum) calculated from HOBO data logger recordings as the dependent variable, site as a fixed effect, and corresponding weather station statistic (mean, maximum, or minimum) as a covariate. For mean temperature, study site was significant and

the five sites clustered into two distinct groups (GLM, $F_{5,19} = 12.386$, Adjusted $R^2 = 0.703$, $p < 0.001$; Fig. 1): the three low elevation sites (OVR, ASP, and NLE) exhibited significantly warmer means than the two high elevation sites (NSF and NNF).

No statistically significant differences were detected across sites for maximum temperature (GLM, overall: $F_{5,19} = 5.227$, $R^2 = 0.579$, $p < 0.05$; site: $F_{4,19} = 1.839$, $p > 0.1$), but OVR tended to be warmer than the other sites. Likewise, there were no statistically significant differences across sites for minimum temperature, although there was also a strong trend indicative of lower minimum temperatures in the high elevation sites (GLM, overall: $F_{5,19} = 3.516$, $R^2 = 0.418$, $p < 0.05$; site: $F_{4,19} = 3.848$, $p < 0.05$, due to marginal pairwise difference [$p = 0.053$] between NNF [high elevation] and ASP [low elevation]).

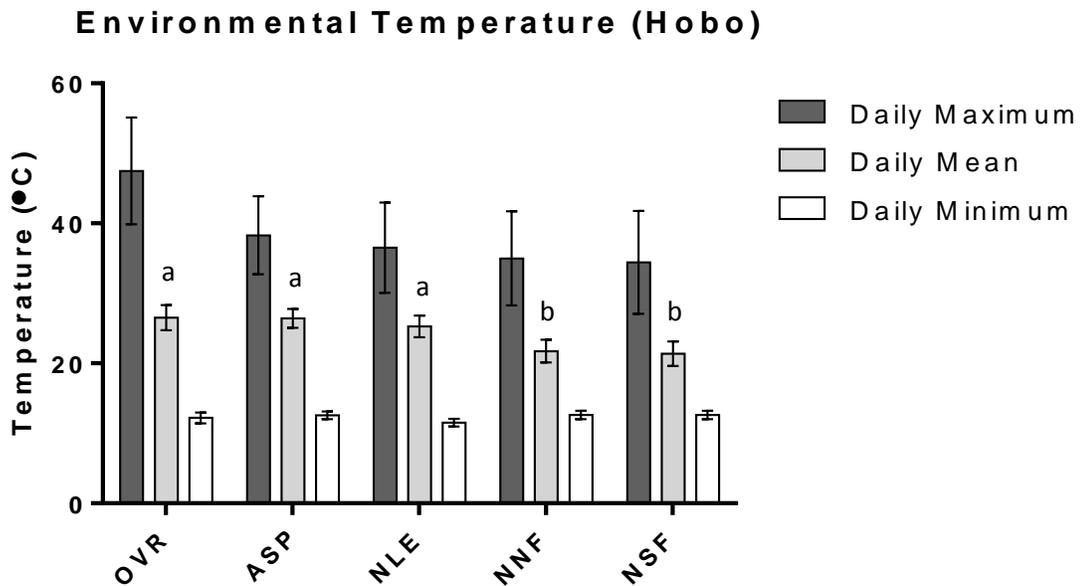


Figure 2. T_e results show that low elevation sites exhibit significantly higher mean temperatures (General Linear Model, $p < 0.001$). Bars display marginal mean values given by our model and error bars represent ± 2 SE. Lower case letters indicate post-hoc results for daily mean: shared letters indicate no significant difference. There were no differences found in daily maximum or daily minimum temperatures.

Field body temperature

To determine differences in T_b across sites, a General Linear Model was created to predict the T_b (the dependent variable, in °C) and included study site, sex of lizard (M/F), and activity (foraging, basking, or hiding) as fixed effects, and lizard SVL (cm) and $T_{\text{substrate}}$ (°C) as covariates (Fig. 3). Site ($p < 0.001$) and activity ($p = 0.004$) were highly significant predictors of T_b (GLM, site: $F_{4,154} = 6.209$, $p < 0.001$; activity: $F_{2,154} = 5.686$, $p = 0.004$). Post-hoc pairwise comparisons revealed significantly higher marginal mean body temperatures in OVR lizards than in lizards from ASP or NLE (Bonferroni corrected post-hoc mean comparisons: $p = 0.004$ and $p < 0.001$, respectively). T_b data were pooled across all sites to compare the differences according to lizard activity. A Kruskal-Wallis test showed significant differences in T_b according to lizard activity ($H_2 = 21.637$, $p < 0.05$), with foraging lizards significantly warmer than hiding lizards (Mann-Whitney U with α adjusted for repeated tests, $U = 2182$, $p < 0.001$). On average, foraging lizards were also warmer than basking lizards across all five study sites, though this trend was not statistically significant.

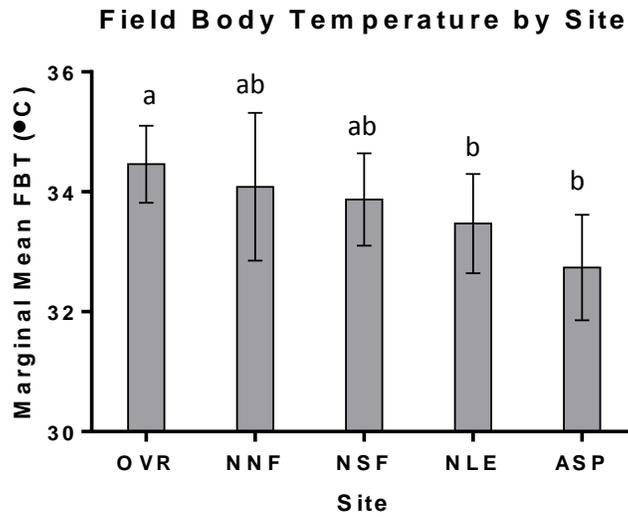


Figure 3. T_b results analyzed by site show differences between Ovriokastro (OVR) and the other two low elevation sites (NLE and ASP; General Linear Model, $p < 0.05$). Bars represent marginal means, with error bars displayed ± 2 SE, with lowercase letters indicating post-hoc results for mean T_b ; shared letters indicate no significant difference.

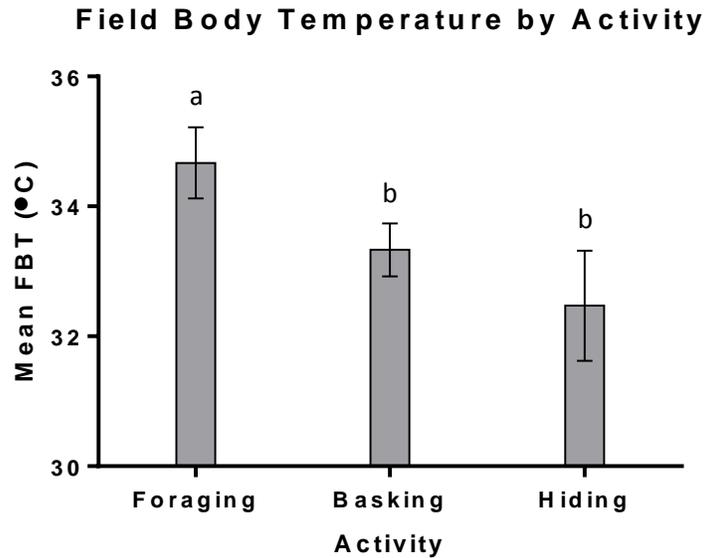


Figure 4. T_b results analyzed by lizard activity reveal that foraging lizards are significantly warmer (Kruskal-Wallis, $p < 0.05$; post-hoc Mann-Whitney U with α adjusted for repeated tests, $p < 0.001$). Bars represent marginal means, with error bars displayed ± 2 SE. Lowercase letters indicate post-hoc results for mean T_b ; shared letters indicate no significant difference.

Thermal preferences

Since no substantial association was found between lab preferred temperature and lizard size in simple linear regressions (T_{pref} vs SVL: $\beta = -0.074$, $p > 0.1$, $R^2 = 0.006$; T_{pref} vs. weight: $\beta = 0.012$, $p > 0.5$, $R^2 = 0.0001$), size was not considered as a covariate in comparisons of mean T_{pref} . We found no significant differences in T_{pref} across the five study populations in mean (ANOVA, $p = 0.705$) or variance (Levene's test, $p > 0.05$). We then pooled data across five study sites to compare males against independently sampled non-gravid and gravid females. We found no significant difference between non-gravid females and males ($p = 0.58$) and consequently pooled these together to increase the sample size of our groups. Gravid females preferred significantly lower temperatures on average than males and non-gravid females (independent samples t-test, $p = 0.006$) with a mean thermal preference 1.18°C lower than males and non-gravid females. Females that were gravid upon capture were kept in captivity until after parturition, at which point thermal preferences were re-measured. Individual females also preferred significantly lower temperatures while gravid vs. non-gravid (paired t-test, $p = 0.001$).

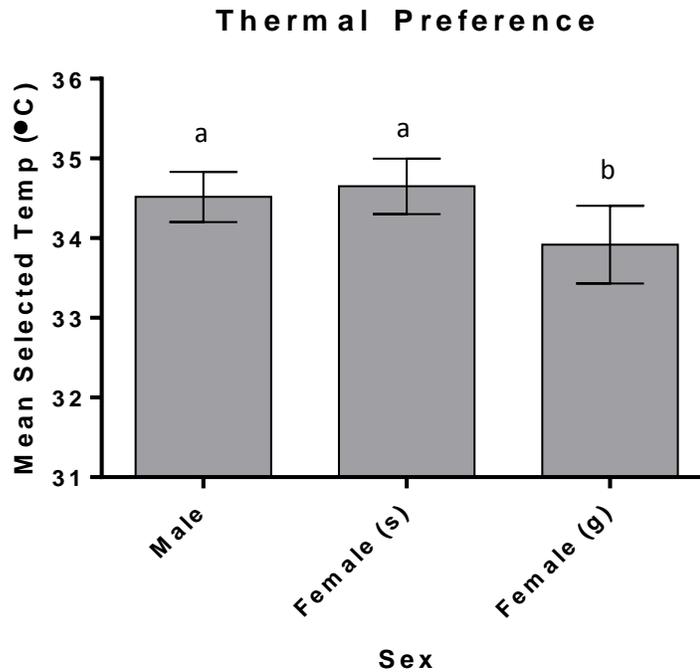


Figure 5. T_{pref} results analyzed by sex and reproductive status (spent vs. gravid) reveal that gravid females lizards prefer significantly cooler temperatures (independent t-test, $p < 0.001$), and that within individual females, thermal preferences are lower while gravid (paired t-test, $p = 0.001$). Bars represent marginal means, with error bars displayed ± 2 SE. Lowercase letters indicate post-hoc results for mean T_{pref} : shared letters indicate no significant difference.

Critical thermal tolerance

General Linear Models were used to compare CT_{max} and CT_{min} across populations.

Preliminary data analyses revealed a potential relationship between size and critical thermal maximum, so lizard size was included as a covariate in the models. For CT_{max} , recorded maximum temperature was used as the dependent variable, SVL as the covariate (this size variable had a lower p-value than lizard weight in the alternate GLM), and site as a fixed effect. There were no significant differences in mean (GLM, $F_{5,48} = 2.922$, $p > 0.05$) or variance (Levene's test, $p > 0.05$) across sites, but a significant association was indicated between CT_{max} and SVL (GLM, $F_{1,48}$, $p < 0.05$), with smaller lizards exhibiting higher CT_{max} values.

For CT_{min} , recorded minimum temperature was used as the dependent variable, weight as the covariate (when SVL was used, error variances were unequal), and site as a fixed effect. There were no significant differences across sites when post-hoc pairwise comparisons were conducted, although marginal differences between sites contributed to a significant overall effect of site (GLM, $F_{4,44} = 2.840$, $p = 0.035$). No significant association was found by our model between size of the lizard and CT_{min} (GLM, $F_{1,44} = 2.909$, $p > 0.05$).

Critical Thermal Tolerance (marginal means)

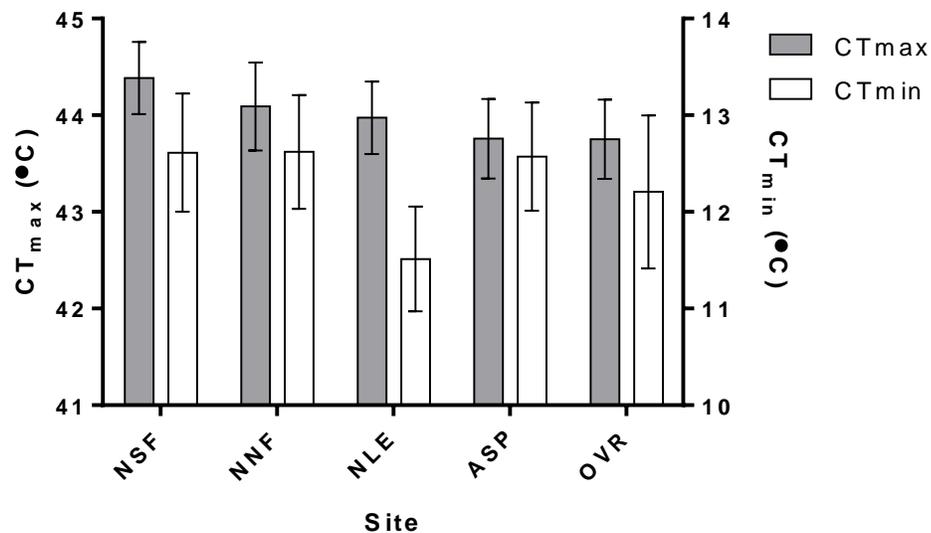


Figure 6. No significant differences were found in CT_{max} or CT_{min} between sites (General Linear Model, $p > 0.05$). Bars represent marginal means, with error bars displayed ± 2 SE.

Evaporative water loss: Adults

EWL data were analyzed using a GLM, with site as a fixed effect, and mean trial temperature as a covariate. We detected no difference in variance among the different groups (Levene's test, $p > 0.05$). We did however detect a significant effect of site on mean EWL was detected (GLM, $F_{3,31} = 7.188$, $p = 0.001$). Post-hoc tests showed that the north-facing high elevation Naxos population (NNF) had the highest water loss rates across the four sites, and the south-facing high elevation Naxos population (NSF) had the lowest. The Naxos low

elevation population (NLE) and the population from Aspronissi (ASP) were not significantly different. The low elevation population also had significantly higher EWL rates than those from the south-facing high elevation site. Soil moisture data from the three Naxos sites (NNF, NSF, NLE) revealed that the environments followed exhibited this pattern of differences as well (Kruskal-Wallis, $H_2 = 11.431$ $p = 0.003$), with the south-facing site having the lowest soil moisture, the low elevation having slightly higher soil moisture (though the difference between this and the south-facing site were non-significant), and the north-facing site having the highest (Mann-Whitney U, $U = 25.00$, $p < 0.01$ for both significant pairwise comparisons).

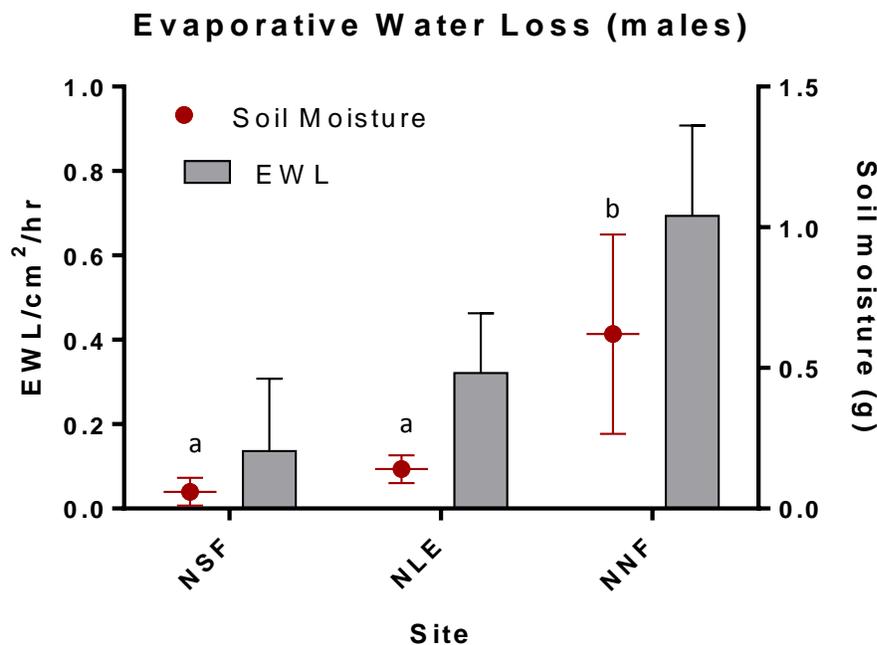


Figure 7. EWL differences across sites correspond to difference in soil moisture. All differences depicted are significant for EWL (General Linear Model, $p < 0.001$). Soil moisture was not significantly different between NSF and NLE but was significantly greater in NNF (Kruskal-Wallis, $p < 0.05$; Mann-Whitney U post-hoc test with adjusted alpha used for pairwise comparisons represented by lowercase letters: shared letters indicate no significant difference.). Bars represent marginal means, with error bars displayed ± 2 SE.

Evaporative water loss: Heritability

EWL measurements for females collected from sites around Naxos were verified to exhibit no significant differences between sampling sites (Kruskal-Wallis $p > 0.05$), which allowed us to pool all females into a single group to test against offspring. Juvenile EWLs were averaged within each clutch and a linear regression weighted according to clutch size (ranging from 1-3 offspring) showed a marginally non-significant relationship between mother and offspring EWL ($h^2 = 0.36$, $p = 0.059$, $R^2 = 0.248$).

DISCUSSION

Our results indicate no significant differences in mean T_b , T_{pref} , or CT_{max} and CT_{min} across the study populations (Figs 3-6). We did, however, detect a difference in mean EWL rate across populations, with differences in site soil moisture exhibiting a correlation with this pattern. Since differences in variance were not detected for the various physiological traits, we posit that genetic impoverishment may not be an important factor in determining variability in traits related to thermal ecology. However, it appears that characteristics of the site, notably maximum T_e and soil moisture content, may contribute to differences across populations. These differences do not extend to variation in selected lizard body temperatures in either a field (T_b) or lab (T_{pref}) setting, even though in other species T_{pref} may differ among populations from differing environments, e.g., along an altitudinal gradient (Sinervo and Adolph, 1989; Van Damme et al., 1989). Relegation to sub-optimal habitats may therefore be a more important short-term impact, especially for small ectotherms which rely on heterogeneous habitat structure for refugia from predators and sub-optimal temperatures

(Sarris et al., 2006). Our results suggest that differences in habitat quality can impact water flux in this species, a critical component of ectotherm physiology (Lorenzon et al., 1999).

We detected higher rates of EWL in the mesic population at NNF, the most mesic site of all those sampled for soil moisture (Fig. 7). This pattern has been demonstrated in several other lizard species (Bentley and Schmidt-Nielsen 1966; Gunderson and Leal, 2012; Dmi'el et al., 1997). It is not clear whether these differences in EWL are genetically determined or whether they are the result of labile behavioral adaptation to local conditions. Our results suggest potential heritability of these differences; however, our heritability study was performed on dam-progeny pairs so it remains confounded by both maternal effects and dominance variation (Lynch and Walsh, 1998). These limitations notwithstanding, our results are suggestive of at least a partial genetic component to the observed differences. Climate in the Aegean Sea region is expected to become both warmer and drier, and our results indicate that it is changes in patterns of precipitation, rather than temperature, that are more likely to affect the lizards. Given the differences exhibited in water loss across our study populations, it is possible that *P. erhardii* populations living in mesic environments may be the first impacted by increased habitat dryness resulting from climate change. This corroborates paleo-historical reconstructions of reptile extinctions on the islands which appear to have been driven by patterns of increasing Holocene desiccation (Foufopoulos et al., 2011).

It remains to be determined which mechanisms underlie differences in EWL across populations. Have populations evolved different EWL rates over time in response to directional selection according to the environment? Or does physiology adjust plastically to the environment experienced by the lizards? If this is a plastic response, or potentially maternal effects-related plasticity (Mousseau et al., 2000), is it reversible later in life? If, for

instance, water loss rates can shift with increasing habitat aridity, this may allow lizards to adapt to relatively rapid fluctuations in climate. Even if this trait lacks plasticity, reduction of precipitation under a changed global climate may not translate into a decline in species abundance. For example, we might reasonably expect range expansions by xeric habitat populations into currently mesic localities as these become drier with progressive climate change, resulting in zero net change in overall abundance. However, if this occurred concomitantly with extinctions in the increasingly dry xeric habitat, this could result in an overall reduction in species abundance. The threshold of habitat dryness beyond which *P. erhardii* populations cannot persist is currently unknown, making these potential future range shifts difficult to predict.

Population demographics appear to contribute to differences within populations. Sex and reproductive status shape differences in T_{pref} , with gravid females selecting significantly lower temperatures than either males or non-gravid females (Fig. 5). Past studies have suggested that this may be related to temperature sensitivity in embryonic development, and that the negative consequences of improper thermoregulation during pregnancy may have lasting impacts on offspring fitness (Burger, 1989; Mathies and Andrews, 1997; Wapstra, 2000). Climate warming therefore would likely have direct impacts on successful recruitment in this species. Size, which can be used as a proxy for age given lifelong growth in this species, also appears to impact thermal tolerances, with larger (older) lizards less able to tolerate higher temperatures than smaller (younger) lizards. Therefore, assuming equal thermal opportunity, we may expect rapid increases in temperature to remove older individuals first, shifting the age/size structure of populations. Coupled with significantly

reduced clutch size in genetically impoverished populations (Belasen, unpubl. data), this may have severe implications for persistence of populations on small islets.

Overall, our results do not indicate a direct impact of genetic impoverishment on thermal ecology. This could be due to highly conservative genetic infrastructure and resistance to directional selection (Hertz and Nevo, 1981; but see Scheers and Van Damme, 2002). Alternatively, this could be the result of diversifying selection on thermal preferences. Although we did not detect any differences associated with island size, prior research suggests that genetic impoverishment is still likely to impact adaptability or evolutionary potential of small populations (Willi et al., 2006). This may be especially likely for the ASP lizard population which consists of only a few hundred individuals. Genetic impoverishment combined with a lack of selection pressure may also result in canalization, or a decline in the propensity for plasticity (Aubret and Shine, 2010; Via et al., 1995). In addition, our study focused on a single species, which interacts with numerous predator, prey, and competitor species. Without assessing potential responses of these allied species to climate change, including spatial or temporal shifts in activity, it is difficult to obtain a clear picture of how the focal species may be impacted (Parmesan, 2006).

Global climate change will not just increase mean temperature, but also will likely increase variability in temperature across the globe (Walther et al., 2002). Ectotherms are sensitive to both increases and decreases in environmental temperature, as both represent deviations from the optimal range and thus a decline in thermal habitat quality (Hertz et al., 1993; Vickers et al., 2011; but see Diaz, 1997). Moreover, changes in habitat structure could have direct impacts on this species' ability to thermoregulate. For ectotherms, temperature is likely the most important factor in determining climate-linked local extinctions (Sinervo et

al., 2010), and therefore restriction of thermoregulatory opportunities could impact these animals directly (Kearney et al., 2009). It is difficult to predict how vegetation may respond to shifts in climate, but with improved parameterization of vegetation models combined with understanding of past versus current habitat use by focal species (Kearney and Porter, 2004; Lawing and Polly, 2011), we may achieve a better understanding of the future for these ecosystems.

The potential synergistic effects of global climate change and habitat fragmentation are likely complex, and warrant further research. Through our studies of the Cycladic lizard populations, we have determined that impoverishment of genetic diversity due to fragmentation may not be as important in shaping thermal ecology as population characteristics such as age and reproductive status. It also appears that environmental conditions have a significant effect on reptile physiology, and habitat moisture appears to be a most important factor. This finding is at odds with the traditional view that humidity is less important for reptiles than other species with more permeable skin. However, we are currently unable to tease apart the interactions between temperature and humidity, or assess how these two abiotic factors may give rise to phenotypic differences across populations. These interactions could potentially be addressed by conducting experiments that vary hydration of individuals and examining whether this alters thermal preferences.

Our results indicate that although thermal ecology of *P. erhardii* appears to be relatively rigid, hydric physiology may be subject to adaptive change in response to environmental habitat characteristics. This lends support to the idea that ectotherms may be among the first vertebrates impacted by changes to the habitat, especially those resulting from climatic shifts (Gunderson and Leal, 2012). The central location of these animals in

food webs means the loss or reduction of their biomass can have cascading effects throughout the ecosystem. Therefore, deeper understanding of anthropogenic impacts on these animals is likely integral to the successful management of broader biological communities in this region.

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