Received: 18 September 2025 | Accepted: 27 July 2026

DOI: 10.1111/1365-2435.70428

Functional Ecology

RESEARCH ARTICLE

Urban oases relax desiccation risk for an arid-adapted lizard

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Funding information
National Science Foundation Postdoctoral Research Fellowship in Biology, Grant/Award Number: 2109710; National Science Foundation Graduate Research Fellowship Program, Grant/Award Number: 2022296896

Handling Editor: Anthony Herrel

Abstract

1. Urbanization from expanding human development has radically altered the structure, ecology and microclimate of landscapes worldwide. These dramatic environmental alterations subject organisms to novel ecological conditions and may select for distinct ecophysiological traits.
2. Here, we investigate the effects of urbanization on cutaneous evaporative water loss (CEWL) in the Aegean Wall Lizard (*Podarcis erhardii*) and explore the potential environmental factors impacting physiology. In this Mediterranean setting, urban microhabitats were cooler and wetter, and urban lizards displayed higher CEWL than nonurban lizards. Increased urban lizard CEWL is a potential response to relaxed pressure for water conservation in areas with increased water availability from human activities, such as irrigation and ornamental water features.
3. Our findings demonstrate that urbanization may shift microclimates and thus alter ectotherm ecophysiology. Quantifying these changes advances our understanding of how urbanization shapes organismal responses to novel environments and offers insights into adaptation and persistence in human-modified landscapes.

KEYWORDS
cutaneous evaporative water loss (CEWL), Cyclades, ecophysiology, plasticity, *Podarcis*, urbanization

1 | INTRODUCTION

Urban environments impose unique pressures, forcing species to adapt, relocate or perish (Lowry et al., 2013; Shochat et al., 2006). Urban ecosystems are characterized by habitat fragmentation, artificial and impervious surfaces, irrigation, pollution and dense human populations, all of which alter microclimates and resource availability (Anderies et al., 2007; Johnson & Munshi-South, 2017; Le Roux et al., 2014; McKinney, 2008; Winchell et al., 2016). While urbanization often limits some resources for wildlife (McKinney, 2008), cities can also be resource havens where food, shelter and water are more abundant than in nonurban habitats, particularly in gardens and green spaces (French et al., 2018; Gibbons et al., 2023; Goddard et al., 2010). In today's rapidly urbanizing world, it is increasingly important to understand the ecological and environmental factors that make cities hospitable or hostile to wildlife.

Water availability and hydration are fundamental factors that affect physiological performance, fitness and survival for

taxa across all environments, and changes in water availability can have significant impacts on species persistence (Belasen et al., 2017; Kearney et al., 2018; McCluney et al., 2012; Rozen-Rechels et al., 2019; Sannolo & Carretero, 2019; Tracy et al., 2014). Urban environments can exhibit a range of humidity levels due to the interplay between human demand for water, impervious surfaces, altered vegetation cover and irrigation practices, resulting in both drier and wetter microclimates (Broadbent et al., 2018; Lin et al., 2018; Ramamurthy & Bou-Zeid, 2014). Impervious surfaces in urban habitats modify microclimates by raising temperatures and altering water infiltration, runoff and evapotranspiration (Beegam & Arulraj, 2018; McGrane, 2016; Shuster et al., 2005; Weng & Lu, 2008), increasing pressure for behavioural and physiological adaptations to adequately maintain thermal and hydric homeostasis (French et al., 2018; Hall & Warner, 2018). These pressures are especially relevant for ectotherms that rely on the external environment to regulate key bodily functions (Huey & Stevenson, 1979).

Lizards are useful study organisms for understanding the ecological consequences of urbanization because they can exhibit rapid shifts in behaviour (Putman et al., 2024), morphology (Donihue, 2016) and ecophysiology (Campbell-Staton et al., 2020) in response to human-mediated environmental change (Camargo et al., 2010; Putman & Tippie, 2020). For example, lizards can reduce evaporative water loss by selecting humid microenvironments or acclimating to drier conditions, making them more resilient to shifts in microclimates than some other taxa (Bodineau et al., 2024; Heatwole & Veron, 1977; Kattan & Lillywhite, 1989; Pintor et al., 2016; Weaver et al., 2022, 2023). However, despite a recent rise in interest in urban ecology and evolution, few studies have directly linked lizard urban microclimates to ecophysiological traits, like evaporative water loss (French et al., 2018; Vardi et al., 2023).

We investigated the effect of urbanization on the hydric physiology of ectotherms by studying urban and nonurban populations of the Aegean Wall Lizard on the island of Naxos, Greece. Naxos experiences long, hot, dry summers that should create strong pressures for water conservation among its inhabitants, and the landscape has been shaped by human presence for thousands of years (Belasen et al., 2017; Brock et al., 2015; Krawczyk et al., 2019). The Aegean Wall Lizard (*Podarcis erhardii*) is a generalist lizard that occupies habitats ranging from undisturbed sand dunes to ancient and modern towns (Brock et al., 2015; Donihue, 2016; Foufopoulos et al., 2024), making it well-suited for assessing the effects of urbanization. We measured microclimate, vegetation and hydric physiology to identify differences between urban and nonurban lizards and their microhabitats. We expected urban areas on Naxos to be more humid due to irrigation and water use, and thus urban lizards would face less desiccation risk, leading to higher evaporative water loss—measured as cutaneous evaporative water loss (CEWL). This study provides insight into the potential positive effects of human activity on wildlife, and how urban oases might influence ecophysiology.

2 | MATERIALS AND METHODS

2.1 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Individuals	Sites	103 (57 urban; 46 nonurban)
Sites	Pooled Sites	5 urban, 3 nonurban

2.2 | Study site and species

This study was conducted May–June 2023 on Naxos, Greece, the largest island in the central Aegean Sea (approximately 448 km^2). The island has a Mediterranean climate with long, hot, dry summers and short, wet winters (Krawczyk et al., 2019). Human activity—agriculture, settlement, mining and tourism—has shaped the landscape for millennia, leaving patches of undeveloped habitat such as juniper dunes, rocky southern slopes and remnant forests in mountain gullies (Grove & Rackham, 2003; Krawczyk et al., 2019). Ancient civilizations such as the Minoans and Mycenaeans cultivated terraced fields on the island slopes to grow olive, grape and garden crops, creating lush habitat for small, non-pest fauna such as lizards, as well as their arthropod prey. Across unsettled areas, ancient deforestation for human settlement and seafaring and contemporary goat herding has left much of the Aegean island landscape deforested and dominated by short sclerophyllous evergreen maquis and diverse, summer-deciduous dwarf scrub or phrygana (Fielding & Turland, 2008).

The Aegean Wall Lizard (*P. erhardii*) is a widespread habitat generalist that occurs in a variety of habitats from sea level to 2000 m in elevation (Valakos et al., 2008). Their common name epitomizes *P. erhardii's* ability to exploit urban microhabitats, such as dry stone walls, gardens and paved surfaces. On Naxos, urban populations of wall lizards have larger bodies, wider heads and larger hindlimb-to-forelimb ratios, all of which may be tied to factors like locomotion, competition and resource acquisition in urban habitats (Donihue, 2016; Stadler et al., 2023).

2.3 | Field work and environmental data

We sampled five urban and three nonurban sites during May and June of 2023 once each and in a random order (Figure 1). Urban sites consisted of dense settlements, stone walls, roads and irrigation. Nonurban sites lacked permanent structures, walls, roads or irrigation and had substrates natural to the island including sand, soil, sandstone and granite.

We used lassos to collect adult lizards (>45 mm snout-vent length, SVL) during their diurnal activity periods (08:00–13:00 and 16:00–18:00). SVL measurements were taken as the average

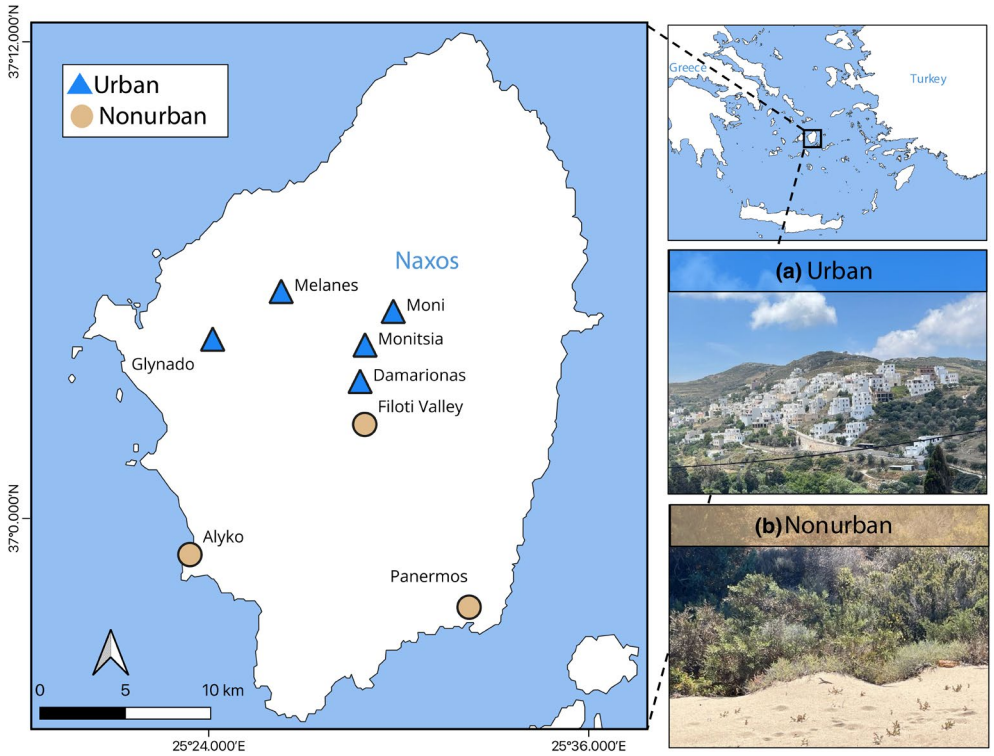

FIGURE 1 Map of field sites on Naxos, Greece. (a) Photo of Melanes, a typical urban environment on Naxos. (b) Photo of Alyko, a nonurban site with natural sand dune substrate and without permanent human settlement.

of two measurements within 10% error of one other, and all measurements were taken by a single person (D.J.S.). Lizards were held in breathable cloth bags and taken to the laboratory to acclimate under standardized conditions (see below) for 24 h before measurement.

At the capture point of each lizard, we estimated the vegetation cover (%) of a 2 m^2 plot around where we first observed each lizard using a quadrat and visual surveys. We also measured ambient temperature (°C) and relative humidity (%) with a digital thermohygrometer (R6001; Reed Instruments, Wilmington, NC, USA) and calculated ambient vapour pressure deficit (VPD; kPa) defined as the difference between the amount of moisture in the air versus how much moisture the air could hold at saturation (Riddell et al., 2017; Weaver et al., 2023).

To investigate whether microclimate differences were driven by urbanization or simply prevailing macroclimate, we extracted WorldClim monthly mean, maximum and minimum temperatures, solar radiation, water vapour and precipitation for the midpoint of each site (v2.1; 1970–2000 1 km^2 scale) (Fick & Hijmans, 2017). We calculated annual precipitation as the sum of all months and monthly VPD using water vapour pressure and maximum temperature. We also extracted normalized difference vegetation index (NDVI) and normalized difference moisture index (NDMI) values from Karra et al. (2021) for the midpoint of each site for May to June 2023. By comparing each lizard's experienced microclimate to the site macroclimate, we can determine whether microclimate differences are impacted by urban development.

2.4 | Physiological measurements

We chose to use CEWL as our measure of water loss, as it is unlikely to be controlled exclusively by behaviour such as water loss through the mouth, cloaca or eyes (DeNardo et al., 2004). Thus, CEWL is subject to greater ecological and evolutionary pressures, so changes in CEWL are more likely to be a physiological response to habitat rather than behavioural changes. We measured CEWL with an AquaFlux evaporimeter (AF200; BioX Systems, London, UK), which quantifies instantaneous flux of water across a 3 mm diameter area of the skin ($\pm 0.02\ g\ m^{-2}\ h^{-1}$). All lizards were maintained under constant laboratory conditions of 26.1°C ± 0.3 SD (range, 25.8–26.5), RH 47.6% ± 0.3 (47–48) and VPD 1.78 kPa ± 0.03 (1.75–1.82) for 24 h prior to CEWL measurement. This laboratory acclimation period served to minimize variability in CEWL due to instantaneous flexibility relative to capture habitat (Davis et al., 2024; Weaver et al., 2022). Thus, our measurements control for the effect of plasticity, and any differences detected can be attributed to lizards' response to their habitat. We measured CEWL in ~5–10 replicates on the mid-dorsum, removed any outliers (0–3 per lizard, 65 total) and averaged remaining replicates (3–10 per lizard) (mean SD = $1.15\ g\ m^{-2}\ h^{-1}$). To ensure body temperature did not influence CEWL, we measured internal body temperature by inserting a thermocouple into the cloaca immediately after measuring CEWL (±0.1°C; K-Type Thermometer, model DM6801; Minnesota Measurement Instruments LLC). We recorded ambient temperature (±0.1°C) and relative humidity (±0.1%) by the evaporimeter for each lizard at the time of measurement to test

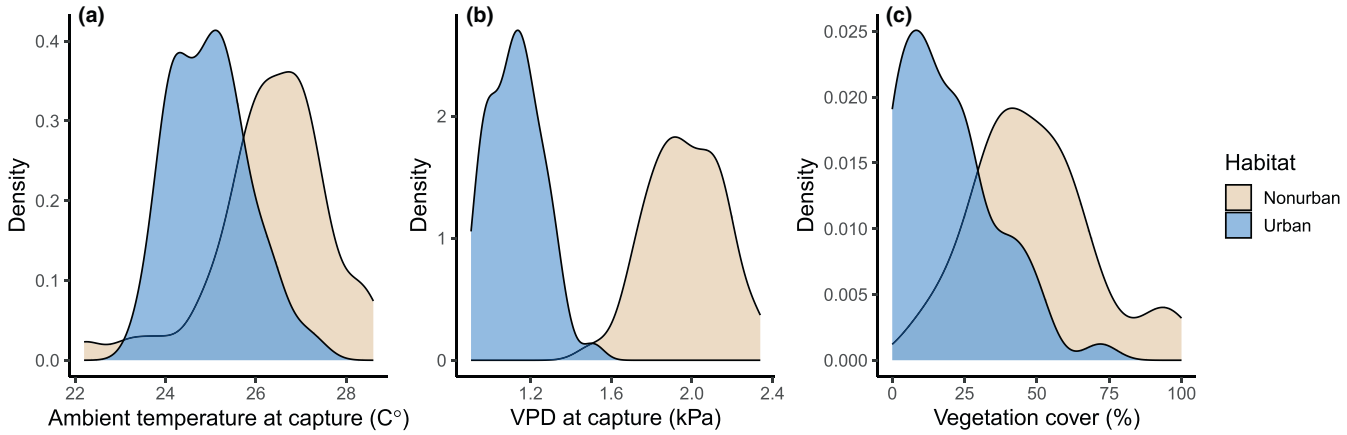

FIGURE 2 Urban microhabitats used by lizards on Naxos, Greece are characterized by lower ambient temperatures (a) lower vapour pressure deficit (VPD) (b) and less vegetation cover (c) than nonurban habitats.

if these factors influence CEWL. Work with live animals was conducted with permission from the University of California Berkeley IACUC (Protocol AUP-2021-08-14567) and the Greek Ministry of Environment (permit ΥΠΕΝ/ΔΔΔ/18726/601 to K.M.B).

2.5 | Statistical analysis

We performed all analyses in R v4.2.0 (R Core Team, 2022) and model assumptions were assessed by visually inspecting residual versus fitted-value plots, normal Q-Q plots and Cook's distance. Residuals exhibited no substantial deviations from normality, residual variance was homogeneous, and no influential observations were detected. To explore the impact of habitat type on CEWL, we fit linear models with habitat type as the primary predictor and sex and SVL as covariates. We initially included site as a random intercept using linear mixed effect models in the *lme4* package (Bates et al., 2026), but site explained no additional detectable variance and was excluded from final analyses.

To test if variation in CEWL was explained by microclimatic differences, we fit linear models with CEWL as the response variable and VPD, ambient temperature and percent vegetation cover measured at the lizard capture location as explanatory variables. We initially included site as a random intercept, but it explained no additional variation and was excluded from the final models. Variance inflation factors (VIFs) were calculated using the *car* package (Fox et al., 2026) to assess multicollinearity among predictors. Final VIFs were low for all microclimatic predictors (VIF <2.48). When habitat type was added to the same model, VIF values increased significantly (Habitat = 10.16; VPD = 12.82), indicating collinearity between habitat type and VPD at lizard capture. Thus, habitat type and microclimatic variables were analysed separately.

To evaluate differences in habitat microclimate, we summarized lizard capture microclimatic variables (ambient temperature, VPD and percent vegetation cover) using a principal components analysis (PCA). Similarly, we summarized site-level macroclimatic variation using PCA based on NDVI, NDMI, annual precipitation, mean monthly precipitation, mean monthly solar radiation, mean monthly water vapour pressure, mean monthly maximum temperature, mean monthly minimum temperature, mean monthly average temperature and mean monthly VPD derived from WorldClim data. We then tested whether microclimate differed between habitat types after accounting for macroclimatic variation using a linear model with microclimate PC1 as the response variable and habitat type, macroclimate PC1 and their interaction as predictors. All PCAs were conducted on centred and standardized variables using the *prcomp* function. Estimated marginal means and pairwise comparisons were calculated using the *emmeans* package (Lenth et al., 2025).

3 | RESULTS

We collected ecophysiological measurements from 103 lizards: 76 males (48 urban and 28 nonurban) and 27 females (9 urban and 18 nonurban). Urban males had an average CEWL rate of 20.98 ± 2.01 g/m^{2}h (±SD) while nonurban males had an average CEWL of 18.54 ± 1.64 g/m^{2}h (±SD). Urban and nonurban females had average CEWL rates of 20.52 ± 2.15 g/m^{2}h (±SD) and 18.67 ± 1.88 g/m^{2}h (±SD), respectively.

3.1 | Micro and macroclimatic variation

Microclimates experienced by urban lizards were characterized by significantly lower temperatures ($F_{1,101} = 42.77$, $p < 0.001$), lower VPD ($F_{1,101} = 734.6$, $p < 0.001$) and less vegetation cover ($F_{1,101} = 62.07$, $p < 0.001$) when compared to their nonurban microclimates (Figure 2). PCA of capture microclimates yielded a PC1 that explained 70.7% of the total environmental variation, with strong loading scores for ambient temperature, vegetation cover and VPD (loadings = −0.57, −0.53 and −0.63, respectively; Figure 3a; Tables S1 and S2). Microclimate PC1 represented an environmental gradient separating hotter, drier, more vegetated microhabitats from cooler, wetter, less vegetated microhabitats.

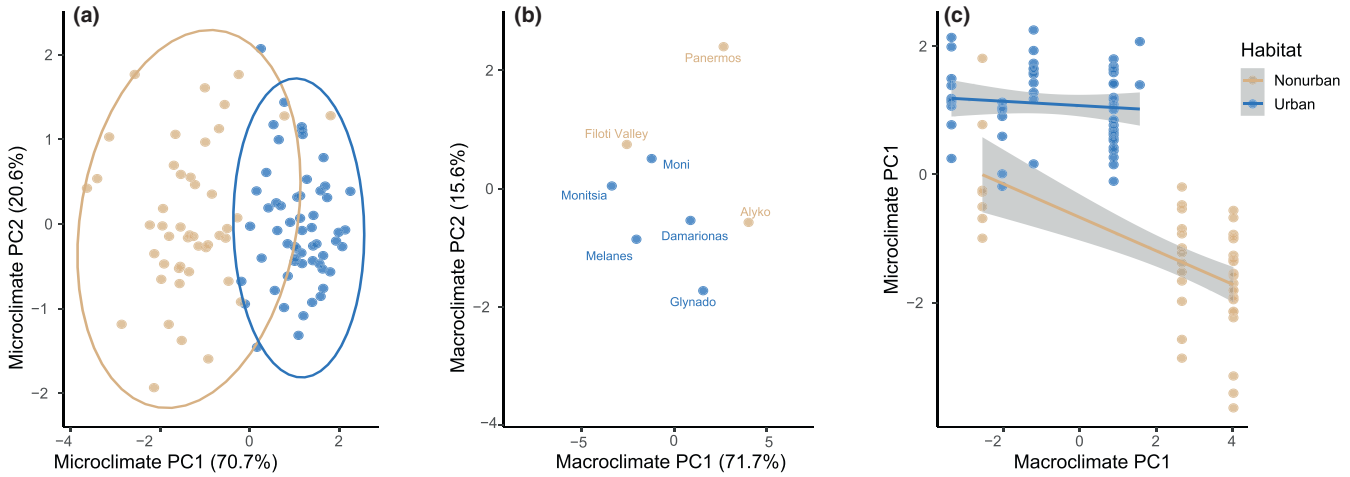

FIGURE 3 Principal component analyses of micro and macroclimatic variables in Naxos, Greece, with percent of variation explained. (a) Principal components analysis (PCA) of microclimatic variables measured at capture locations of individual Aegean Wall Lizards. (b) PCA of macroclimatic variables summarized at the site level. Ellipses represent 95% confidence intervals in both PCA plots. (c) Relationship between microclimatic PC1 and macroclimatic PC1, where solid lines show fitted linear regressions with shaded 95% confidence intervals.

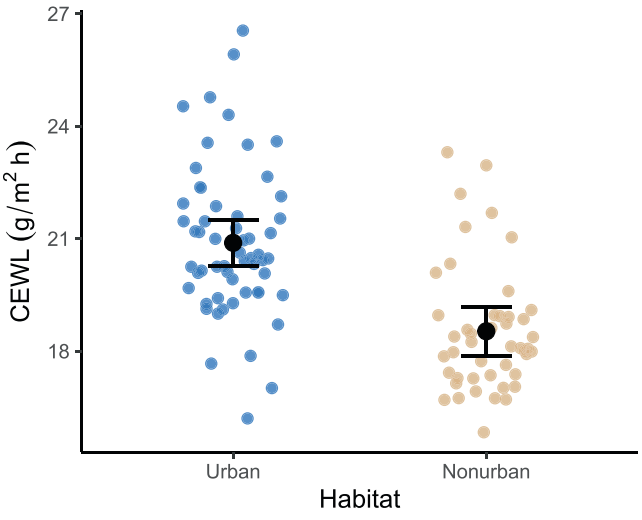

FIGURE 4 Urban Aegean Wall Lizards on the island of Naxos, Greece, exhibited significantly higher cutaneous evaporative water loss (CEWL) than their counterparts found in nonurban habitats. Smaller coloured points represent individual lizards, while larger black points represent estimated marginal means from our linear models with 95% confidence intervals.

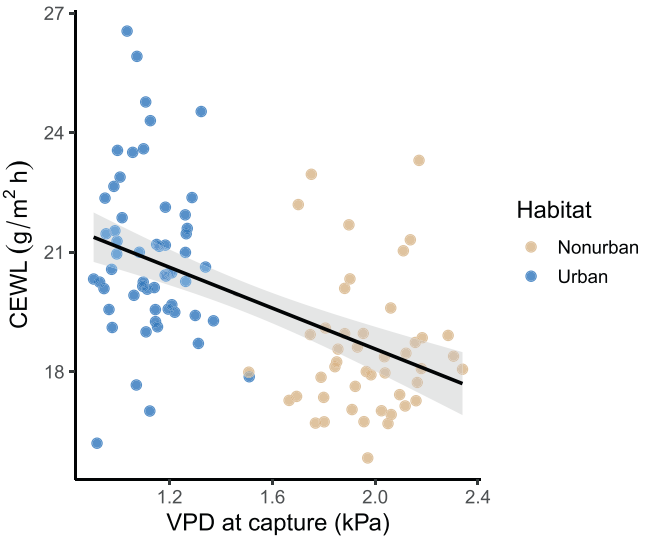

FIGURE 5 Vapour pressure deficit (VPD) in the lizard's habitat was a significant predictor of cutaneous evaporative water loss (CEWL) in Aegean Wall Lizards, with CEWL decreasing as VPD increases. Points represent individual lizards.

Macroclimatic PC1 explained 71.7% of the variation among sites, with mean monthly minimum temperature (loading = 0.37), water vapour pressure (0.37), mean monthly average temperature (0.37), mean monthly maximum temperature (0.36), annual precipitation (−0.36) and mean monthly precipitation (−0.36) contributing most strongly to PC1 (Figure 3b; Tables S3 and S4). Macroclimate PC1 separated warmer, higher-radiation sites from sites characterized by more precipitation and lower VPD.

Microclimates in microhabitats selected by lizards differed strongly between habitat types even after accounting for macroclimatic variation (Habitat: $F_{1,99} = 328.10$, $p < 0.001$). Macroclimate PC1 was also a significant predictor of microclimate PC1 ($F_{1,99} = 24.21$, $p < 0.001$; Figure 3c; Table S5). Additionally, the relationship between macroclimate and microclimate differed between habitat types, as indicated by a significant Habitat × Macroclimate interaction ($F_{1,99} = 10.85$, $p = 0.001$). In nonurban habitats, microclimatic PC1 decreased with increasing macroclimatic PC1 (slope = −0.260 ± 0.044 SE, 95% CI = −0.348 to −0.173), whereas no significant relationship was detected in urban habitats (slope = −0.034 ± 0.053 SE, 95% CI = −0.138 to 0.071). The habitat-specific slopes differed significantly (difference = 0.226 ± 0.069 SE, $t_{99} = 3.29$, $p = 0.0014$), indicating that macroclimate was associated with microclimate variation in

nonurban habitats but not in urban habitats. Together, these results indicate that urban and nonurban lizards occupy distinct microclimates and that the relationship between macroclimate and microclimates differs between habitat types.

3.2 | CEWL variation between habitats

Urban lizards exhibited significantly higher CEWL than nonurban lizards ($\beta = 2.36 \pm 0.48$ [±SE], $F_{1,99} = 39.78$, $p < 0.001$; Figure 4; Table S6), while sex and SVL had no significant impact ($F_{1,99} = 0.014$, $p = 0.905$ and $F_{1,99} = <0.001$, $p = 0.997$, respectively; Table S6).

Only VPD at capture was a significant predictor of lizard CEWL, with CEWL declining as VPD increased (VPD: $\beta = -2.82 \pm 0.67$ [±SE], $F_{1,99} = 36.78$, $p < 0.001$; Figure 5; Table S7), while ambient temperature and percent vegetation cover did not predict CEWL variation (ambient temperature: $F_{1,99} = 0.67$, $p = 0.415$; percent vegetation cover: $F_{1,99} = 0.04$, $p = 0.842$).

4 | DISCUSSION

Physiology is an important trait mediating adaptive responses to environmental change, such as urbanization. Urbanization can act as a resource haven for select species in naturally arid regions such as the Cyclades islands, reshaping thermal and hydric conditions and thus ecophysiology. The Aegean Wall Lizard demonstrates strong adaptability to these changes, with urban lizards exhibiting higher CEWL rates. Urban and nonurban lizards occupy distinct microclimates despite a broadly similar macroclimate, and VPD is the primary microclimatic variable associated with CEWL variation. The higher CEWL exhibited in urban populations may reflect relaxed selection for water conservation in more humid urban microclimates. Thus, urban areas may be oases that provide novel ecological opportunities for wildlife to exploit.

4.1 | Micro and macroclimatic variation

Urban and nonurban lizards occupied distinct microhabitats even after accounting for macroclimatic variation. Urban microclimates were characterized by lower temperatures, lower VPD and less vegetation cover than microclimates in nonurban areas. Macroclimatic variables were associated with microclimate, but habitat type remained a strong predictor even after accounting for broader environmental variation. Additionally, the significant interaction between habitat type and macroclimate indicates that the relationship between site-level macroclimate and lizard-experienced microclimate differs between habitat types, where macroclimatic variables had a significant impact on nonurban microclimates, but had no impact on urban microclimates. These results indicate urbanization may be directly impacting the microclimates occupied by lizards. Urban Aegean Wall Lizards on Naxos are not only exposed to significantly different substrate and habitat structure, but also to completely different microclimates than their nonurban counterparts. The stark contrast in environmental factors between urban and nonurban Naxos is due to a combination of the prevailing Mediterranean climate and human design, culture and behaviours. Nonurban habitat on Naxos is Mediterranean scrub that is often hot, dry and characterized by dense phrygana/maquis vegetation. Conversely, urban habitats on Naxos have been under construction for thousands of years and dry stone wall terraces that the lizards eponymously inhabit have been used to concentrate water and increase the amount of arable land across the island (Grove & Rackham, 2003). Additionally, much of Naxos's development is constructed with naturally occurring and/or light-coloured materials that potentially have higher levels of albedo than typical urban construction (Chapman et al., 2017). Concentrated water use in urban areas, in combination with a higher level of heat reflection by light-coloured buildings, works to moderate Naxos's typically hot and dry climate. Additionally, both micro- and macroclimate analyses found reduced vegetation cover and greenness in urban areas, indicating that expansive, green, more natural habitat does not necessarily provide the same level of water resources as the dense pockets of ornamental greenery found in urban spaces. Despite reduced vegetation cover and a uniform prevailing hot and dry Mediterranean macroclimate, urban oases may offer more favourable conditions than surrounding natural habitats, especially in the context of global climate change that is expected to increase aridity in the Mediterranean (Ali et al., 2022).

4.2 | CEWL variation between habitats

Urban lizards lost more water through CEWL, and this difference is likely due to environmental differences between urban and nonurban habitat. Environmental VPD was the sole microclimatic variable associated with CEWL variation, with lower VPD corresponding to higher CEWL rates. Biophysically, higher VPD increases atmospheric demand for water and would thus be expected to cause an increase in CEWL. However, organisms can alter their physiology to reduce CEWL in dry environments. The negative relationship we measured suggests there has indeed been a physiological response of CEWL to site-level microclimates in Aegean Wall Lizards. Importantly, CEWL for all populations was measured in the laboratory under identical conditions, showing that CEWL differences persisted even without continued exposure to their respective habitat conditions. Nonurban lizards may have altered their anatomy and/or physiology to counteract the physical demand of high-VPD microclimates by minimizing CEWL in their dry, natural habitat to prevent desiccation. Alternatively, in urban environments, reduced VPD might relax pressures to minimize water loss, allowing for increased water loss through CEWL without increased risk of dehydration (DeNardo et al., 2004; Loughran & Wolf, 2023; Tattersall et al., 2006). Additionally, although our analyses did not find ambient temperature to be a significant predictor of CEWL, higher temperatures in nonurban habitats may still contribute indirectly to water stress by

increasing evaporative demand and dehydration risk, potentially reinforcing physiological responses that promote water conservation. Cutaneous water loss in reptiles seems to be primarily controlled by changes in skin lipid composition and/or quantity (Champagne et al., 2015; Roberts & Lillywhite, 1980). Mechanisms associated with minimizing water loss in arid climates may come with physiological and energetic costs. Thus, reduced water stress may relax the pressures associated with minimizing water loss and allow for fitness advantages. However, studies have not yet quantified the energetics of reptile skin permeability. Recent studies suggest that lizard CEWL is highly plastic, with rapid responses to humidity and temperature, and further research is needed to explore the mechanisms behind shifting CEWL rates in human-altered environments and to distinguish between plasticity, acclimation and genetic adaptation (Davis et al., 2024; Weaver et al., 2022, 2023).

The island of Naxos often experiences water scarcity, and in response, humans have been controlling water supply through rainwater harvesting and irrigation, directing it towards gardens, crops, water features and urban areas for centuries (Zarikos et al., 2023). These practices increase water availability in developed areas for all inhabitants, significantly alter the local microclimate and serve as a potential source of water supplementation for Naxos's urban lizards (Krawczyk et al., 2019; Zarikos et al., 2023). Another potential driver of increased CEWL in our urban sites is shifts in dietary preferences. Frugivory has been documented in *Podarcis* spp., including on the island of Naxos (Brock et al., 2014). Given the higher water content of fruit and plant material and the dietary adaptability of Aegean Wall Lizards, it is possible that urban populations are supplementing water intake through consumption of fruits that are often more prevalent near human development (Pietczak & Vieira, 2017). However, the true water quantity of these food items is unknown, and food alone has been shown to be insufficient in maintaining lizard hydration levels (Chabaud et al., 2023; Kay, 2023; Wright et al., 2013). Thus, the urban habitat and its concentrated water use is likely contributing to differences in local microclimate and VPD between urban and nonurban habitats, and in turn, acting as the primary driver of changes in CEWL (Weaver et al., 2022, 2023). Microhabitat alterations, behaviour, dietary changes and water supplementation might play secondary roles in reducing osmotic stress and creating urban oases that allow for increased CEWL in urban populations of Aegean Wall Lizards. Future work should investigate the potential pathways of water sensing, acquisition and use in Aegean Wall Lizards.

5 | CONCLUSION

Naxos' urban Aegean Wall Lizards appear to be thriving amidst increased resource availability, lower temperatures, more water and decreased VPD, where they exhibit relaxed water conservation through higher CEWL. The evolution and plasticity of traits that can maintain key physiological equilibria is critical for survival in these rapidly changing environments (Belasen et al., 2017; Gunderson & Stillman, 2015). Importantly, our findings suggest that urbanization does not universally impose hotter and drier conditions. Instead, cities, particularly those in arid climates, may create novel, wetter microclimates compared to the surrounding unirrigated land. Natural arid environments favour water conservation by wildlife, but if this is costly or poses trade-offs, water conservation should be relaxed in more humid environments. This study shows one way in which organisms may physiologically respond to climate change and human development and highlights the impact urbanization may have on local environmental variables. We should expect further changes in species traits, populations and distributions worldwide, but as demonstrated here, some populations are taking advantage of the urban scene.

AUTHOR CONTRIBUTIONS

Savannah J. Weaver, Tanmayi Patharkar and Kinsey M. Brock conceived the ideas and designed methodology; Savannah J. Weaver, David J. Stroud, Sara Ahlich, Tanmayi Patharkar, Annika Pohlo and Kinsey M. Brock collected the data; Tucker C. Heptinstall, Savannah J. Weaver, Emily N. Taylor, Kinsey M. Brock, and Rory Mendelow analysed the data; all authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Dr. Panayiotis Pafilis for his assistance in obtaining permits to perform research in Greece. Thanks to Brock Lab members and several anonymous reviewers for their constructive feedback that improved this manuscript. This research was supported by a National Science Foundation Postdoctoral Research Fellowship in Biology to KMB (Award No. 2109710) and a National Science Foundation Graduate Research Fellowship to SJW (Award No. 2022296896).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available for download at https://github.com/theptin/Urban-and-Nonurban-Lizards/blob/main/CEWL_final_analysis_data.xlsx and Zenodo: https://doi.org/10.5281/zenodo.21707618 (Heptinstall, 2026a). Additionally, the original code used for analyses can be found in both GitHub (https://github.com/theptin/Urban-and-Nonurban-Lizards/blob/main/CEWL_Lizards_Code_GitHub.R) and Zenodo: https://doi.org/10.5281/zenodo.21652338 (Heptinstall, 2026b).

STATEMENT ON INCLUSION

Our study here was conducted as a sub-project of a larger project on ecophysiology in Aegean wall lizards across the Aegean archipelago in collaboration with Dr. Panayiotis Pafilis from the National and Kapodistrian University of Athens (mentioned in the Acknowledgements). Additionally, whenever relevant, literature published by scientists from the region (e.g. Valakos, Pafilis, Foufopoulos, etc.) was cited.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Variable loadings for the principal components analysis (PCA) of lizard capture microclimates based on ambient temperature, vegetation cover and vapour pressure deficit (VPD).

Table S2. Variance explained by each principal component in the PCA of lizard capture microclimates.

Table S3. Variable loadings for the principal components analysis (PCA) of site-level macroclimatic variables derived from WorldClim data and vegetation indices.

Table S4. Variance explained by each principal component in the PCA of site-level macroclimatic variables.

Table S5. ANOVA results for the linear model relating microclimate PC1 to habitat type, macroclimate PC1 and their interaction.

Table S6. ANOVA results for the linear model testing the effects of habitat type, sex and body size (log-transformed SVL) on cutaneous evaporative water loss (CEWL).

Table S7. ANOVA results for the linear model testing the effects of vapour pressure deficit (VPD), ambient temperature and vegetation cover on cutaneous evaporative water loss (CEWL).

How to cite this article: Heptinstall, T. C., Weaver, S. J., Mendelow, R., Stroud, D. J., Ahlich, S., Patharkar, T., Pohlo, A., Taylor, E. N., & Brock, K. M. (2026). Urban oases relax desiccation risk for an arid-adapted lizard. *Functional Ecology*, *00*, 1–10. https://doi.org/10.1111/1365-2435.70428