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SYMPOSIUM

Comparison of Hydric and Thermal Physiology in an Environmentally Diverse Clade of Caribbean Anoles

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Synopsis As the world becomes warmer and precipitation patterns less predictable, organisms will experience greater heat and water stress. It is crucial to understand the factors that predict variation in thermal and hydric physiology among species. This study focuses on investigating the relationships between thermal and hydric diversity and their environmental predictors in a clade of Hispaniolan anole lizards, which are part of a broader Caribbean adaptive radiation. This clade, the "cybotoid" anoles, occupies a wide range of thermal habitats (from sea level to several kilometers above it) and hydric habitats (such as xeric scrub, broadleaf forest, and pine forest), setting up the possibility for ecophysiological specialization among species. Among the thermal traits, only cold tolerance is correlated with environmental temperature, and none of our climate variables are correlated with hydric physiology. Nevertheless, we found a negative relationship between heat tolerance (critical thermal maximum) and evaporative water loss at higher temperatures, such that more heat-tolerant lizards are also more desiccation-tolerant at higher temperatures. This finding hints at shared thermal and hydric specialization at higher temperatures, underscoring the importance of considering the interactive effects of temperature and water balance in ecophysiological studies. While ecophysiological differentiation is a core feature of the anole adaptive radiation, our results suggest that close relatives in this lineage do not diverge in hydric physiology and only diverge partially in thermal physiology.

Introduction

Climate change is rapidly impacting biodiversity across the globe (Pearce-Higgins et al. 2015; Riddell et al. 2019; Bennett and Classen 2020; Zhang et al. 2020; Briscoe et al. 2023). Rising temperatures, for example, are imposing heat stress and constraining activity patterns (Bradshaw and Holzapfel 2008; Sunday et al. 2012; Pecl et al. 2017; Catullo et al. 2019; Kelly 2019). Along with this increase in global temperatures, anthropogenic climate change is also altering global precipitation patterns (Dore 2005; Trenberth 2011; O'Gorman 2015). The frequency and intensity of both floods and droughts are predicted to increase (Dai et al. 2018; Allan et al. 2023), and constraints on water balance present an existential threat to biodiversity (Riddell et al. 2019). While ongoing global change impacts all organisms, its pernicious effects are expected to be especially pronounced in tropical ectotherms (Huey et al. 2010; Sinervo et al. 2010; Huey et al. 2012). This increased vulnerability to climate change is attributed to their temperature-dependent performance, their tendency for physiological specialization, and the fact that many of these organisms are already operating near their upper physiological limits (Huey et al. 2009; Sinervo et al. 2010; Huey et al. 2012). Mechanistic models that predict vulnerability to global change require detailed information about the behavioral and physiological capacities of organisms (Riddell et al. 2023a). This study focuses on

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investigating hydric and thermal specialization in a clade of tropical lizards and the environmental predictors for their ecophysiological diversity.

Water and temperature play a crucial role for life at all levels of biological organization. At the cellular level, for example, water serves as a solvent of biochemical reactions, and temperature influences the speed of those reactions (Franks et al. 1990; Chaplin 2006; Angilletta 2009). At the level of organisms, maintaining water balance and performance within thermal boundaries is paramount, and navigating complex hydric and thermal environments presents several challenges (Angilletta 2009; Sears and Angilleta 2015; Rozens-Rechels et al. 2019). The saturation vapor pressure increases exponentially with temperature, so the evaporative demand of the air (known as the vapor pressure deficit, VPD) is higher at warmer temperatures. Yet, in many ectothermic organisms, optimal thermal performance increases (until a threshold) with temperature (Angilletta et al. 2010); the same thermal features that can boost thermal performance also increase hydric demand. Additionally, there are often costs associated with hydro- and thermoregulatory behaviors, such as energy expended to select the optimal microclimate or greater exposure to predation (Huey and Slatkin 1976; Herczeg et al. 2008). The coupling of body temperature and evaporation rates means that there may be a trade-off between optimal thermal regulation and optimal hydric regulation (Pintor et al. 2016; Pirtle et al. 2019; Weaver et al. 2022).

The intrinsic link between hydric and thermal physiology inspires comparative inquiry. While many studies focus on either thermal physiology or hydric physiology, few provide data for both. Whereas the thermal physiology of lizards has long been the subject of comparative studies (reviewed in Bodensteiner et al. 2021; Muñoz 2022), comparatively less attention has been paid to water balance regulation and the interaction between water balance and thermal physiology (Pintor et al. 2016; Rozens-Rechels et al. 2019). There are several factors influencing thermo- and hydroregulatory strategies that shape organismal phenotypes, performance, and potential fitness. For example, dehydration can reduce a lizard's voluntary thermal maximum and/or critical thermal maximum (Herrando-Perez et al. 2020; Camacho et al. 2023). Impacts of temperature extremes can be magnified due to low precipitation (Wang et al. 2016), and low precipitation can additionally reduce the quality of microhabitat thermal refugia (Scheffers et al. 2014). Physiological stress influences thermo-hydro regulatory behavior: reptiles alter their preference for specific microhabitats relative to recent rainfall events (Ryan et al. 2016), temperature increases (Pintor et al. 2016), and water restriction (Rozen-Rechels et al. 2020). In addition to altering microhabitat selection because of hydric stress, some species have shown reduced activity to maintain their water balance (Davis and Denardo 2010; Kearney 2013; Kearney et al. 2018). Modeling approaches have made major contributions to better understanding organismal responses to changing environmental conditions mediated by energy-temperature-water interactions (Kearney et al. 2013; Riddell et al. 2018; Kearney and Porter 2020). Empirical studies bridging thermal and hydric physiology, however, remain relatively rare (Rozens-Rechels et al. 2019).

Anole lizards have long been the focus of thermal physiology studies, offering a rich dataset spanning several decades of research (Ruibal 1961; Rand 1964; Van berkum 1986; Hertz et al. 2013; Muñoz et al. 2014; Gunderson et al. 2018; Salazar et al. 2019). *Anolis* lizards from the Caribbean Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico) are a classic example of adaptive radiation, characterized by the independent evolution of ecomorphological and ecophysiological specialists (Williams 1972; Losos 2009; Hertz et al. 2013; Gunderson et al. 2018; Bodensteiner et al. 2024). This natural replication in ecological and phenotypic specialization has positioned anoles as a model system in ecology and evolution (Losos 2009; Muñoz et al. 2023). Ecomorphological specialization has long been the subject of investigation, resulting in a rich understanding of the connection between structural microhabitat use and variation in body size and shape. Anoles in the "twig" ecomorph, for example, have relatively small limbs and are diminutive in size, allowing them to cling to the distal ends of narrow branches. Patterns of ecophysiological evolution vary among Caribbean islands. On Puerto Rico, within-ecomorph niche partitioning occurred along the sun-shade axis, prompting specialization in heat tolerance to "warm" and "cool" microclimatic niches (Rand 1964; Williams 1983; Gunderson et al. 2018). Although physiological data are not available for Cuban anoles, within-ecomorph lability in canopy use follows a similar pattern, suggesting that comparable processes are at play (Ruibal 1961; Schettino et al. 2010). Yet, on Hispaniola, the patterns are different: close relatives on this island seem to be kept apart by allopatric and parapatric barriers, with limited signatures of ecophysiological divergence (Muñoz et al. 2014; Bodensteiner et al. 2024). Such variation urges a deeper exploration into the factors that predict ecophysiological evolution. While there are far fewer data available for hydric divergence along climatic gradients in *Anolis* lizards, a study on the Puerto Rican anole (*A. cristatellus*) found that lizards from a more mesic site (Cambalache) were more desiccation-prone than lizards from a more xeric

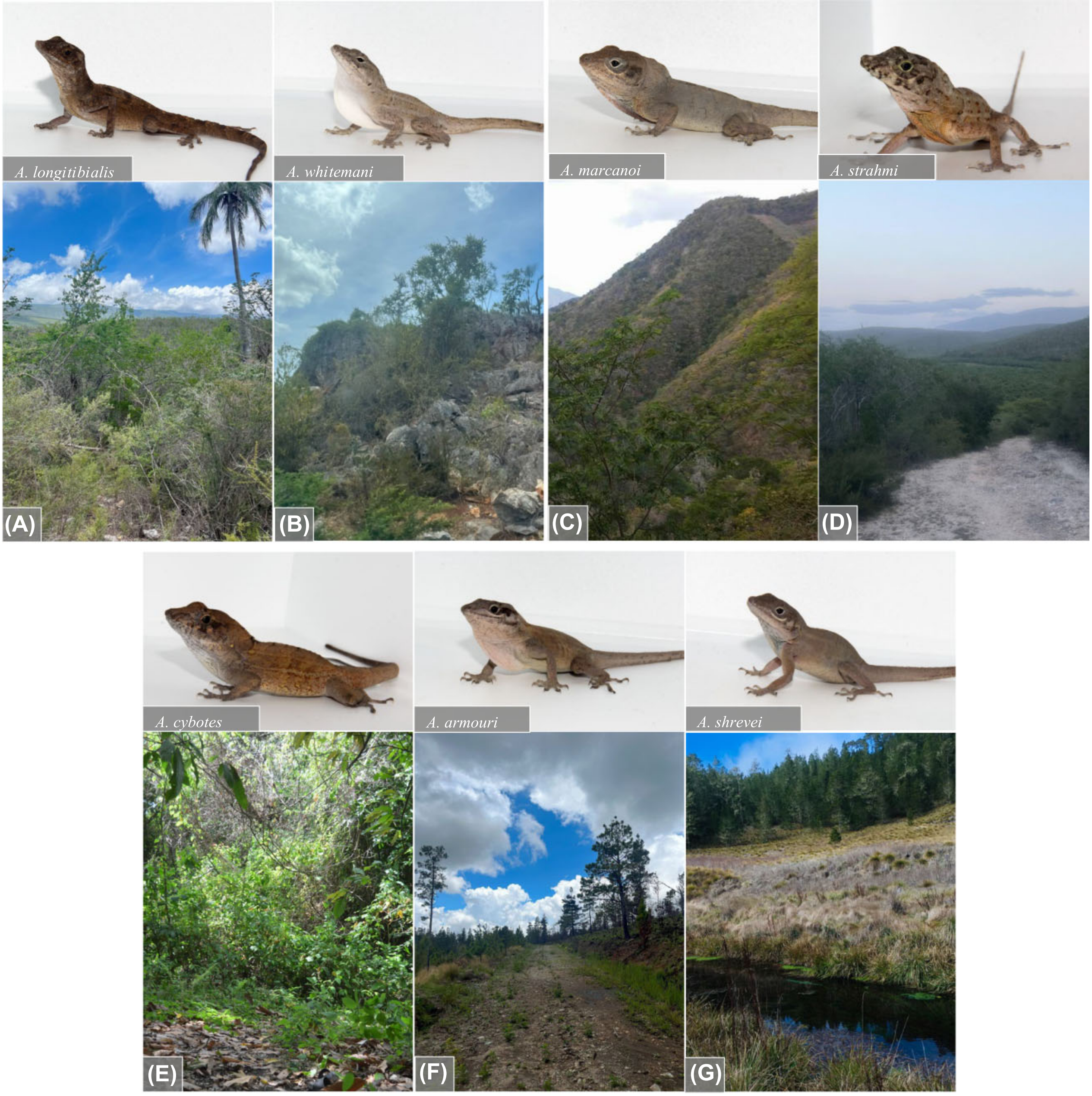

Fig. 1 Photos of cybotoid species, as well as the habitats from which lizards were collected in the Dominican Republic. Elevational range for each species is also provided. (A) *Anolis longitibialis*; Jaragua National Park, Pedernales province (∼0–100 m.a.s.l.). (B) *Anolis whitemani*; Hatillo Forest Reserve, Azua province (∼0–518.16 m.a.s.l.). (C) *Anolis marcanoi*; San José de Ocoa province (∼450–1800 m.a.s.l.). (D) *Anolis strahmi*; Loma Charco Azul Biological Reserve, Independencia province (∼0–900 m.a.s.l.). (E) *Anolis cybotes*; Francisco Alberto Caamaño Deñó National Park, Azua province (∼0–1200 m.a.s.l.). (F) *Anolis armouri*; Sierra de Bahoruco National Park, Independencia province (∼762–2438.4 m.a.s.l.). (G) *Anolis shrevei*; Valle Nuevo National Park, La Vega province (∼1555–2500 m.a.s.l.). Photo credit: *A. longitibialis*, *A. whitemani*, *A. marcanoi*, *A. strahmi*, *A. cybotes*, *A. armouri*, and *A. shrevei* by Saúl F. Domínguez-Guerrero; Habitat images for A, B, D, and F by Brooke Bodensteiner; E and G by Isabela Hernández Rodríguez; C by Ydsell Bonilla.

site (Guanica) (Gunderson et al. 2011). In *Anolis* lizards, there have been mixed results relating to water loss patterns and environmental conditions. Whereas some studies have found that lizards from more arid habitats were more resistant to water loss (Hillman and Gorman 1977; Hillman et al. 1979; Dmi'el et al. 1997; Gunderson et al. 2011), others have not detected a strong relationship between habitat aridity (microhabitat openness in the case of Hertz 1980) and water loss (Hertz 1980; Muñoz-Nolasco et al. 2019; Baeckens et al. 2023). The methodologies used varied among studies and often did not account for phylogenetic

Table 1 Species averages are given for size-corrected residuals of evaporative water loss (EWL) and the thermal sensitivity of EWL (Q10), which is a unitless metric. environmental variables related to sampling localities are also given, specifically mid-point elevation (m), mean monthly maximum temperature (°C), mean monthly minimum temperature (°C), and mean monthly precipitation (mm) from 1980–2023..

Species	EWL at 23°C ± SE (*n*)	EWL at 33°C ± SE (*n*)	Q10	Elevation	T_{max}	T_{min}	Precip.
Anolis armouri	0.22 ± 0.00(8)	−0.12 ± 0.26 (9)	2.80	2165	21.8	10.1	131
Anolis cybotes	−0.06 ± 0.18 (8)	−0.06 ± 0.10 (7)	2.49	45	32.4	22.2	71
Anolis longitibialis	0.09 ± 0.15 (7)	0.07 ± 0.19 (8)	2.17	177	31.9	21.2	66
Anolis marcanoi	0.12 ± 0.19 (4)	0.10 ± 0.03 (4)	4.85	940	25.7	12.8	100
Anolis shrevei	0.05 ± 0.25 (6)	0.04 ± 0.44 (8)	2.84	2359	16.9	5.4	140
Anolis strahmi	0.04 ± 0.03 (7)	−0.002 ± 0.26 (7)	2.34	515	30.6	18.6	81
Anolis whitemani	−0.23 ± 0.13(6)	−0.03 ± 0.12 (4)	1.34	3	32.0	21.7	69

relatedness or body size, limiting our ability to generalize findings.

Here, we investigate the thermal and hydric physiology and their environmental predictors in the cybotoids, a clade of Hispaniolan *Anolis* lizards. As a clade, these anoles are found across a wide elevational range, from sea level to more than three kilometers above it, and correspondingly occur in various types of habitats, including lowland xeric scrublands, mesic broadleaf forests, and upland pine forests and savannas (Fig. 1; Table 1). The precipitation and temperature patterns from the field sites utilized by Gunderson et al. (2011) in Puerto Rico (study described above) were comparable to the thermal/hydric conditions observed at our field sites in the Dominican Republic, setting up the possibility for different patterns of hydric specialization among the cybotoid species (Supplementary Fig. S3). Additionally, we have an extensive amount of thermal physiological and behavioral data relating to the cybotoid anoles (Muñoz et al. 2014; Muñoz and Losos 2018; Muñoz and Bodensteiner 2019), serving as a strong basis for comparison with hydric physiology.

Prior work on the thermal ecology and physiology of the cybotoids indicates that some traits co-vary with the thermal environment more strongly than others. Heat tolerance (the critical thermal maximum, *CTmax*), the preferred temperature (*Tpref*), and the field-measured body temperature (*Tb*) exhibit little variability across elevation (Muñoz et al. 2014; Muñoz and Bodensteiner 2019). This stability in body temperature and heat tolerance reflects, at least in part, strong diurnal thermoregulatory behavior, as these anoles precisely maintain their body temperature within a relatively narrow preferred range (Muñoz and Losos 2018), owing to the high thermal variability of lizard habitats during the daytime (Muñoz and Bodensteiner 2019). This behavioral buffering reduces exposure to environmental variation, which in turn can limit selection that organisms experience, a phenomenon known as the Bogert effect or behavioral inertia (Bogert 1949; Huey et al. 2003; Muñoz 2022). Nevertheless, thermoregulatory behavior cannot buffer all traits from environmental selection equally. Anoles are inactive at night and sleep exposed on branches and leaves, limiting behavioral buffering from cold exposure. Correspondingly, cold tolerance (*CTmin*) varies among species. Specifically, lizards from higher elevations (where nighttime temperatures are colder than at lower elevations) are more cold-tolerant (lower *CTmin*) than their low-elevation counterparts (higher *CTmin*) (Muñoz et al. 2014). Certainly, thermal physiology and behavior are important aspects of organismal function and fitness; nevertheless, hydric physiology is just as important, but has received notably less attention.

In general, species, populations, and individuals from drier habitat types are more resistant to water loss than counterparts from mesic habitats, but results vary among studies, even within the same study system (Gunderson et al. 2011; Cox and Cox 2015; Belasen et al. 2017). As described above, work focused on the hydric physiology of *Anolis* lizards has yielded mixed evidence for desiccation specialization, limiting directional hypotheses. Nevertheless, we predicted that cybotoid species from more xeric habitats (*A. whitemani, A. strahmi, and A. longitibialis*) would have lower levels of evaporative water loss (EWL) than their closely related counterparts from more mesic environments (*A. shrevei, A. armouri, A. cybotes, and A. marcanoi*). Alternatively, we may find that hydric physiology is similar among species, perhaps owing to a strong hydroregulatory capacity, as observed for their thermoregulatory behavior (but see Sears and Angilleta 2015; Sears et al. 2019; Rozens-Rechels et al. 2019).

Here, we examined and compared thermal physiology and hydric physiology across environmental gradients in seven species of closely related anoles (the "cybotoids") from the Caribbean island of Hispaniola.

We measured evaporative water loss at two temperatures (23 and 33°C) using flow-through respirometry, and we calculated the thermal sensitivity of evaporative water loss (Q10, the change in performance across a 10°C increase in measurement temperature). We examined the relationships between hydric physiology and climatic variables, as well as the relationships between hydric traits and thermal traits. We discuss how specialization varies among thermal and hydric physiology, and how the patterns observed in this clade of anoles relate more broadly to their adaptive radiation across the Caribbean.

Methods

Study species and study sites

Caribbean anoles are a classic case of adaptive radiation, characterized in part by the convergent evolution of distinct habitat specialists, termed "ecomorphs" (Losos 2009). Ecomorphs exhibit a suite of behavioral and morphological features specialized to the specific portion of the structural microhabitat (e.g., trunks, canopy, and twigs) that species most commonly utilize. The species in this study all belong to the "trunk-ground" ecomorph category; when compared to other anoles, species in this ecomorph are medium-sized (∼50–70 mm in snout-to-vent length), have relatively long hind limbs, and are commonly found on tree trunks, rocks, and other broad, near-ground perches (Schwartz 1989; Losos 1990). We obtained thermal and hydric data from seven species of cybotoid anoles (*A. cybotes* and its close relatives). From July 28, 2023–August 6, 2023, we collected up to ten individuals from each species (from 1–3 populations per species) from the Dominican Republic for the hydric physiology measures (Supplementary Fig. S1). Of note, there are elevational and thermal-hydric habitat differences between and within cybotoid species. *Anolis cybotes*, for example, is found nearly island-wide, occupying a range of hydric and thermal habitats. *Anolis armouri* and *A. shrevei*, by contrast, are montane species, restricted to high elevation in the Sierra de Baoruco and Cordillera Central, respectively. Due to permitting constraints on sample sizes, we collected ten individuals per species and recognized that there may be within-species diversity that we could not sample in this study. We only collected male lizards to reduce potential effects of sex, and sampled only from adjacent populations with similar thermal-hydric regimes (Table 1). Lizards were brought to the lab at Yale University and allowed 4 weeks to acclimate to lab conditions. Lizards were kept under constant conditions of 28°C, 70% RH, and 12:12 light schedule (overhead and UVB). Anoles were watered twice daily (including days during which water loss was measured) by spraying all interior walls of their cages and fed twice a week with 4–6 calcium and vitamin dusted crickets.

Measuring thermal physiological traits

To investigate thermal physiological evolution in the cybotoid anoles, we focused on four key traits: the critical thermal minimum (CT_{min}), the critical thermal maximum (CT_{max}), the field-measured body temperature (T_b), and the preferred temperature (T_{pref}). CT_{min} and CT_{max} describe the lower and upper limits, respectively, for locomotor function and are widely used for estimating the thermal limits of performance in ectotherms (Spellerberg 1972; Lutterschmidt and Hutchison 1997). The preferred temperature refers to the average of the central 50% of body temperatures measured in lizards that have been placed in a thermal gradient and allowed to choose where to sit (i.e., in the absence of environmental or ecological constraints) (Huey 1982; Hertz et al. 1993). Thermal data were gathered for these seven species from our previously published work (Muñoz et al. 2014; Muñoz and Bodensteiner 2019; Bodensteiner et al. 2024; Supplementary Table S1).

Measuring evaporative water loss

To measure rates of evaporative water loss (EWL), we used a flow-through respirometry system. Each individual lizard was measured first at 23°C and then at 33°C (due to logistical constraints with temperature and calibration of equipment), and given at least a week of rest between experimental runs. The setup for the respirometry experiments began with outside air being drawn through the Bev-A-Line® IV Tubing (Thermoplastic Processes, Georgetown, DE, USA) by a sub-sampler (SS4, Sable Systems International [SSI], North Las Vegas, NV, USA), which was then humidified through a bubbler and passed through a dewpoint generator (DG-4, SSI). The dewpoint generator allowed us to precisely control the water vapor pressure, which was kept at a constant 1.5 kPA.

The airstream was then split through a manifold (MF-8, SSI) to eight acrylic cylindrical chambers. We covered the outside of each chamber with colored tape to minimize any potential stress associated with seeing another lizard. Smaller lizards had mesh fabric in the chamber to decrease their ability to move around. We kept the last chamber empty for the baseline reading. The lizards were placed in an incubator with an air fan to maintain the temperature at either 23 or 33°C. The air fan was controlled by a thermal controller (PELT5, SSI).

During a given run, each lizard was sampled three times over the course of approximately three hours.

Between each lizard reading, we sampled the empty chamber to get a stable baseline reading. We sampled using a multiplexer (MUX-8, SSI) and the airstream was then passed through a water vapor analyzer (RH-300, SSI), which measured the change in water vapor pressure. The RH-300 was calibrated with pure nitrogen gas periodically throughout the experiments.

During the experiment, the lizards were left in the dark to simulate a time when they are the least active. If there was any activity during the reading or if the lizards excreted waste (when the readings were abnormally high and sporadic), then we re-ran experiments for those individuals after giving them at least one week of rest.

We used Expedata Software (Version 1.9.27, SSI) to estimate EWL. All equations used came from Lighton (2018) Oxford University Press.

The flow rate was corrected with Equation (1):

$$\mathrm{FRc} = \mathrm{FRsel} * (\mathrm{BP} - \mathrm{WVP})\,/\mathrm{BP}, \tag{1}$$

where FRsel is the flow rate of the selected chamber, BP is barometric pressure, and WVP is water vapor pressure measured from the RH-300. The data were then corrected from the baselines. The data were then converted to water vapor density (WVD) using Equation (2):

$$\mathrm{WVD} = \mathrm{WVP}/\left(\left(273 + \mathrm{Deg\_C}\right) * 461.5\right), \tag{2}$$

where Deg_C is the temperature of the incubator and converted to Kelvin (adding 273). The temperature (in Kelvin) is multiplied by the gas constant for water (Rw), which is 461.5 $\mathrm{J/kg^{-1}/K^{-1}}$.

Lastly, EWL was calculated multiplying the WVD by the corrected flow rate of the incurrent air (FRc) and then multiplying it by (1/60) to get the units to g/s using Equation (3):

$$\mathrm{EWL} = (\mathrm{WVD} * \mathrm{FRc}) * (1/60) \tag{3}$$

We calculated each species' mean thermal sensitivity (Q10) of EWL using only individuals that were measured at both temperatures. Lastly, to account for body size variation, we phylogenetically size-corrected evaporative water loss values by regressing log-transformed EWL against log-transformed SVL using the phyl.resid function in the phytools (Revell 2012) R package. All evaporative water loss data used in the analysis are the residuals of evaporative water loss and mass. We used the ultrametric maximum clade credibility (MCC) mtDNA phylogenetic tree for Caribbean anoles from Mahler et al. (2010, 2013), which we pruned down to the seven species included in this study.

Climatic data

We extracted monthly climate variables from our sampling localities from the TerraClimate database (Abatzoglou et al. 2018) using the package ClimateR (https://github.com/mikejohnson51/climateR). TerraClimate utilizes climatically aided interpolation to combine relatively high-spatial resolution (1/24°) data from various sources (Abatzoglou et al. 2018). We extracted monthly variables, including precipitation (mm), maximum temperature (°C), minimum temperature (°C), wind speed (m/s), and vapor pressure deficit (kPa).

Statistical methodology

To investigate the relationship between environmental predictors on ecophysiology, we ran phylogenetic generalized least squares using maximum likelihood in phytools (Revell 2012). We examined hydric physiology relative to species-specific climate variables (mean monthly precipitation, mean monthly maximum temperature, mean monthly minimum temperatures, mean monthly wind speed, and mean monthly vapor pressure deficit) and thermal physiological traits (thermal tolerance limits, preferred temperature, and field-measured body temperature). All analyses were conducted in the R environment (Team 2017).

Results

Thermal physiology

Cold tolerance (*CTmin*) is inversely correlated with the elevation (which is positively correlated with precipitation, but negatively correlated with temperature; Supplementary Fig. S2), such that lizards found at higher elevations are more cold-tolerant. We found no relationship between elevation and the other thermal physiological traits (CT_{max}, T_b, and T_{pref}) (Fig. 2). These relationships have been previously established (e.g., Muñoz and Bodensteiner 2019), and are presented here simply to facilitate comparison with the hydric traits.

Hydric physiology

We found no relationship between the residuals of mass and evaporative water loss at either temperature and our climatic variables (Table 2). Similarly, we found no relationship between the thermal sensitivity of EWL (Q10) and our climatic variables (Table 2). When we examined the relationship between hydric and thermal physiology, we found a negative relationship between evaporative water loss at 33°C and critical thermal maximum (Fig. 3). In particular, lizards that are more heat-tolerant (higher CT_{max}) are also more resistant to the water loss at higher temperatures (lower EWL at 33°C).

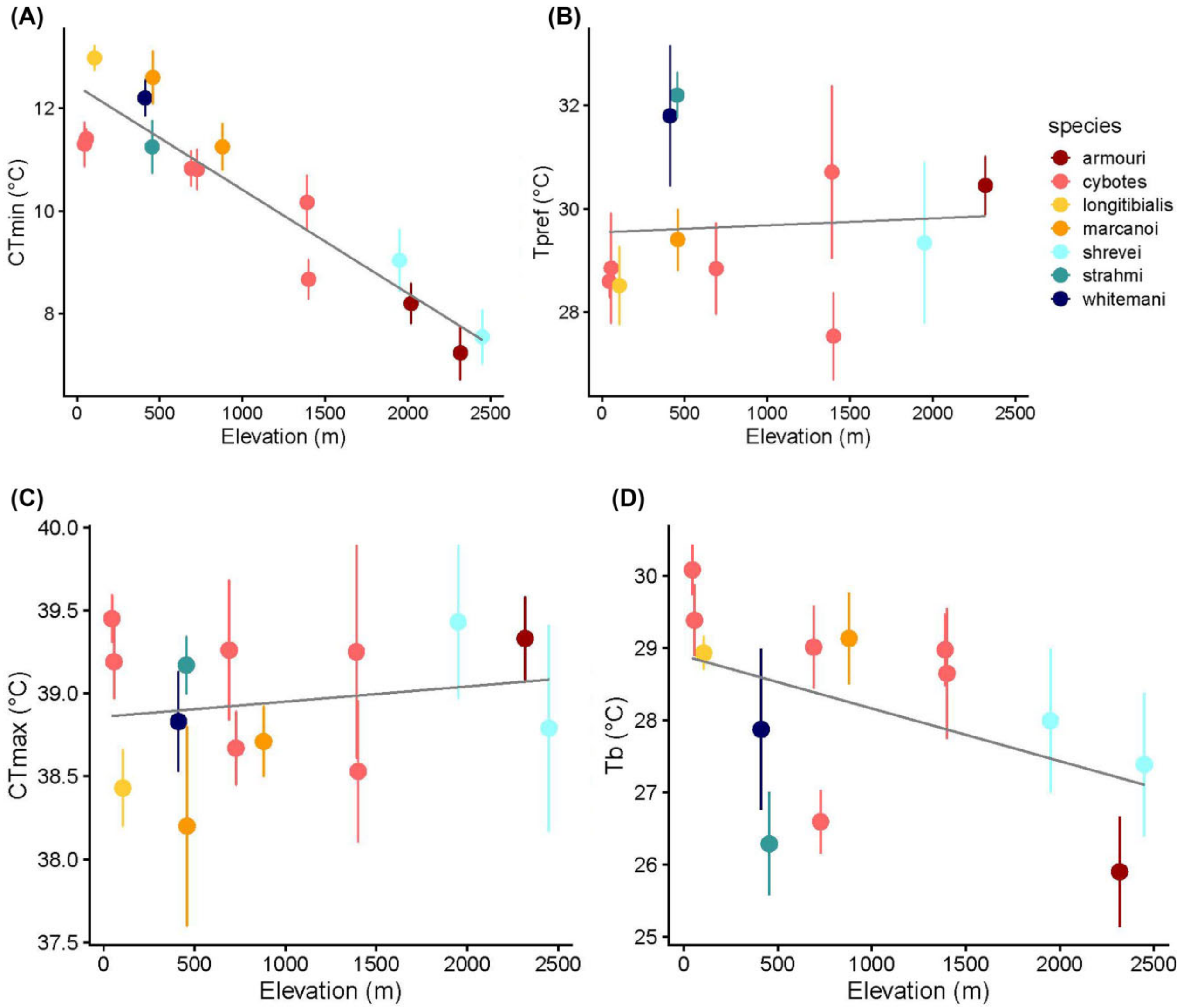

Fig. 2 Species at a high elevation are more cold-tolerant than species at low elevation. No other thermal traits shifted with elevation. Thermal physiological traits of populations of cybotoid species across elevations. (A) Cold tolerance decreases with elevation (PGLS: R2 = 0.95, $P < 0.001$). (B) Thermal preference does not vary across elevation (PGLS: R2 = 0.17, $P = 0.739$). (C) Heat tolerance does not vary across elevations (PGLS: R2 = 0.34, $P = 0.097$). (D) Body temperature does not vary across elevations (PGLS: R2 = 0.21, $P = 0.167$). Figure modified from Muñoz et al. (2014); Muñoz and Bodensteiner (2019), supplemented with additional data from Bodensteiner et al. (2024).

Discussion

Limited evidence for hydric specialization in the cybotoid anoles

Environmental factors shape physiological trade-offs in performance that may constrain organismal responses to climate change (Cohen et al. 2012; Riddell et al. 2023b). Thermoregulation, for example, often constrains hydric regulation (Pirtle et al. 2019), potentially limiting how organisms can dynamically respond to shifts in both ambient temperature and moisture. The implications of climate change for “dry skinned” ectotherms have primarily been investigated through the lens of temperature (Deutsch et al. 2008; Sinervo et al. 2010; Vickers et al. 2011), while research on the combined impacts of thermal and hydric variation is less common (Chown et al. 2011; Pintor et al. 2016). Here, we aimed to better understand hydric and thermal physiology in a group of “dry skinned” ectotherms, the cybotoid anoles from the Caribbean island of Hispaniola. Our findings generally defy the expectation that lizards from xeric environments are more resistant to water loss than their counterparts from more mesic environments (Lillywhite et al. 2006; Cox and Cox 2015). We found limited evidence for hydric specialization among these species. Cybotoid species from more xeric environments (e.g., *A. whitemani* and *A.*

Table 2 Results from PGLS analyses showing no relationship between evaporative water loss and climatic predictor variables.

Trait	Predictor	F-statistic	Adj. R^2	*P*-value
EWL at 23	Precipitation	$F_{1,5} = 2.63$	0.21	$P = 0.166$
	Maximum temperature	$F_{1,5} = 2.06$	0.15	$P = 0.211$
	Minimum temperature	$F_{1,5} = 2.70$	0.22	$P = 0.162$
	Wind speed	$F_{1,5} = 0.71$	−0.05	$P = 0.437$
	Vapor pressure deficit	$F_{1,5} = 2.55$	0.21	$P = 0.171$
EWL at 33	Precipitation	$F_{1,5} = 0.10$	0.18	$P = 0.770$
	Maximum temperature	$F_{1,5} = 0.26$	0.14	$P = 0.634$
	Minimum temperature	$F_{1,5} = 0.10$	0.18	$P = 0.765$
	Wind speed	$F_{1,5} = 1.87$	−0.20	$P = 0.230$
	Vapor pressure deficit	$F_{1,5} = 0.00$	0.13	$P = 0.969$
Q10 of EWL	Precipitation	$F_{1,5} = 1.37$	0.06	$P = 0.294$
	Maximum temperature	$F_{1,5} = 1.38$	0.06	$P = 0.293$
	Minimum temperature	$F_{1,5} = 2.16$	0.16	$P = 0.202$
	Wind speed	$F_{1,5} = 0.00$	−0.20	$P = 0.954$
	Vapor pressure deficit	$F_{1,5} = 2.31$	0.18	$P = 0.189$

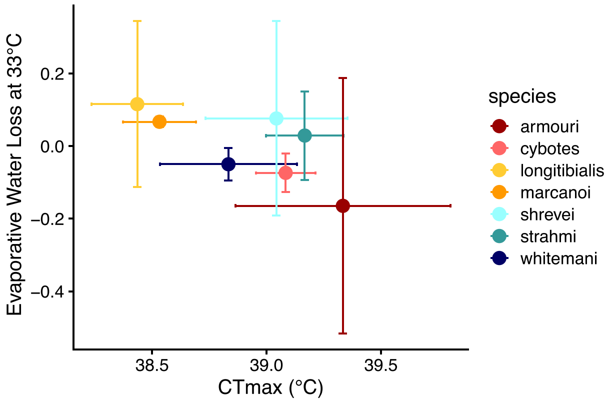

Fig. 3 Lizards that are more heat-tolerant are also more resistant to water loss at higher temperatures. The relationship between residuals of EWL and mass at 33°C and critical thermal maximum (PGLS: $F1,5 = 10.8$; Adj. $R2 = 0.62$; $P = 0.022$).

longitibialis) were not appreciably more desiccation-tolerant than species from more mesic environments (e.g., *A. marcanoi*). It is additionally possible that these species may exhibit more variation in desiccation tolerance at warmer temperatures, approaching their heat tolerance limit. More comparative data, particularly relating to thermo-hydric ecology and physiology, are needed to better understand the multidimensional nature of this and other adaptive radiations (Castro-Insua et al. 2018; Martin and Richards 2019). Nevertheless, we did find patterns that point to shared ecophysiological specialization between heat tolerance and water conservation at warmer temperatures.

While there are some previous studies on hydric physiology in the cybotoid lizards (Le Galliard et al. 2021), drawing direct comparisons is challenged by differences in methodology and species sampling. Hertz (1980), for example, examined differences between *A. cybotes* and *A. marcanoi* and found no difference in water loss rates or in the ability to withstand dehydration, but we highlight that body size was not taken into account in the statistical analyses. Hillman and Gorman (1977) examined the differences in water loss rates between 11 Caribbean anole species and found that *A. cybotes* had lower rates of water loss than anole species from more mesic habitats, but no other cybotoid species were considered. More broadly, there seems to be a general lack of consensus about the relationship between hydric physiology and climatic conditions in “dry skinned” ectotherms, owing in large part to the use of different methodologies. There is a long history of varied measures associated with organismal water balance (e.g., water loss rates, evaporative water loss, or cutaneous water loss), methodologies utilized to measure that water balance (e.g., weighing before and after heat and/or “dry” air exposure or flow-through respirometry), and adequately controlling for body size and the evaporative power of the air (i.e., VPD; Le Galliard et al. 2021). By contrast, our study simultaneously controlled for body size and VPD while measuring EWL.

The similarity in hydric physiology among species that we observe may reflect the homeostatic influence of hydroregulation on physiological divergence across gradients (i.e., the Bogert effect; Huey et al. 2003; Muñoz 2022). At the macroenvironmental scale of our climatic data, we can detect clear differences in ambient moisture that reflect the steep hydric gradients the cybotoids occupy, from xeric lowland scrub to moist broadleaf forest. Yet, there may be variation in microclimatic conditions that we are not capturing at the relatively broad spatiotemporal scale for which we have data (Supplementary Fig. S4). In other words, there may be microclimatic variation in ambient moisture that allows cybotoids to hydroregulate to avoid desiccation, even in sites that are comparatively dry at the macroclimatic scale (Farallo et al. 2020). The cybotoid anoles are precise thermoregulators in large part because they occupy habitats along forest edges, which provide ample sun and shade structure for thermal shuttling behavior (Muñoz and Losos 2018 and Bodensteiner et al. 2024). Such habitats may likewise be propitious for hydroregulatory behavior. Whereas thermoregulatory behavior has been relatively well established in the cybotoid anoles (Hertz and Huey 1981; Muñoz et al. 2014; Conover et al. 2015; Boronow et al. 2018; Muñoz and Losos 2018), we lack the necessary ecological data to make comparable inferences about the Bogert effect in hydric behavior (Muñoz 2022), but encourage future investigation of this possibility. Although the cybotoid anoles are edge/open habitat species, other Hispaniolan anole species are true closed canopy specialists, occupying mid-elevation cloud forests. Such closed canopy species are less heat-tolerant than their edge habitat counterparts, reflecting a more limited thermoregulatory capacity in their habitats (Bodensteiner et al. 2024). In addition to being spatially homogenous in temperature, cloud forests are also notably wet. We hypothesize that resistance to water loss will be considerably lower in anole species that inhabit closed-canopy forest interiors.

The heat tolerance and water loss trade-off

Although we saw no compelling relationships between hydric specialization and environmental conditions, we did find that species with higher CT_{max} exhibited lower water loss rates at the higher experimental temperature (33°C). This temperature is above the lizards' preferred range, but below their heat tolerance (∼39°C), and so desiccation tolerance may be even stronger at higher temperatures. The ability to better retain water and maintain locomotion at higher temperatures could be correlated due to the inherent link between the hydric and thermal environment. As temperatures rise, so too does the drying capacity of air, leading to increased EWL at warmer temperatures and creating strong selection to limit desiccation (Albright et al. 2017). Dehydration can negatively affect thermoregulatory behavior and locomotor performance in ectothermic animals (Anderson and Andrade 2017; Sannolo and Carretero 2019). Maintaining high heat tolerance while reducing water loss rates at elevated temperatures can therefore confer an adaptive advantage for the anoles observed in this study. Indeed, the relatively high heat tolerance (among anoles) that the cybotoids exhibit should allow them to maintain (or even increase) activity patterns under rising temperatures (Muñoz et al. 2022), but only if they are also able to maintain water budgets. This inverse correlation is particularly intriguing given the limited variation in CT_{max} observed among cybotoid species (∼1 degree), meaning even slight shifts in thermal physiology can be associated with appreciable changes in hydric tolerance at warm temperatures. Across the broader radiation of Hispaniolan anoles, heat tolerance varies by ∼10 degrees, and species from forest interiors (e.g., cloud forests) are particularly intolerant of heat (Bodensteiner et al. 2024). This sets up the possibility for even stronger patterns of hydrothermal tradeoffs when explored across the broader Hispaniolan anole radiation.

Neither CT_{max} nor EWL change across environmental gradients (elevation, mean precipitation, and mean annual temperature) in the cybotoid lizards. This lack of variation in thermal physiology holds true when examining thermal micro- or macro-habitat differences across this environmental gradient; there is no impact of scaling (macro-micro) environmental conditions on CT_{max} in the cybotoids (Muñoz et al. 2014; Muñoz and Losos 2018). Instead, behavioral thermoregulation has buffered CT_{max} from changing across this gradient (Muñoz and Losos 2018), suggesting that thermo-hydro-regulatory behaviors may be driving this relationship. The Bogert effect has proven a powerful force shaping thermal physiological evolution in squamate reptiles, including the cybotoid anoles we examined here (Huey et al. 2003; Muñoz and Losos 2018; Bodensteiner et al. 2021; Muñoz 2022). However, behavioral hydroregulation is less frequently examined in squamates (Rozen-Rechels et al. 2019), although there are some clear examples of active hydroregulation. For example, following prolonged exposure to dry air, Asp vipers (*Vipera aspis*) spend more time in shelters with a moist microclimate to mitigate physiological stress (e.g., dehydration and muscle wasting) (Dezetter et al. 2023). When rainforest rainbow skinks (*Carlia rubrigularis*) are exposed to higher temperatures, they choose a more humid refuge, even if that means they are spending time below their preferred substrate temperature (Pintor et al. 2016). The extent to which anoles exhibit hydroregulatory behavior remains relatively unknown, but there is evidence that gravid females tend to preferentially select humid microsites for nests (Pruett et al. 2022; Muñoz et al. 2023). Methods for better incorporating the interactive effects of temperature and hydric conditions in the wild are necessary for better understanding the capacity of hydrothermal regulatory behaviors to shape trait variation in wild populations.

Looking to the future

As climate change marches on, organisms must find ways to simultaneously contend with abrupt shifts in temperature and precipitation. Great strides have been made in understanding how higher temperatures impact organismal fitness (i.e., increased metabolic demand, reduced activity times; Kearney et al. 2013; Huey and Kingsolver 2019), but less is known about the effect of changing moisture on organismal performance, fitness, and population stability (Riddell et al. 2018; Riddell et al. 2021; Wu et al. 2024b). Explicit incorporation of the interaction effects of hydrothermal physiology and regulatory behavior is even less common but is especially relevant (Riddell et al. 2018; Riddell and Sears 2020).

We find that hydric physiology is largely unrelated to the hydrothermal environment in the cybotoid anoles. Do the patterns in hydric physiology we observe exemplify strong environmental buffering due to hydroregulatory behavior (i.e., the Bogert effect; Huey et al. 2003; Muñoz 2022)? Do patterns reflect a limited capacity to adapt hydric physiological traits (Beever et al. 2016)? How does physiological diversity in the cybotoids compare to other species on Hispaniola, and to species on other islands (Bodensteiner et al. 2024)? Caribbean anoles are a diverse, highly endemic radiation of tropical ectotherms, meaning they are highly vulnerable to climate change (Huey et al. 2009; Sinervo et al. 2010; Huey et al. 2012). Comparative data are necessary to better parse out eco-evolutionary patterns of hydrothermal physiologies. However, it is challenging to coalesce different studies into a single framework because of different methodologies employed and other data limitations (e.g., lack of controlling for body size and/or VPD; Le Galliard et al. 2021). Moving forward, having a standardized approach will help to build comparative data sets, allowing for a more complete picture of organismal vulnerability in a rapidly changing world (Riddell et al. 2023b; Wu et al. 2024a).

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Supplementary data

Supplementary data available at *ICB* online.

Conflict of interest

The authors declare no conflict of interest.

Data availability

Data will be made available via dryad upon publication.

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