Ecology: Report

Climatic Variability Shapes Plasticity of Hydric and Thermal Physiology in Tropical Geckos

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KEYWORDS

evaporative water loss, geckos, physiological plasticity, reptiles, seasonal plasticity, seasonal tropics, thermal preference

Abstract

Phenotypic plasticity in reptiles is a key mechanism enabling individuals to maintain and optimize physiological responses to changing environments. The ability to adjust metabolic rates and thermal physiology in response to seasonal changes is known to be central to the physiological ecology of some reptiles, but less is known about reptiles' ability to exhibit seasonal flexibility in rates of evaporative water loss (EWL). Physiological acclimatization to seasonal changes was measured in six species of geckos in the genus *Gehyra* from the highly seasonal tropics of northern Australia. Four species from a mesic, more thermally stable site did not have seasonal differences in thermal preference (T_p), but T_p was significantly lower during the cooler dry season in three species from a semi-arid, more thermally variable site. EWL was significantly lower (42% to 78%) during the dry season compared to the wet season for all species. For most species, EWL decreased rapidly from wet to early dry season, then continued to a minimum in the late dry season. There was no relationship between extent of plasticity and geographic range size. These results demonstrate high plasticity and imply a cost to maintaining low EWL, the basis of which requires further study.

INTRODUCTION

Seasonal fluctuations in climate can expose ectothermic animals to regular periods of unfavourable conditions that can present challenges to survival, such as prolonged dry periods where moisture is limiting, or extreme temperatures. Physiological plasticity (or acclimatization), the ability to adjust physiological responses to compensate for environmental changes, can enable animals to persist during temporarily adverse conditions, or cope with a changed climate (Basson and Clusella-Trullas, 2015; Bozinovic & Naya, 2014; Canale & Henry, 2010).

Reptiles can modify a variety of behavioural and physiological traits across seasons in response to changed abiotic variables (Christian et al., 1998; 2023; Clusella-Trullas & Chown, 2014). In some reptiles, preferred body temperatures change seasonally as measured in the field or measured from animals immediately after capture (Christian et al., 1983; 1998; Christian & Bedford, 1995; Clusella-Trullas & Chown, 2014). Compared to thermal physiology, seasonal evaporative water loss (EWL) in reptiles is understudied (Rozen-Rechels et al., 2020; Weaver et al., 2023), with the limited research suggesting a trend for lower EWL in reptiles in dry seasons compared to humid conditions (Blamires and Christian, 1999; Weaver et al., 2023).

The extent to which a species can acclimatize by varying physiological responses may, in part, determine its distribution. Greater plasticity increases tolerance to a broader range of environmental conditions and the lack of plasticity could restrict activity times or decrease survival (Bozinovic & Naya, 2014; Li et al., 2016; Muñoz & Bodensteiner, 2019; Pither, 2003; Slatyer et al., 2013). Greater physiological plasticity is therefore expected in species with larger and more climatically variable distributions.

We investigated seasonal plasticity in thermal preferences (T_p) and EWL of nocturnal *Gehyra* geckos from the seasonal tropics of northern Australia. Geckos were sampled from two sites where they were active year-round and that varied in aridity and seasonal temperature patterns. Rainfall and humidity vary greatly between wet and dry seasons across the region in association with the summer monsoon, and even relatively arid sites are humid during wet seasons.

We hypothesized that T_p would be higher in wet season (warm) than the dry (cool) season and that EWL would be lower in the dry season compared to the wet. We also predicted to find greater physiological plasticity in species with large distributional (climatic) ranges. These predictions assume the geckos have the physiological capacity to adjust to seasonal conditions.

METHODS

Species and sites

Six species of *Gehyra* were sampled from two sites (Litchfield National Park and Kidman Springs Station, Figure 1a), both with strong seasonal changes in rainfall (Figure 1). Litchfield has mesic conditions (mean annual rainfall 1675 mm) with low seasonal fluctuation in temperature, and Kidman Springs is semi-arid (mean annual rainfall 914 mm) with greater seasonal changes in temperature (Figure 1b, based on data averaged over 2000–2009 inclusive, acquired from the Australian Bureau of Meteorology, *http://www.bom.gov.au/climate*).

Each species was sampled from a single location except for *G. nana*, which was sampled from both locations (Table 1). The species identity of all individuals was confirmed by sequencing of mtDNA which provides a reliable diagnostic for these taxa, some of which are difficult to distinguish based on morphology (Oliver et al. 2020). Range sizes for each species (Table 1) were estimated using QGIS v. 3.20 by taking the area (km^2) of a convex hull polygon fitted to geographic records for the respective species, which was then clipped to the Australian coastline, inspected, and modified if needed. See Supplementary Materials for full details.

Geckos were sampled during the wet (October–April), early dry (May–June), and late dry (referred to as 'dry', July–September) seasons (Table 1). They were located in the field by spotlight, captured by hand, and adult individuals were transported to Charles Darwin University in cloth bags. EWL was measured in the laboratory over the following 24 h, followed by T_p experiments over the next three days. When not in experiments, geckos were housed individually in clear plastic cages (40 × 25 × 13.5 cm) containing a plastic hide and were supplied with a spray of clean water daily and live food three times per week until release at the site of capture.

Thermal preference

Geckos were individually placed in a 60 × 30 × 35 cm glass tank with an artificial crevice made from a 55 × 15 cm length of ceramic tile elevated 1.5 cm by terracotta blocks. The tank was housed in a temperature-controlled room set to 20 ˚C and a 50 W infrared heat globe was placed at one end of the crevice to create a linear temperature gradient of ~ 20–40 ˚C (Belasen et al., 2017; Christian et al., 1998; Carneiro et al., 2017; Rozen-Rechels et al., 2020). A thermal imaging camera (Testo 868, 0.08 ˚C thermal sensitivity) was used to photograph the geckos at hourly intervals, for a total of 12 measurements per gecko. We extracted temperatures using Testo IRSoft thermal imaging software (v4.8) from the lower abdomen of the animal (Figure 2a). This location was selected as an approximation of cloacal temperature. The mean T_p was calculated from the central 50% of readings (the set-point range, Hertz et al., 1993; Pintor et al., 2016; Stellatelli et al., 2018).

Evaporative water loss

EWL includes components due to evaporation across the skin, from the eyes, and from respiratory water loss (Mautz, 1982). These components were not partitioned; however, gecko skin temperatures were measured immediately after removal from the experiment using a calibrated infrared thermometer (Thomas Scientific Traceable, model 123D37) for evidence of seasonal differences in cutaneous EWL.

EWL was measured with an open-flow system (Mautz, 1982; Young et al., 2005). Air was drawn through a silica gel drying column and into a cylindrical experimental chamber (12.5 × 3 cm, 70 mL volume) at a rate of 0.2 L/min using a calibrated low-flow air pump (Sensidyne Gilian LFS-113D). This chamber was contained within an A&E Lab 18 L portable incubator (model AE-PI-100) set to 30 °C. A Vaisala HUMICAP® Humidity and Temperature Probe HMP110 (0–100 ± 1.5% RH, -40–80 ± 0.1 °C) connected to an ADInstruments PowerLab data acquisition apparatus placed downstream of the chamber to continuously record temperature and relative humidity of the air exiting the chamber. Baseline measurements were taken from stable readings before an animal was introduced in the chamber.

After a gecko was placed in the chamber, temperature and relative humidity of the air was monitored until readings stabilized and the animal remained at rest for 10 min. The lowest humidity reading was taken during this rest period, provided humidity remained similarly low for at least 2 min. Trials lasted no longer than 2 h. After experiments, a digital caliper was used to measure the length and width of the body (snout-vent-length), limbs, and tail of geckos to 0.1 mm, and body mass was measured to 0.01 g.

The difference between the reading with the animal in the chamber and the baseline is a measure of the amount of water lost via evaporation by the animal, and this value was analyzed with respect to body surface area, which was estimated for each individual by assuming the trunk, tail, and limbs to be one-ended cylinders, similar to previous studies (Belasen et al., 2017; Chukwuka et al., 2020). This approach was validated by confirming that the calculated surface areas matched those obtained by measuring the area of tape that had been meticulously wrapped over the surface of realistic plastic lizard models.

Statistical analysis

Analyses were performed with R v4.3.1 in Rstudio v2023.06.2 with the stats package unless otherwise specified (R Core Team, 2023; R Studio Team, 2020). Seasonal comparisons were conducted for each species separately, including separate analyses for the two sampled populations of *G. nana*. We assessed differences in body condition (mass/snout-vent-length; Sion et al., 2021) between seasons with generalized linear models (GLM) with a log-link. Repeated-measures ANOVAs were used to compare T_P between wet and dry seasons. GLMs (with a Gamma distribution and log-link, and surface area as a covariate) were used for species comparisons of EWL by season. EWL is presented as predicted values from the GLMs. As a measure of variability of EWL between wet, early dry, and dry seasons, paired t-tests were performed to test for differences in standard deviation within each species of predicted EWL (adjusted for surface area). Seasonal differences between air temperature and skin temperature at the end of EWL experiments were compared by ANOVA. Lastly, we tested if mean change in EWL from wet to dry season per species (% depression and absolute change, separately) correlated with species' range sizes with a rank-based estimation regression in the Rfit package (Kloke & Mckean 2012). Tukey's honest significant difference (HSD) test was used for post hoc testing, using $p < 0.05$ as the level for significant difference.

RESULTS

Body condition was not different between seasons for any species except *G. koira* ($p < 0.01$), where body condition was significantly higher in the wet season compared to both early dry and dry seasons. Seasonal body condition was not considered in further analyses.

Thermal preference

Mean T_P varied from 28.9–33.9 ˚C across species and seasons. There were no differences in T_P between seasons in the four species from Litchfield ($p > 0.05$ for all), but all three species from Kidman Springs had significantly lower T_P in the cooler dry season (Figure 2b; *G. koira*, $F_{(1,21)} = 18.41$, $p = 0.0003$; *G. gemina*: $F_{(1,21)} = 6.35$, $p = 0.02$; *G. nana* (KS), $F_{(1,22)} = 7.77$, $p = 0.01$.

Evaporative water loss

EWL was significantly lower in the dry season compared to the wet for all geckos except the Kidman Springs population of *G. nana*, which had consistently low values (Table 2, Figure 2c). Most species showed significantly lower EWL in the early dry compared to the wet season but no difference between early dry and dry. Exceptions were: *G. nana* and *G. australis* from

Litchfield with no significant difference in EWL between wet and early dry seasons, and *G. nana* had significantly lower EWL in the dry season compared to the early dry (Table 2). Mean EWL was depressed by 42–78% from wet to dry season. Standard deviations of EWL in the dry season were significantly lower (34–98%) compared to the wet (paired-t = 2.72, p = 0.03, n = 6 removing Kidman Springs *G. nana*). At the end of EWL experiments, geckos had significantly lower skin temperatures (relative to air temperature) in wet season than dry season (two-way ANOVA, $F_{(1, 161)} = 7.44$, p = 0.007), confirming higher cutaneous evaporation in the wet season. Mean change in EWL from the wet to the dry season did not correlate with species range (% EWL depression: t = -0.63, p = 0.6; absolute EWL change: t = -0.84, p = 0.4).

DISCUSSION

If there is heterogeneity in the thermal environment (Muñoz et al., 2014), nocturnal geckos can regulate body temperatures during the day through selection of retreat sites (Kearney & Predavec, 2000; Shah et al., 2004), which can change seasonally (Kearney, 2002). For some *Gehyra*, behavioural thermoregulation is a high priority when thermal conditions are sub-optimal (Grimm-Seyfarth et al., 2018). Although T_P did not differ between seasons for the four *Gehyra* species from the mesic site with relatively stable seasonal temperatures (Litchfield), all three species from the semi-arid site with a greater range of seasonal temperatures (Kidman Springs) had significantly lower T_P in the dry season. The different patterns between the two sites are consistent with plasticity being correlated with variability in environmental conditions (Christian et al., 2023; Muñoz & Bodensteiner, 2019), and this conclusion is strengthened by the results from the two populations of *G. nana* in which only the population from the more variable environment showed seasonal plasticity.

There were strong and significant reductions in EWL from wet to dry season in all six species. This result aligns with our prediction and the limited field-based observations of other tropical reptiles (Blamires & Christian, 1999). The significant difference in EWL between wet and early dry seasons for most species suggests that EWL changes rapidly in response to reduced humidity. However, the results showed that EWL is not maximally reduced until late in the dry season. In recent laboratory experiments, lizards decreased EWL after only 8 d of exposure to constant dry conditions (Weaver et al., 2023). However, in the field, the transitional period would likely be influenced by local conditions and variable weather events.

Contrary to our predictions, plasticity in EWL (% depression or absolute change) was not associated with the size of distributional ranges. Strong seasonal responses were observed regardless of range size (Tables 1 & 2). For example, *G. nana* from Litchfield and *G. paranana* had the two greatest proportional reductions in mean EWL from wet to dry season (78% and 67% respectively), yet *G. paranana*'s distributional range equates to just 4% of that of *G. nana*.

The significant reduction in variability of EWL between wet and dry seasons suggests that the geckos may converge on a biologically minimum EWL in the dry season. In the wet season, the release from hydric stress results in higher EWL generally, but differences in local conditions may result in higher variability among individuals. This seasonal pattern suggests a significant cost associated with maintaining low EWL. Plasticity in EWL apparently provides greater benefits than fixing EWL at a low rate due to this unquantified cost of maintaining low EWL. In laboratory acclimation experiments in other lizards, decreased EWL was attributed to changes in skin permeability caused by lipid redistribution (Kattan & Lillywhite, 1989). Research into the mechanics of EWL reduction, including the energetic consequences, is needed.

Metabolic rates may also have been depressed in the dry season (Christian et al., 1999; 2023), which would have resulted in lower respiratory water loss. However, higher skin temperature (relative to air temperature) associated with EWL measurements of geckos in the dry season as compared to the wet season is evidence of less evaporative cooling at the skin, indicating that reduced skin permeability is a factor in the depressed EWL (Kattan & Lillywhite, 1989).

Arguments that the relative stability in environmental conditions in some tropical regions negates the need for physiological plasticity (Sun et al., 2022) have been over-generalized to include the entire tropics despite there being substantial evidence for a link between physiological plasticity and the wet-dry tropical climate (Christian et al., 2023). Metabolic plasticity in the seasonal tropics has been well-documented (Berg et al., 2017; Christian et al., 1999; Christian et al., 2023), and there is growing evidence with respect to EWL plasticity in reptiles from wet-dry tropical regions (K. Christian, unpublished data). The general lack of attention to EWL plasticity (Weaver et al., 2023) means that little is known about seasonal plasticity of EWL of reptiles in the field from the wet tropics and other climatic zones.

In the context of climate change, our results demonstrate that geckos from the seasonal tropics can physiologically adapt to changes in humidity. The mechanism driving differences in thermal plasticity between the two sites is unknown. Specifically, we do not know if the absence of seasonal plasticity of preferred body temperature in the geckos from the relatively stable site (Litchfield) indicates that they lack the genetic capacity for thermal plasticity, as is the case for some forest-dwelling lizards in the aseasonal tropics (Huey et al., 2009). If so, these populations may be sensitive to temperature changes if appropriate thermal refugia are no longer available.

ACKNOWLEDGMENTS

The Parks and Wildlife Commission of the Northern Territory provided permits (64816, 66691, 69132), and the work was approved by the Charles Darwin University's Animal Ethics Committee (A19005). Financial support was provided by the Australian Research Council

(DP190102395, DP210102176), a Charles Darwin University Covid-19 Supplementary Project grant, and an Australian Government Research Training Program Scholarship (KS). Mirjam Kaestli provided statistical advice. For assistance with animal capture, we thank Leo Tedeschi, Octavio Jiménez Robles, Brenton von Takach, Jake Christian, Chris Jolly, and Alana de Laive.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.25116158.

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Table 1. Species and locations of *Gehyra* geckos sampled between 2019–2021 for experiments comparing evaporative water loss (EWL) and thermal preference (T_P) among seasons.

Species	Species Range (km^2)	Sampling Location(s)	N		
			Season	EWL	T_P
G. australis	133,822	Litchfield	wet	13	12
			early dry	10	
			dry	12	5
G. gemina	536,949	Kidman Springs	wet	11	12
			early dry	8	
			dry	8	11
G. koira	181,501	Kidman Springs	wet	11	12
			early dry	5	
			dry	9	11
G. lapistola	4,205	Litchfield	wet	12	13
			early dry	8	
			dry	32	20
G. nana	250,493	Kidman Springs	wet	9	12
			early dry	12	
			dry	10	12
		Litchfield	wet	15	15
			early dry	8	
			dry	22	14
G. paranana	9,528	Litchfield	wet	11	11
			early dry	10	
			dry	17	7

Table 2. Mean evaporative water loss (EWL) (mg/min) of *Gehyra* species from Litchfield and Kidman Springs, and EWL depression expressed as the percentage decrease from wet to dry season mean EWL.

Species	Mean EWL			EWL	Season	Seasonal Comparisons (*p*-Values)		
	wet	early dry	dry	Depression (%)	*p*-Value	wet - early dry	early dry - dry	dry - wet
G. australis	0.13	0.09	0.06	54	<0.01*	0.6	0.2	0.01*
G. gemina	0.12	0.06	0.07	42	<0.0001*	0.0009*	0.7	0.003*
G. koira	0.24	0.07	0.1	58	<0.0001*	0.0004*	0.3	<0.001*
G. lapistola	0.17	0.07	0.08	53	<0.0001*	<0.0001*	1	<0.0001*
G. nana (KS)	0.06	0.05	0.05	17	0.4	-	-	-
G. nana (L)	0.09	0.05	0.02	78	<0.0001*	0.3	0.02*	<0.0001*
G. paranana	0.12	0.06	0.04	67	<0.0001*	0.004*	0.1	<0.0001*

(KS) = Kidman Springs population, (L) = Litchfield population

Statistically significant p-values are marked with ‘*’.

Figure Captions

Figure 1. Study sites from which *Gehyra* gecko species were sampled for physiological plasticity studies; **(a)** map of the northern portion of the Northern Territory displaying sampling locations. Color overlay provided for context; represents mean annual 3 pm relative humidity (% RH) between 1976–2005. Figure modified from map provided by the Australian Bureau of Meteorology, *http://www.bom.gov.au/climate*. **(b)** Mean monthly total rainfall and mean maximum and minimum temperatures for the two sites between 2000–2009 inclusive. Litchfield data (blue) were sourced from the Batchelor Airport weather station, and Kidman Springs data (orange) were sourced from the Kidman Springs weather station.

Figure 2. **(a)** Thermal image of a *Gehyra* gecko showing the temperature sampling site in the lower abdominal region (M1) and the corresponding temperature scale as displayed in the Testo IRSoft thermal imaging software (v4.8) interface. **(b)** Mean preferred body temperatures of *Gehyra* geckos in the wet and dry seasons. **(c)** Mean evaporative water loss (EWL) rates for Northern Territory *Gehyra* species across tropical seasons. A seasonal effect on EWL was significant for all groups except *G. nana* from Kidman Springs. Boxplots represent data from all species combined, depicting median values, upper and lower quartile ranges, and outliers (black circles). Colored data points are mean values for each species. Blue = Litchfield species (L), orange = Kidman Springs (KS). Shapes represent separate species within a sampling site. Error bars represent ± 1 standard deviation.

Figure 1

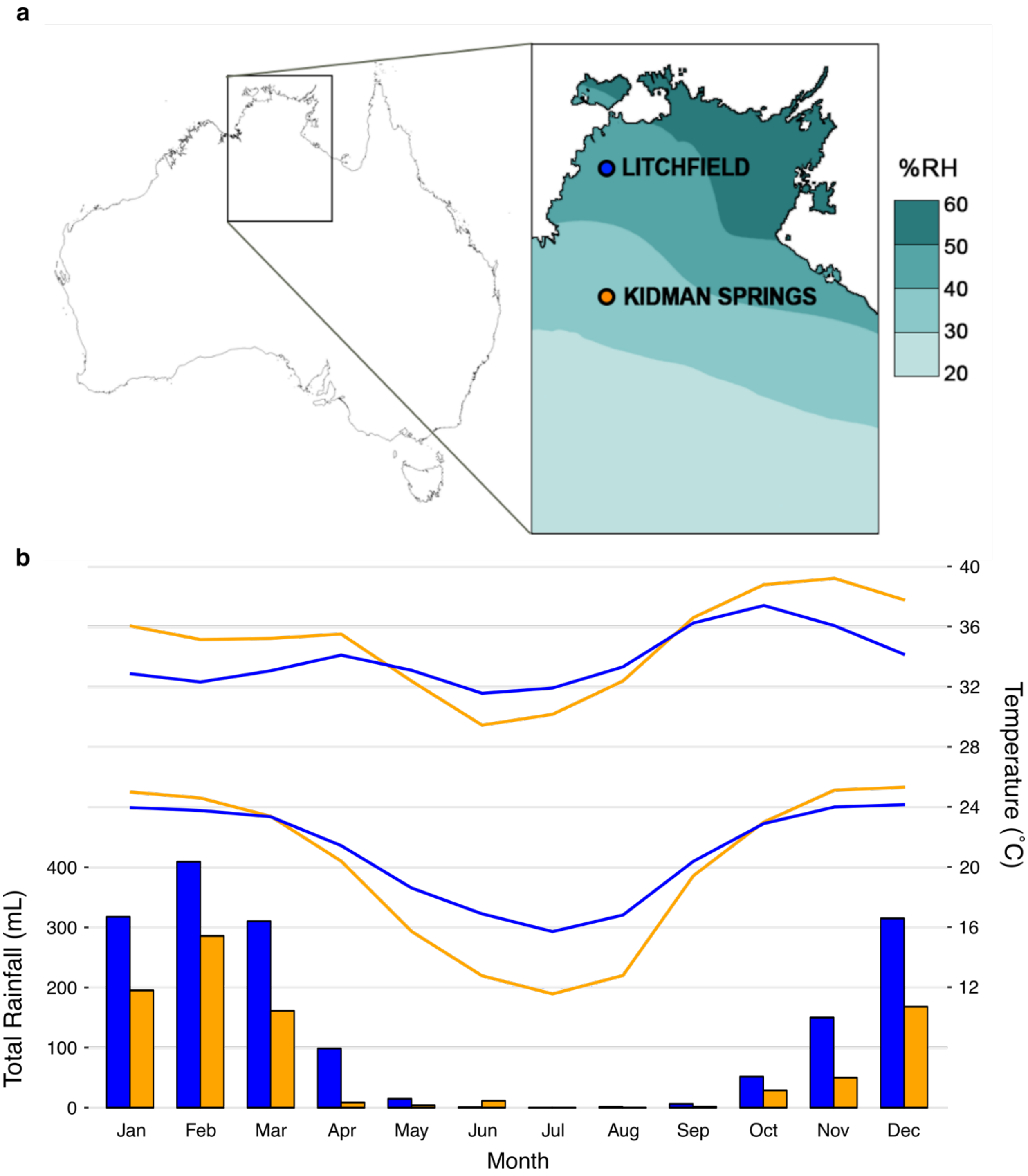
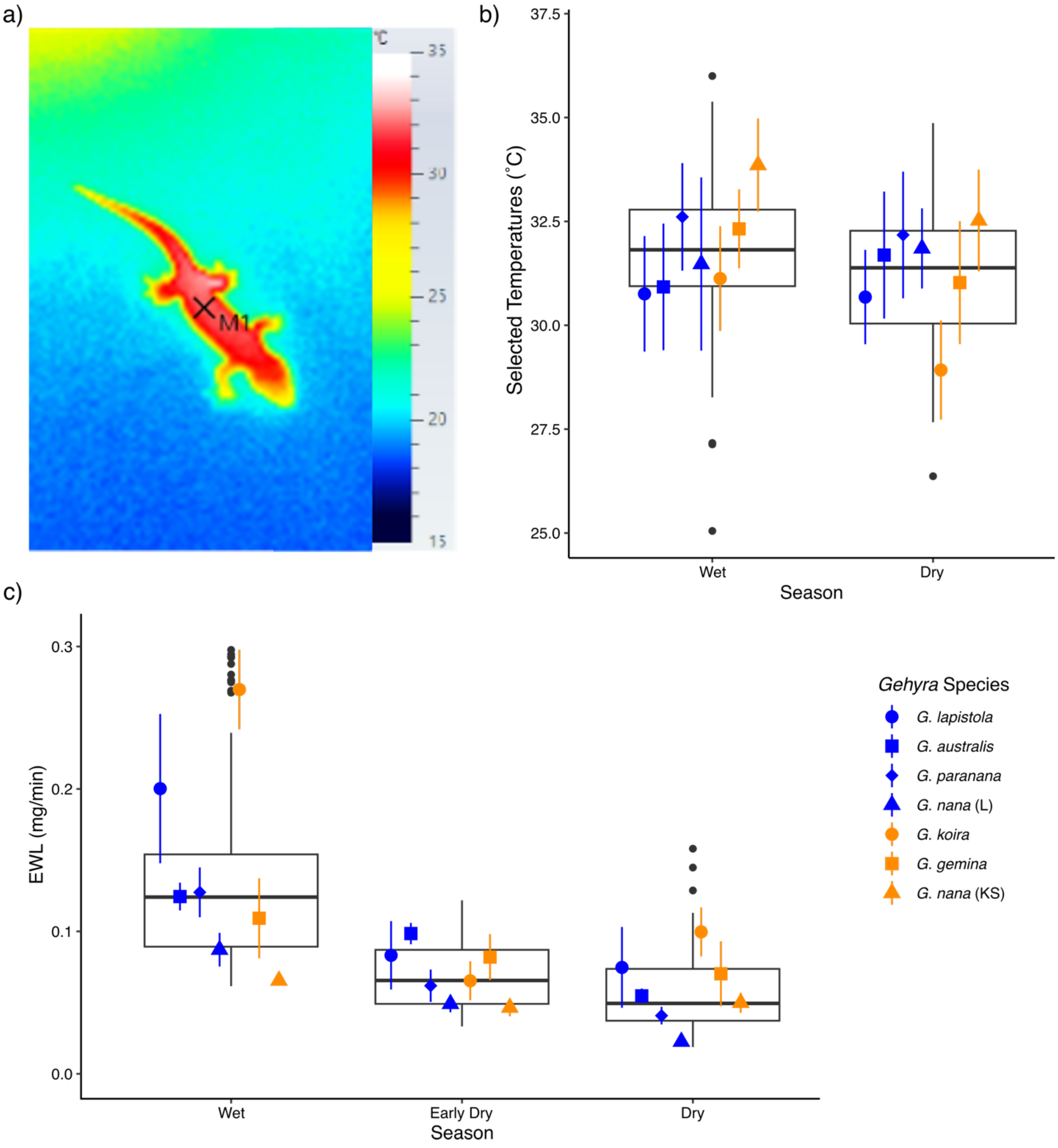

a
LITCHFIELD
KIDMAN SPRINGS
%RH
60
50
40
30
20
b
40
36
32
28
24
20
16
12
Temperature (°C)
400
300
200
100
0
Total Rainfall (mL)
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Figure 2.


a)
℃
35
30
25
20
15
M1
b)
Selected Temperatures (˚C)
37.5
35.0
32.5
30.0
27.5
25.0
Wet
Dry
Season
c)
EWL (mg/min)
0.3
0.2
0.1
0.0
Wet
Early Dry
Dry
Season
Gehyra Species
G. lapistola
G. australis
G. paranana
G. nana (L)
G. koira
G. gemina
G. nana (KS)

Ecology: Report

Supplementary Materials

Climatic Variability Shapes Plasticity of Hydric and Thermal Physiology in Tropical Geckos

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KEYWORDS

evaporative water loss, geckos, physiological plasticity, reptiles, seasonal plasticity, seasonal tropics, thermal preference

Range Size Estimation

Range sizes were estimated using QGIS v. 3.20 by taking the area (km^2) of a convex hull polygon ('Minimum bounding geometry' function) fitted to geographic records for the respective species, each of which was then clipped to the Australian coastline. Polygons were then inspected and modified, if needed, to produce more realistic distributions. This was done for *G. australis* to extend its polygon across the western Top End, where no specimen records exist but where the species is known to occur throughout woodland habitat (S. Zozaya pers. obs.). Because many *Gehyra* are difficult to differentiate, only records verified by sequence data or else of easily identified species were used to calculate polygons. These records were obtained from published studies (Hutchinson et al. 2014; Moritz et al. 2018; Ashman et al. 2018; Kealley et al. 2018; Oliver et al. 2020; Fenker et al. 2021) or else represent new records by the authors. Note that the polygon for *G. nana* is based on the distribution of the "nana2" lineage (*sensu* Moritz et al. 2018) because *G. nana* remains an unresolved species complex, and so lumping all of what is currently recognised as *G. nana* would overinflate the range size with respect to populations sampled herein.

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