Climate Does Not Predict Thermal and Hydric Traits in Northern Australian Geckos

Kade Skelton[1], Craig Moritz[2], Kimberley Day[1], Chava L. Weitzman[1], Christine Schlesinger[1], Michael Kearney[3], Stephen M. Zozaya[2], Keith Christian[1*]

[1]Charles Darwin University, Research Institute for the Environment and Livelihoods, Ellengowan Drive, Brinkin, NT 0810 Australia
[2]Division of Ecology and Evolution, Research School of Biology, and Centre for Biodiversity Analysis, The Australian National University, Building 46, Sullivans Creek Road, Acton, ACT 2601, Australia
[3]School of Biosciences, The University of Melbourne, Parkville, Victoria, Australia

* Corresponding author: Charles Darwin University, Research Institute for the Environment and Livelihoods, Ellengowan Drive, Brinkin, NT 0810 Australia;
Keith.Christian@cdu.edu.au

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CONFLICT OF INTEREST STATEMENT

We have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

Keith Christian, Craig Moritz, Kade Skelton and Kimberley Day conceived the ideas and designed methodology; Keith Christian, Craig Moritz, Kade Skelton, and Kimberley Day collected the data; Kade Skelton, Michael Kearney, Stephen Zozaya, and Chava Weitzman analysed the data; Kade Skelton, Keith Christian and Christine Schlesinger led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

STATEMENT ON INCLUSION

Our study brings together authors from different countries, including scientists based in the country where the study was carried out. All authors had the opportunity to express diverse sets of perspectives they represent.

DATA AVAILABILITY STATEMENT

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.25116158 (for review, temporary Figshare link: https://figshare.com/s/0ec4706d590c48d8782c).

Abstract

1. Reptiles are challenged with maintaining stable hydric states and viable body temperatures in a variable terrestrial environment. Reptiles can use behaviour to select favourable microhabitats as well as physiological adaptations, such as increased skin resistance to water loss to regulate their hydric and thermal states. The degree to which a species' physiology is adapted to overcome environmental challenges can indicate if species have become specialised to local conditions; for example, reptiles from arid locations tend to have lower rates of evaporative water loss (EWL).

2. EWL rates were measured in 18 species of Australian geckos in the genus *Gehyra* collected from 11 Northern Territory and Western Australian locations during the dry season, and preferred temperatures were measured for the nine species sampled from the Northern Territory.

3. Rates of EWL did not differ significantly among most species except between a few species with the highest and lowest rates. There was no association between EWL and the aridity of capture locations, and microhabitat conditions (temperature and humidity in rock crevices) did not explain this lack of association. Thermal preferences differed among species, with *G. koira* selecting significantly cooler temperatures than all other species. *Gehyra moritzi*, from the most arid location (Kurundi Station), had the highest preferred body temperature, overlapping only with two sympatric species (*G. minuta* and *G. purpurascens*).

4. Unlike some reptiles, *Gehyra* geckos do not specialise in their EWL to match the local climate despite the strong gradient in aridity across sampling sites. Their nocturnal activity and seasonal plasticity in EWL may explain the lack of association between their physiological traits and climate.

KEYWORDS

aridity, climate, evaporative water loss, *Gehyra*, phylogeny, thermal preference

1 INTRODUCTION

Terrestrial reptiles are challenged with maintaining stable thermal and hydric states in variable environments. They rely on environmental temperatures to regulate body temperatures and metabolic processes, with warmer temperatures enabling increased sprint speed and digestion efficiency, but extreme thermal conditions can be lethal (Christian & Tracy, 1981; Harwood, 1979; Hertz et al., 1982). Although acting on a longer time-scale than thermal stress, cumulative water loss can result in dehydration with both sublethal and lethal consequences (Pirtle et al., 2019).

Reptiles can overcome thermal and hydric stress by adapting to local conditions. For example, reptiles from warmer environments tend to select higher body temperatures, reflective of adaptations to local conditions through physiological and behavioural processes (Clusella-Tullas & Chown, 2014; Liz et al., 2019). Measuring preferred temperatures in a controlled setting can identify the optimal body temperatures of reptiles when they are unaffected by environmental variables that may restrict thermoregulatory behaviours in the field (Hertz et al., 1993). Comparing this measure across species from varying environments can then indicate whether species have adapted to their local conditions.

Similarly, species that live in arid climates typically have lower evaporative water loss (EWL) rates than those from more mesic conditions (Belasen et al., 2017; Bentley & Schmidt-Nielsen, 1966; Cox & Cox, 2015; Dmi'el et al., 1997; Dmi'el, 1998; Dmi'el, 2001; Mautz, 1982a; Shoemaker & Nagy, 1977). Cutaneous EWL accounts for most of the non-excretory water loss in reptiles, and the rate of EWL is dependent on various factors including environmental humidity, air flow, and skin permeability (Bentley & Schmidt-Nielsen, 1966; Mautz, 1982a; Shoemaker & Nagy, 1977; Snyder, 1979), the latter of which is subject to selective pressures. Lower rates of water loss have evolved in arid environments due to species' long-term exposure to dry conditions, allowing them to persist in environments with high levels of hydric stress by reducing the amount of water passively lost across surface membranes. Historically, colonisation of arid environments by reptiles is associated with adaptive changes in EWL (skin permeability), indicating that this process is driven by climate even where a phylogenetic signal is present (Cox & Cox, 2015). This association between EWL and aridity has been documented primarily in species originating from a temperate climate, but has been broadly accepted as applying to reptiles more generally. Such associations have not, however, been documented for Australian geckos. It has been suggested this may relate to their nocturnal habit which protects them from diurnal aridity extremes (Vucko, 2008; Withers et al., 2000).This is supported by observations that annual EWL is lower in reptiles with nocturnal compared to diurnal activity patterns (Pirtle et al., 2019). Also, it is possible that seasonal changes in EWL may represent an alternative physiological adaptation that precludes the advantages of a fixed association between EWL and aridity (Blamires & Christian, 1999; Skelton, 2024).

Identifying whether species have adapted to their environment through specialisation of their physiological traits can provide information on species' evolutionary history of dispersal and trait development, explain the co-existence of sympatric species and, when combined with phylogenetic data, predict how species will cope with anticipated environmental changes in the future(Garcia-Porta et al., 2019; Piantoni et al., 2019; Sannolo et al., 2018). This approach is especially effective if multiple congeneric species from varied climatic habitats are measured, allowing for consideration of both phylogenetic and ecological influences on physiological traits.

In this study, we compared field-sampled physiological traits across gekkonid species of the genus *Gehyra* (dtellas) from northern Australia (Western Australia and the Northern Territory). This region has a seasonal tropical climate, with all locations within the study area experiencing a wet (high humidity or rainfall) and dry (low humidity and rainfall) season. Conditions range from mesic to arid as latitude increases, such that the mesic locations experience strong seasonal differences in water availability but minor shifts in environmental temperature. Arid locations experience similarly strong seasonal fluctuations in water availability—though with harsher dry season conditions and less total rainfall—and comparatively greater changes in temperature. *Gehyra* species are found throughout this region, allowing for strong comparisons across varying climatic environments.

The evolutionary history and radiation of the Australian *Gehyra* species complex have recently been described and new species identified (Hutchinson et al., 2014; Moritz et al., 2017; Oliver et al., 2019; Oliver et al., 2020), but physiological information is required to enhance current understandings of *Gehyra* ecology. This genus is found across mainland Australia, where some species are restricted to small ranges and others are widespread in their distribution. The variety of distribution patterns and inhabited environments within *Gehyra* provides opportunities to determine if species' biological differences are driven by adaptations to local environments or shared evolutionary history. This information can provide further insight into species evolution and the degree of species' specialisation to local environments. We predicted that dtellas adapt their physiology to match the local environment to reduce hydric and thermal stress, and that adaptation to local conditions has a stronger effect on physiological traits than phylogenetic relatedness.

We hypothesised that EWL would differ across *Gehyra* species and that species from arid locations would have comparatively low EWL. Despite there being no established association between EWL and aridity in Australian geckos (Withers et al., 2000), the diversity of species and climates included in this comparison allowed for a stronger test for such an association than has previously been undertaken. We also predicted that phylogenetic signal of EWL would be weak, with environmental conditions, not phylogeny, being the driving force behind potential species differences. This prediction is also supported by the lack of correlation between EWL and phylogeny reported in a previous study comparing physiological traits of Australian geckos, including members of the *Gehyra* genus (Withers et al., 2000).

In addition to the EWL measurements, preferred temperatures were measured for nine species from the Northern Territory; Western Australian species were excluded due to logistical challenges related to interstate transport for laboratory-based experiments. Because the three Northern Territory sites used in this study are distinct in their climatic conditions, we predicted that preferred temperatures would differ among species and sampling locations.

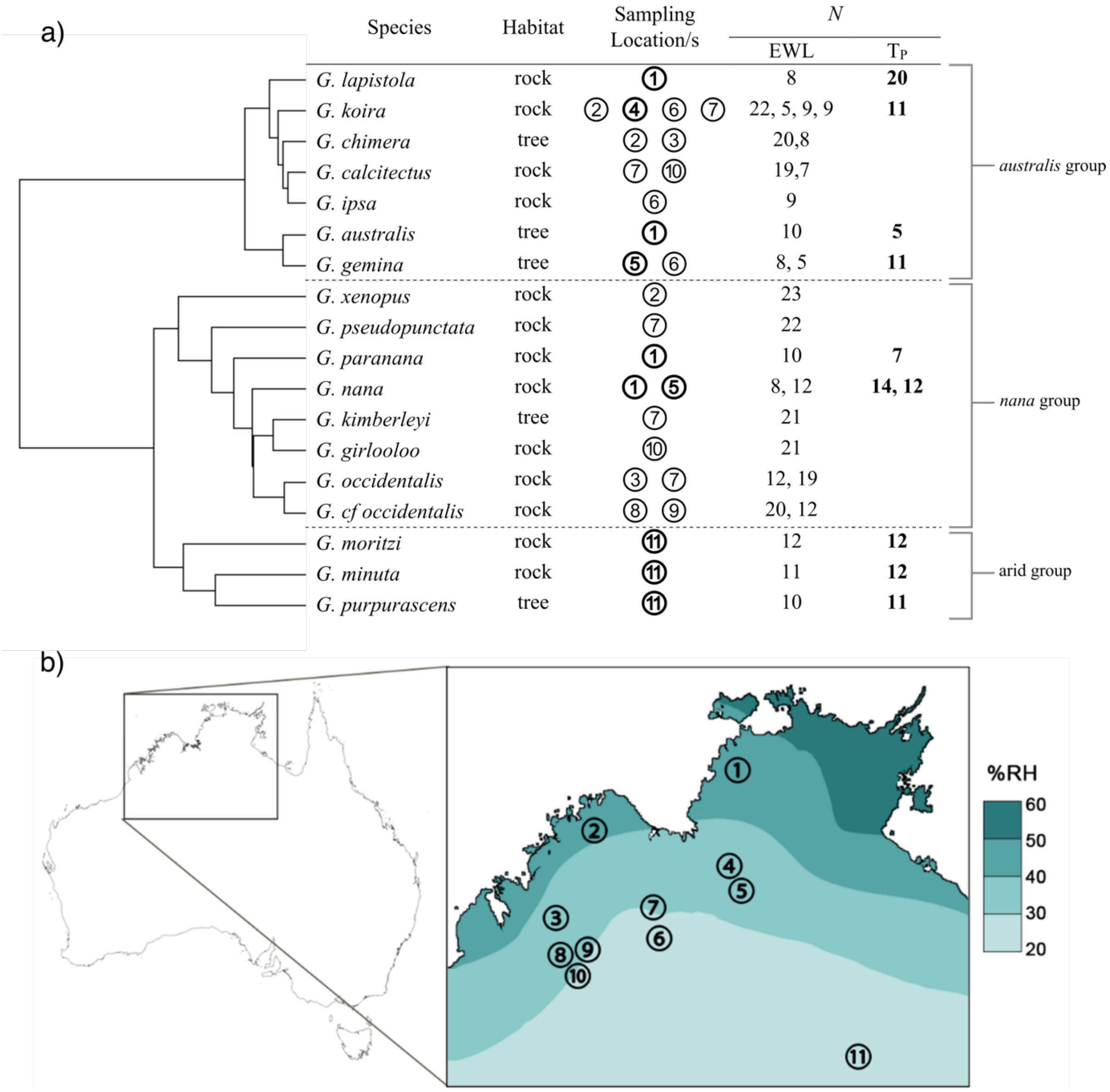
2 MATERIALS AND METHODS

2.1 Sample Species & Sites

Eighteen *Gehyra* species were sampled during the dry season (May to September) from eleven locations in the Northern Territory and Western Australia between 2019–2021 (Figure 1). Sampled species spanned three deeply divergent, phylogenetic clades: the largely tropical *australis* and *nana* clades, and a group of arid zone species (Figure 1, Figure S1). The species identity of all individuals was confirmed by mtDNA sequencing, which provides reliable diagnosis for the sampled taxa, some of which are difficult to distinguish morphologically (Doughty et al., 2018; Oliver et al. 2020). Although five species are tree-dwelling, most species are rock-dwelling, with the type of rock habitat varying across locations (Figure 1; Figure S2). Spotlighting methods were used to locate and capture dtellas at night. Spotlighting sessions typically lasted 4 h, from the early evening until sightings diminished. Spotlighting was repeated on consecutive nights with the aim of acquiring at least 10 of each target species from each location. Hatchlings and dtellas with an incomplete tail, or broken skin, were excluded from the study and released if captured. All other dtellas were captured by hand and immediately transferred into individual cloth bags. For all species from all sampling sites, field EWL measurements were taken within 48 h of capture; species from Western Australia were measured in the field, species from Kidman Springs were measured in makeshift laboratory conditions, and all other species from the Northern Territory were transported to Charles Darwin University and measured in a laboratory using the same equipment used in the field.

The nine species sampled from the Northern Territory were also used in laboratory-based thermal preference experiments. After initial measurements were acquired, dtellas were housed individually in clear plastic holding enclosures of 40 × 25 × 13.5 cm (for moderate/large species) or 17 × 23 × 15 cm (for small species) containing a plastic hide and were supplied with a spray of clean water daily and offered live food three times per week. Dtellas were kept in these enclosures when not used in experiments and were released at their original location within six months of capture.

Sampling sites were assigned numeric aridity scores calculated through environmental modelling using NicheMapR (Kearney & Porter, 2004; Kearney & Porter, 2017) (Figure 1). Scores reflect the annual amount of water loss for a typical lizard at each site, assuming nocturnal behaviour and average local rainfall patterns; higher scores indicate greater aridity.



Species	Habitat	Sampling Location/s	*N*	
			EWL	T$_P$
G. lapistola	rock	**①**	8	**20**
G. koira	rock	② **④** ⑥ ⑦	22, 5, 9, 9	**11**
G. chimera	tree	② ③	20,8	
G. calcitectus	rock	⑦ ⑩	19,7	
G. ipsa	rock	⑥	9	
G. australis	tree	**①**	10	**5**
G. gemina	tree	**⑤** ⑥	8, 5	**11**
G. xenopus	rock	②	23	
G. pseudopunctata	rock	⑦	22	
G. paranana	rock	**①**	10	**7**
G. nana	rock	**①** **⑤**	8, 12	**14, 12**
G. kimberleyi	tree	⑦	21	
G. girlooloo	rock	⑩	21	
G. occidentalis	rock	③ ⑦	12, 19	
G. cf occidentalis	rock	⑧ ⑨	20, 12	
G. moritzi	rock	**⑪**	12	**12**
G. minuta	rock	**⑪**	11	**12**
G. purpurascens	tree	**⑪**	10	**11**

Key	Location*	Rock Type$^{\$}$	Rock Structure	Aridity Score
1	Litchfield (NT)	SS	boulders, ground	12.8
2	Theda (WA)	SS	boulders	16.7
3	Silent Grove (WA)	SS	boulders, cliffs	23.1
4	Buchannan Limestone (NT)	LS	cliffs	23.4
5	Kidman Springs (NT)	B	ground	23.9
6	Purnululu (WA)	SS, LS	cliffs	26.7
7	Mt. Nyulasy / Lissadell (WA)	SS / LS	boulders, cliffs	28.6
8	Boab Quarry (WA)	LS	boulders, cliffs	
9	Danggu (WA)	LS	boulders	30.7
10	Gogo Station (WA)	LS	boulders, cliffs	31.3
11	Kurundi Station (NT)	SS	ground	38.2

*NT = Northern Territory, WA = Western Australia
$^{\$}$SS = sandstone, LS = limestone, B = basalt

Figure 1 **(a)** Phylogenetic tree and corresponding sampling locations for *Gehyra* geckos sampled during the dry season between 2019–2021 for evaporative water loss (EWL) and thermal preference (T$_P$) analyses. Sampling locations correspond with (b); bold locations indicate sites for T$_P$ analyses in addition to EWL analyses. **(b)** Map of sampling locations and habitat types in the Northern Territory and Western Australia. Locations are numbered in order of increasing aridity score, with Boab Quarry (no aridity calculated) numbered among nearby sites. For context, the map colour overlap represents mean annual 3pm relative humidity (%RH) between 1976–2005. Figure modified from map provided by the Australian Bureau of Meteorology, *http://www.bom.gov.au/*.

To obtain direct measurements of microhabitat conditions, iButton® temperature/humidity loggers (DS1923 Hygrochrons) were deployed at Gogo Station, Kidman Springs, Buchannan Limestone, Litchfield, and Silent Grove sites in 2019. At least four loggers were deployed at each site, with most loggers positioned within crevices identified as dtella microhabitat, and one logger at each site positioned outside crevices in shaded locations, including open rock chasms and tree branches. Data retrieval was not successful in all cases, as only a single logger (crevice) was retrieved at the Silent Grove site. Readings were taken hourly, and for each logger, per month, we calculated mean, mean maximum, and mean minimum temperature and absolute humidity (calculated from relative humidity and air temperature) readings from inside crevice microhabitats for visualisation and analyses comparing conditions among sites. We also calculated a value representing the range of temperature and relative humidity per month as the difference between the mean maximum and minimum temperatures. Most loggers collected data for 11 or more months. We ensured year-round data collection from Litchfield by replacing loggers mid-year, amounting to up to four values per month in open habitat and up to 11 values per month in crevices.

Monthly mean maximum and minimum temperatures from the nearest weather stations (<100 km from sampling sites) for Northern Territory sampling sites are shown in Table 1 for the wet and dry seasons for the years 2000–2009 inclusive. These values were used in thermal preference comparisons (below). The Buchannan Limestone location was treated as a Kidman Springs site for this analysis due to its proximity and similar climatic conditions.

Table 1. Average mean monthly temperatures during dry (May–October) and wet (November–April) seasons in Northern Territory sampling sites between 2000–2009 inclusive and the weather stations from which temperature data was acquired (Ali Curung missing 2009 data). Data acquired from the Australian Bureau of Meteorology, *http://www.bom.gov.au/climate.*

Sampling Site	Weather Station	Mean Monthly Minimum Temperature (°C)		Mean Monthly Maximum Temperature (°C)	
		dry season	*wet season*	*dry season*	*wet season*
Litchfield	Batchelor Airport	18.5	23.4	33.9	33.8
Kidman Springs	Kidman Springs Station	15.9	24.0	33.3	36.5
Kurundi Station	Ali Curung	11.3	21.6	28.4	36.0

2.2 Evaporative Water Loss

Evaporative water loss (EWL) was measured with an open-flow system similar to setups used in previous studies (Mautz, 1982b; Young et al., 2005). This approach to EWL measurement ensured factors that may influence water loss rates were controlled (Mautz, 1980). Air flow rate and temperature were maintained at constant levels and measurements were taken from dtellas at rest. The EWL rate includes evaporation across the skin, from the eyes, and from respiratory water loss, and these components were not delineated (Mautz, 1982b). Skin temperatures of dtellas were measured immediately after removal from the experiment using a calibrated infrared thermometer (Thomas Scientific Traceable, model 123D37), allowing for calculations of cutaneous resistance to water loss (Table S1). This is achieved by comparing EWL rates and skin temperatures of study animals to that of similarly shaped agar models that lack any cutaneous resistance to water loss (Spotila & Berman, 1976).

In the experimental setup, air was drawn through a dehydration column of silica gel and into a cylindrical experimental chamber (12.5 cm long, 3 cm diameter, 70 mL volume) at a rate of 0.2 L/min using a 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 to maintain a stable air temperature. 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 system to continuously record the temperature and relative humidity of the air exiting the chamber. Baseline measurements were taken from stable readings before an animal was introduced into the chamber.

After a stable baseline was recorded, an individual dtella was placed in the experimental chamber. The air temperature and relative humidity of the air output was monitored until readings stabilised 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 1 min. Trials were restricted to 2 h maximum duration to ensure the welfare of the animals used in the experiment. After experiments, a dial calliper was used to measure the length (snout-to-vent) and width of the body, limbs and tail of dtellas to 0.1 mm, and body mass was weighed to 0.01 g.

The difference between the humidity reading with a dtella in the chamber and the baseline reading is a measure of the amount of water lost via evaporation. This value was analysed with respect to body surface area (see *Statistical Analysis* below), which was estimated for each individual by assuming the trunk and limbs to be cylinders with one end, replicating techniques used in similar studies (Belasen et al., 2017; Chukwuka et al., 2020). This approach was validated by confirming that the calculated surface areas of plastic lizard models matched those obtained by measuring the area of tape that had been meticulously wrapped over the surface of these models (Skelton, 2024).

2.3 Thermal Preference

Thermal preference (T_P) experiments were conducted soon after field EWL was measured, within 72 h of collection of animals from the field. An individual dtella was 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 small terracotta blocks. The tank was kept in a temperature-controlled room set to 20 °C and a 50 W heat globe was placed at one end of the tank to create a linear temperature gradient of 20–40 °C in a design similar to those used in other studies (Carneiro et al., 2017; Christian et al., 1998; Christian et al., 2007; Belasen et al., 2017; Rozen-Rechels et al., 2020). A Testo 868 thermal imaging camera (0.08 °C thermal sensitivity) was used to photograph the dtella at hourly intervals, producing a total of 12 thermal images for each dtella. Testo IRSoft thermal imaging software (v4.8) was used to extract temperature readings from the lower abdomen of the animal (Figure 4). This location was selected to replicate the standard procedure of measuring reptile body temperatures via the cloaca.

The central 50% of readings were used to produce a set-point range which considers the variation in selection of temperatures between upper and lower set-points; this is standard practice in studies of thermal preference and allows for a more complete capture of thermoregulatory decisions (Hertz et al., 1993; Pintor et al., 2016; Stellatelli et al., 2018).

Initial results indicated that *G. koira* had the lowest T_P of the nine species measured. Given that this was the only species of the nine that was collected from limestone, this result raised the possibility that the deep crevices found in the limestone may allow lower daytime body temperatures resulting in a low T_P. To test this hypothesis, in November 2023 we collected a sample of 12 *G. koira* from each of two sites: the Buchannan Limestone, and a site 65 km to the NNW near Timber Creek, NT where *G. koira* were found on sandstone. These two samples of *G. koira* were taken to the laboratory and T_P was measured as described above and the two groups were compared as described below.

2.4 Statistical Analysis

Analyses were performed with R v4.3.1 in Rstudio v2023.06.2 (R Core Team, 2023; R Studio Team, 2020). Where relevant, pairwise contrasts were always done via lsmeans (Lenth, 2016) using the Tukey method for p-value adjustments. We performed type II tests using *Anova* (car package; Fox and Weisberg, 2019) to calculate F statistics and p-values for all non-phylogenetic linear models, with Wald's χ^2 tests used for all mixed-effects models.

With the iButton data from five sampling locations, we used linear mixed-effects models with the *lmer* function in the lme4 package (Bates et al., 2015) to test whether crevice conditions differ among sites. We analysed each of the temperature and humidity metrics separately, including month as a covariate and logger ID as a random factor. We had enough iButtons deployed at Litchfield to also compare open and crevice microhabitats for each of the climate metrics with *lmer*.

EWL data were used to test: (i) whether sites differed within species, (ii) whether species differed from each other, (iii) the extent of phylogenetic signal in mean EWL for each species, and (iv) whether there is a relationship between EWL and aridity among species. EWL was log-transformed prior to analyses due to a relationship between mean and variance with respect to surface area (SA), and in all analyses EWL is adjusted for SA. For the seven species sampled at multiple sites (Figure 1), we tested whether EWL values differed among sites using a linear model for each species with SA as covariate. Because within-species values differed only by a single site for *G. koira*, we focus further analysis on species-level differences. We then tested whether EWL differed among species using a linear model, again with SA as a covariate, and performed pairwise contrasts of adjusted EWL among all species pairs. Using the above model, we then produced predicted mean EWL values (using lsmeans) for each species at a given SA (SA = 52.7, the average across all samples) to use for visualisation and for subsequent phylogenetic comparative analysis. Predicted EWL is in the original scale (mg/min) and is not log-transformed. Phylogenetic signal was estimated for predicted mean EWL using Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999) using the *phylosig* function in phytools (Revell, 2012), with 1000 permutations specified for each analysis. We then tested whether among-species differences in SA-adjusted EWL correlates with aridity using the *intra_phylm* function in sensiPhy (Paterno et al. 2018), which can perform phylogenetic linear regression that accounts for intraspecific variation. We used predicted mean EWL values for each species as the response variable and aridity score as the predictor variable, using the lambda model for phylogenetic covariation and incorporating standard deviation in predicted EWL to account for within-species variation. We specified 1000 repetitions, which repeats the analysis with random mean values for each species informed by the given standard deviation, thus yielding a distribution of coefficient estimates and p-values across iterations. Given that the EWL data show negligible phylogenetic signal (see Results), we also performed a non-phylogenetic mixed-effects model across all observations (not just species means) using the *lmer* function (as above), with log-transformed EWL as the response variable, SA as a covariate, and aridity score as the predictor, with observations nested within species as a random factor. Finally with respect to water loss data, we used a linear model to test whether mass (g) predicted log-transformed cutaneous resistance, with species included in the model as a covariate.

Repeated-measures ANOVAs were used to analyse T_P with *aov*, including individual gecko ID in the error term. We first verified that the two sampled populations of *G. nana* did not differ, and then tested for differences among species in the main dry season data set. Lastly, we tested for differences between two *G. koira* sites in data collected in November 2023.

3 RESULTS

3.1 Crevice Conditions

Mean and mean maximum crevice temperatures were significantly different among locations (mean: $\chi^2 = 20.0$, df = 4, p = 0.0005; maximum: $\chi^2 = 25.0$, df = 4, p < 0.0001; Figure 2, Table S3), though mean minimum crevice temperatures did not differ among locations ($\chi^2 = 7.2$, df = 4, p = 0.1). Humidity metrics also differed among the sampling locations (mean: $\chi^2 = 99.0$, df = 4, p < 0.0001; minimum: $\chi^2 = 20.1$, df = 4, p = 0.0005; maximum: $\chi^2 = 33.5$, df = 4, p < 0.0001). Gogo Station crevices maintained lower mean humidity than all other sites except Silent Grove (11.9 g/m^3 compared to 15.7–17.8 g/m^3), and Kidman Springs crevices had significantly higher mean maximum temperatures than all sites except Gogo Station (40.2 ˚C compared to 29.5–32.2 ˚C).

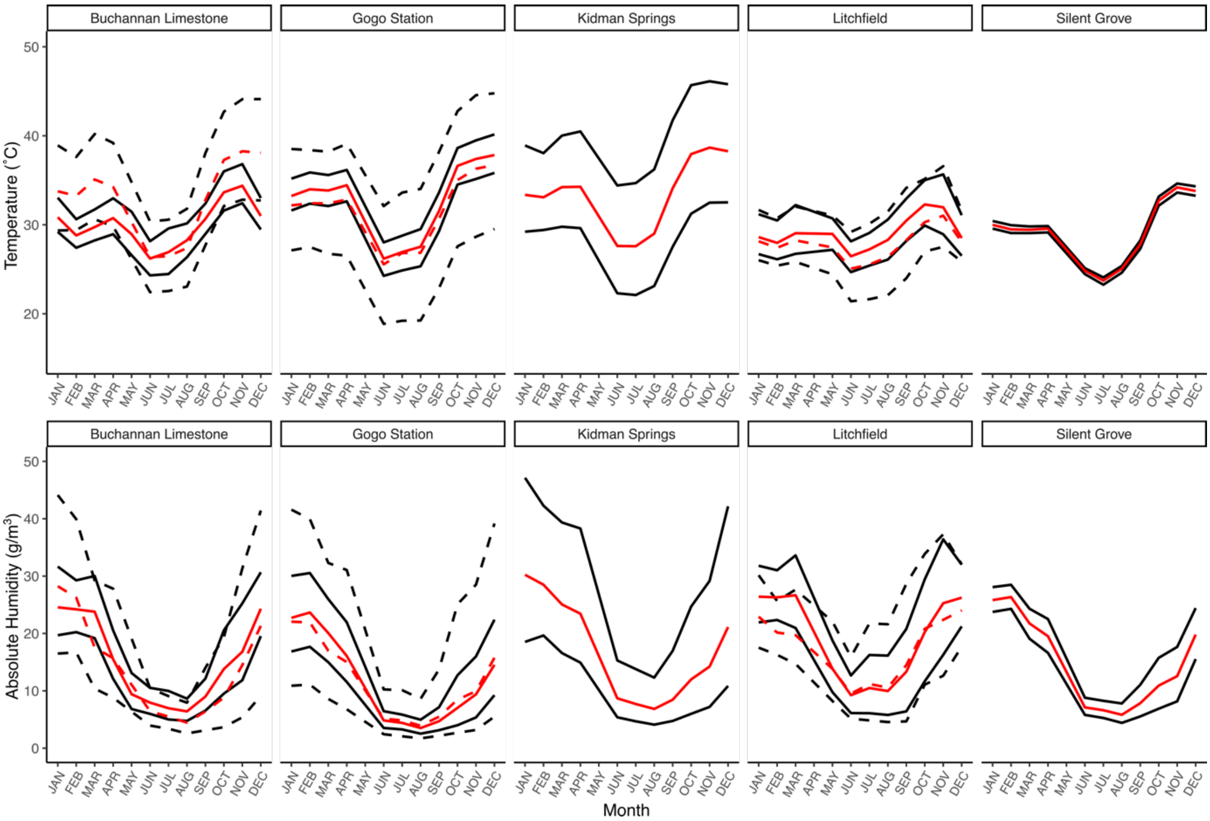


Figure 2. Mean monthly temperature and humidity measured by data loggers placed across sites between 2019–2021. Red lines are grand mean values; black lines are mean maximum and mean minimum values. Solid lines represent data collected from inside crevice microhabitats, dashed lines represent data collected from the external environment in the shade. Significant differences in measures between crevice and external conditions were found in Gogo Station (maximum temperature, minimum temperature, maximum humidity, minimum humidity) and Litchfield (mean temperature, minimum temperature).

The monthly ranges of humidity and temperature differed across locations (humidity: $\chi^2 = 11.6$, df = 4, $p = 0.02$; temperature: $\chi^2 = 17.1$, df = 4, $p < 0.002$). In post hoc test, there were no pairwise differences in range of humidity between sites, aligning with similar aridity across these sites. Kidman Springs had significantly greater temperature range than the other sites (excluding Silent Grove), which may be driven by rock type; the arid limestone sites of Gogo Station and Buchannan Limestone each had a mean range of crevice temperature of ~ 4 °C, whereas the similarly arid Kidman Springs site had a greater mean range of 12 °C in crevice temperature, and is characterised by small, fractured basalt rocks on the ground.

Generally, crevices provided conditions within the range of temperatures and humidity in open environments (Figure 2). At Litchfield, where we deployed enough loggers to compare crevice and open environments and found no significant differences between the two exposure types in all humidity metrics ($\chi^2 < 3.25$, $p > 0.07$ each). However, most temperature values differed between crevice and open environments (minimum: $\chi^2 = 10.8$, $p = 0.001$; average: $\chi^2 = 10.5$, $p = 0.001$; range: $\chi^2 = 4.9$, $p = 0.03$), indicating that crevices at Litchfield provide higher minimum temperatures, higher average temperatures, and a smaller range of temperatures than open environments. Maximum temperatures between the two environments were similar ($\chi^2 = 0.06$, $p = 0.8$).

One iButton deployed at Buchannan Limestone was positioned 5 m deep into a crevice, while the four other crevice iButtons were placed < 1 m deep. This deep data logger recorded lower mean monthly minimum, mean, and maximum temperatures than most other crevice loggers from the same site except one with similar mean monthly minimum temperatures. Temperatures in this deep crevice were also lower and more stable than outside conditions at the same site (Table 2).

Table 2. Monthly mean temperatures recorded by iButton loggers deployed at Buchannan Limestone in varying microhabitat locations between 2019–2020. Deep crevice recordings (1 logger) are lower and more stable than shallow crevices (4 loggers) and outside conditions (1 logger).

iButton Placement	Minimum Temperature (°C)	Mean Temperature (°C)	Maximum Temperature (°C)

	minimum	*maximum*	*range*	*minimum*	*maximum*	*range*	*minimum*	*maximum*	*range*
Deep crevice	22.4	27.9	*5.5*	23.4	28.1	*4.7*	23.8	28.5	*4.7*
Shallow crevices	24.8	33.6	*8.8*	26.9	36.0	*9.1*	29.2	38.9	*9.7*
Outside shade	22.4	32.8	*10.4*	26.3	38.3	*12.0*	30.4	44.1	*13.7*

3.2 Evaporative Water Loss

EWL rates did not differ among sites for any of the seven species that were sampled at multiple localities ($p \geq 0.1$ in all cases). Consequently, we did not include site as a factor in any subsequent models that tested EWL differences among species.

EWL rates differed significantly among species when accounting for SA ($F_{(17, 332)} = 2.07$, $p = 0.008$). Post hoc pairwise contrasts, however, revealed significant differences only between *G. girloorloo*, with the lowest EWL, and the four species at the high end of the EWL range (Figure 3): (*G. koira* ($p = 0.02$), G. *occidentalis* ($p = 0.01$), *G. chimera* ($p = 0.006$), and *G. australis* ($p = 0.04$)). Predicted mean EWL rates ranged from 0.04 to 0.09 mg/min when adjusted to an SA of 52.7.

Phylogenetic signal in predicted mean EWL among lineages was low and not statistically significant ($K = 0.301$, $p = 0.3$; $\lambda = 0.14$, $p = 0.5$), although we do note that our power to detect phylogenetic signal with relatively few species will be low (Blomberg et al., 2003). The phylogenetic linear regression via *intra_phylm* indicates there is no significant relationship between predicted mean EWL and aridity score when accounting for phylogenetic covariance and within-species variation (mean $p = 0.433$, CI = 0.415–0.451). There was also no significant relationship between EWL rates and aridity score in the non-phylogenetic linear model ($\chi^2 = 1.74$, df = 1, $p = 0.2$) (Figure S4). Tests of the effect of body mass on cutaneous resistance (Table S1) indicated that gecko mass had no significant effect on skin resistance to water loss ($F_{(1, 346)} = 0.5$, $p = 0.5$).

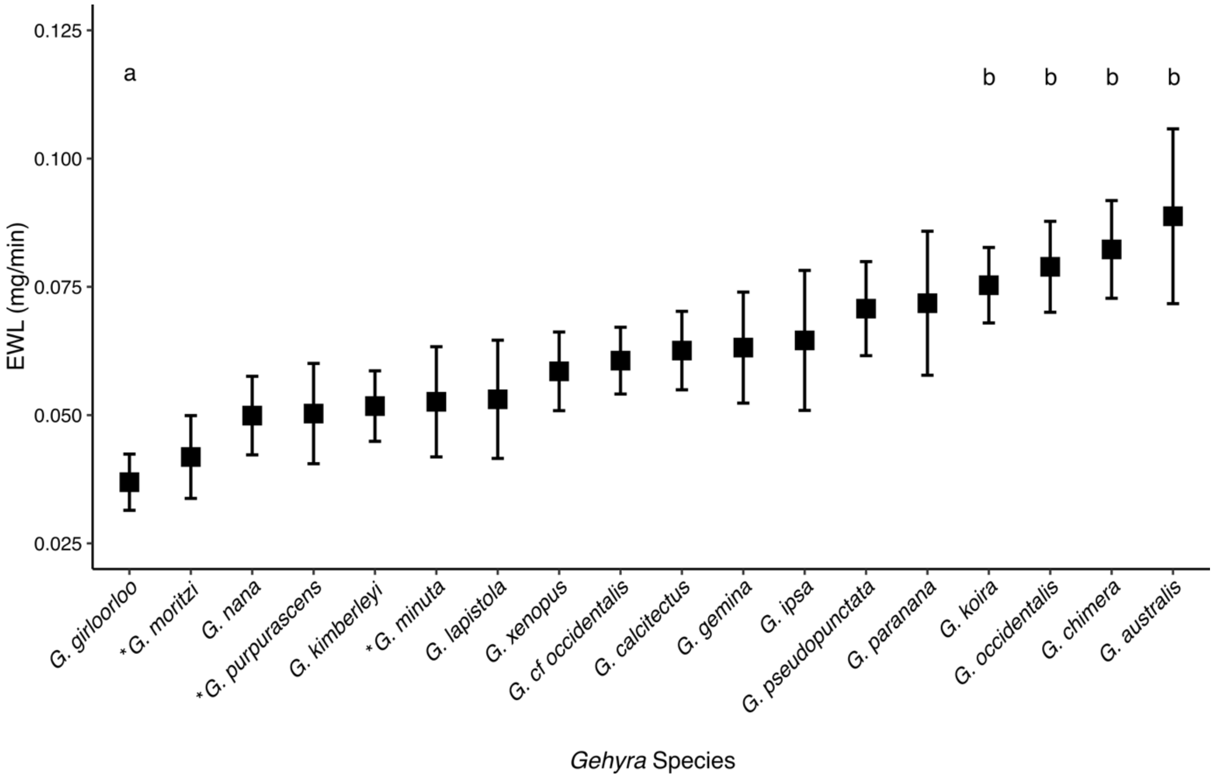


Figure 3. Mean surface area-adjusted evaporative water loss (EWL) rates of *Gehyra* species sampled from the Northern Territory and Western Australia. Data were acquired during May and June, except for species marked with '*' which were sampled in September. Different letters indicate Tukey's post hoc comparisons; species marked '*a*' are significantly different from species marked '*b*'. Error bars display ±1 standard error.

3.3 Thermal Preference

Preliminary testing determined that there was no significant difference in preferred temperatures between the Litchfield and Kidman Springs populations of *G. nana* ($F_{(1,24)} = 2.45$, $p \geq 0.1$). No distinction between these populations is made in the following analysis, aside from consideration of site aridity.

T_P was significantly predicted by species ($F_{(8, 106)} = 17.1$, $p < 0.01$; Figure 4). Post hoc tests identified that *G. koira* had significantly lower T_P, with a mean preferred temperature of 28.9°C, compared to the means of 30.7 - 34.5°C for the other species. When resampled in 2023, the limestone and sandstone populations of this species were not significantly different with respect to T_P ($F_{(1,141)} = 2.149$, $p = 0.1$).

G. moritzi had the highest mean T_P and was significantly different from most species except the other species from Kurundi Station. Phylogenetic signal in T_P was not examined due to the small number of species measured, leading to weak statistical power. Nonetheless, it is notable that the three species from this site are all members of the arid group radiation of *Gehyra* (Figure 1a).

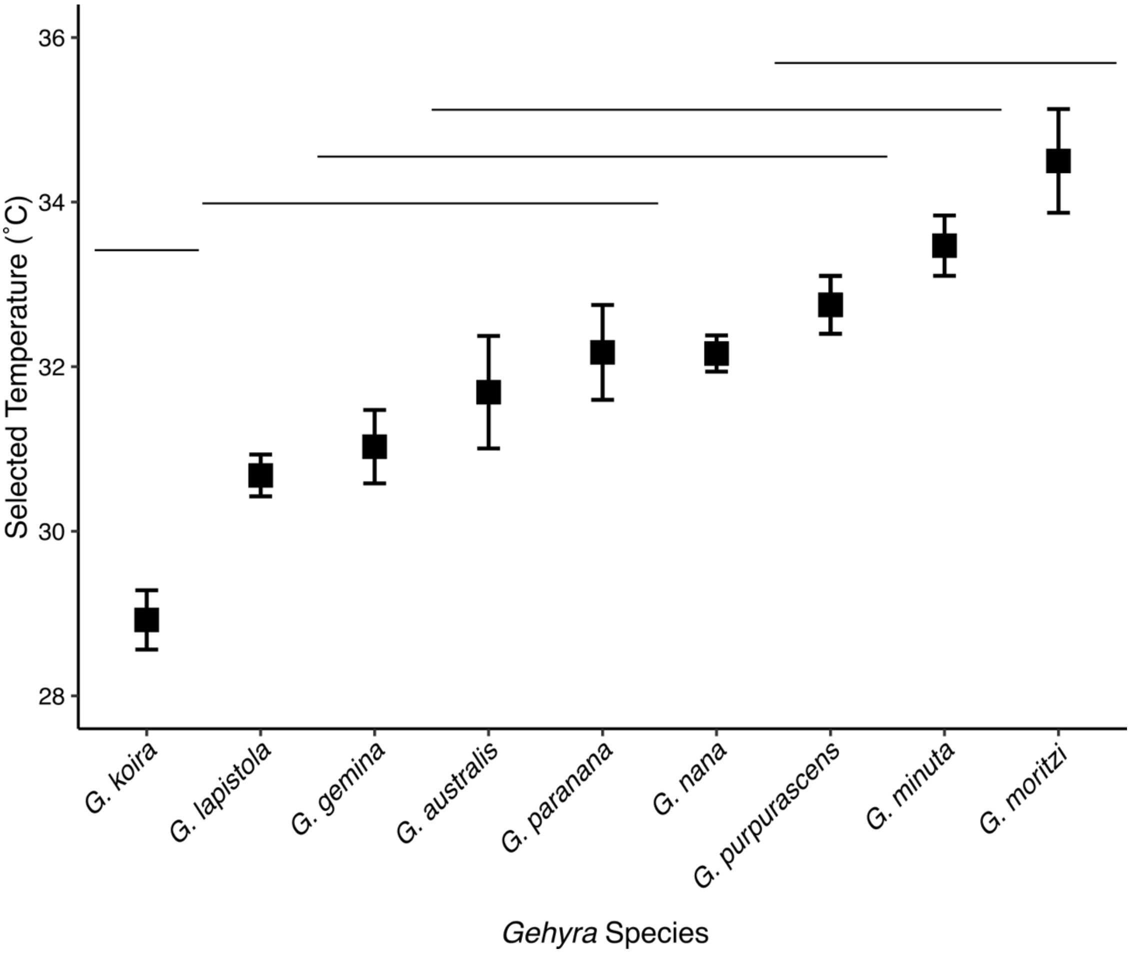


Figure 4. Means of selected temperatures of *Gehyra* species sampled from locations in the Northern Territory. Measurements were taken during the dry season. Horizontal bars indicate species similarities from post hoc tests. Error bars display ±1 standard error.

4 DISCUSSION

4.1 Evaporative Water Loss

Evaporative water loss rates differed among *Gehyra* species when accounting for surface area; however, this difference was largely driven by *G. girloorloo*. This result contradicts our prediction that species would differ in their EWL rates and suggests that hydric physiology is not specialised to local habitat conditions in these species. Estimates of phylogenetic signal for EWL rates were extremely low, which aligns with our predictions; the reasoning for our initial prediction, however, is not supported. In a more phylogenetically diverse comparison, Cox and Cox (2015) concluded that climate, rather than phylogenetic signal, is the primary driver of adaptive physiological trait development in arid-zone reptiles. Considering that EWL and climate were not closely associated in *Gehyra*, phylogenetic signal with respect to adaptive trait development may be of little relevance.

There was no significant association between EWL and aridity among species, contradicting our expectations that EWL would be lower in species from arid locations. This result aligns with findings in studies of other Australian gecko species and, as suggested in these studies, could be attributed to the nocturnal habit of geckos, which shields them from diurnal extremes in environmental conditions (Vucko, 2008; Withers et al., 2000).

If crevice conditions were similar across sites despite differences in broadscale aridity, this could also explain a lack of association between aridity and EWL, as crevices may provide shelter from climatic conditions (Mautz, 1982b). But crevice conditions differed between locations and generally did not differ significantly from external conditions, except in the cases of Gogo Station and Litchfield. The range of within-crevice temperature and humidity was also not associated with site aridity. Thus, neither broad-scale aridity nor microhabitat conditions greatly affected EWL rates. It is notable when comparing arid sites that the limestone crevices at Gogo Station and Buchannan Limestone sites provided a more stable climatic environment compared to the shallow microhabitats of the small basalt rocks of Kidman Springs, however this seems to have little consequence on species' EWL rates.

4.2 Thermal Preference

T_P differed among species, with the most notable result being *G. koira*'s particularly low T_P. The low T_P of *G. koira* was significantly different from all other species and was the only mean T_P less than 30°C. Comparisons between T_P of *G. koira* sampled in limestone and sandstone locations did not support the hypothesis that the low T_P of this species was a consequence of inhabiting limestone with deep, cooler crevices.

G. moritzi also had notable T_P, selecting for high temperatures that were similar only to the high T_P of other species from Kurundi Station. Kurundi Station experiences strong daily fluctuations in temperatures during the dry season, with hot day and cold night temperatures (Table 1). The higher T_P of species from this site may reflect a tolerance of high daytime temperatures and use of patchy warm microhabitats at night, because small rocks can heat up quickly and retain warmth for relatively long periods of time (Kearney, 2002)..

For other species, T_P showed no notable trends. Nocturnal activity patterns may shield dtellas from exposure to diurnal temperature extremes, but they would nevertheless experience daily and seasonal thermal fluctuations. Access to thermal refugia can allow nocturnal reptiles to thermoregulate (Kearney & Predavec, 2000; Nordberg & Schwarzkopf, 2019). Even though thermal conditions were found to be similar within, and different across, our sampling locations, it is unlikely that temperatures would be homogenous throughout the environment at any given time. This may allow dtellas to behaviourally maintain temperatures close to T_P through selection of microhabitats with favourable temperatures, a pattern of habitat preference which has been observed in other geckos (Shah et al., 2004).

4.3 Conclusion

Few differences in EWL were identified across *Gehyra* species during the dry season, suggesting dtellas are not specialising their hydric physiology to their local microhabitats or broadscale climates. The lack of specialisation in this trait could be explained by physiological plasticity; it is possible that the capacity to shift EWL in response to immediate local, seasonal conditions (Skelton, 2024) may obviate the need for specialisation related to habitat aridity.

Differences in T_P across species may be driven by local thermal conditions, but there was substantial overlap across species. Crevice conditions dampen extreme temperatures, but at most sites were not otherwise substantially different from external shade conditions. Despite low variability within local thermal climates, the combination of a nocturnal lifestyle and behavioural thermoregulation within crevices may be sufficient to maintain body temperatures close to a similar T_P for most species.

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Electronic supplementary material

Climate Does Not Predict Thermal and Hydric Traits in Northern Australian Geckos

Kade Skelton[1], Craig Moritz[2], Kimberley Day[1], Chava L. Weitzman[1], Christine Schlesinger[1], Michael Kearney[3], Stephen M. Zozaya[2], Keith Christian[1*]

[1]Charles Darwin University, Research Institute for the Environment and Livelihoods, Ellengowan Drive, Brinkin, NT 0810 Australia

[2]Division of Ecology and Evolution, Research School of Biology, and Centre for Biodiversity Analysis, The Australian National University, Building 46, Sullivans Creek Road, Acton, ACT 2601, Australia

[3]School of Biosciences, The University of Melbourne, Parkville, Victoria, Australia

* Corresponding author: Charles Darwin University, Research Institute for the Environment and Livelihoods, Ellengowan Drive, Brinkin, NT 0810 Australia; Keith.Christian@cdu.edu.au

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Figure S1. Species of the three *Gehyra* clades represented in this study, including **(a)** the *G. australis* clade, characterised by large bodies and preferring trees and rock boulder habitats (*G. lapistola*), **(b)** the small-bodied *G. nana* clade which inhabits various rocky environments (*G. nana*), and **(c)** the arid radiation of *Gehyra* (*G. minuta*). Photography source: Stephen Zozaya, used with permission.

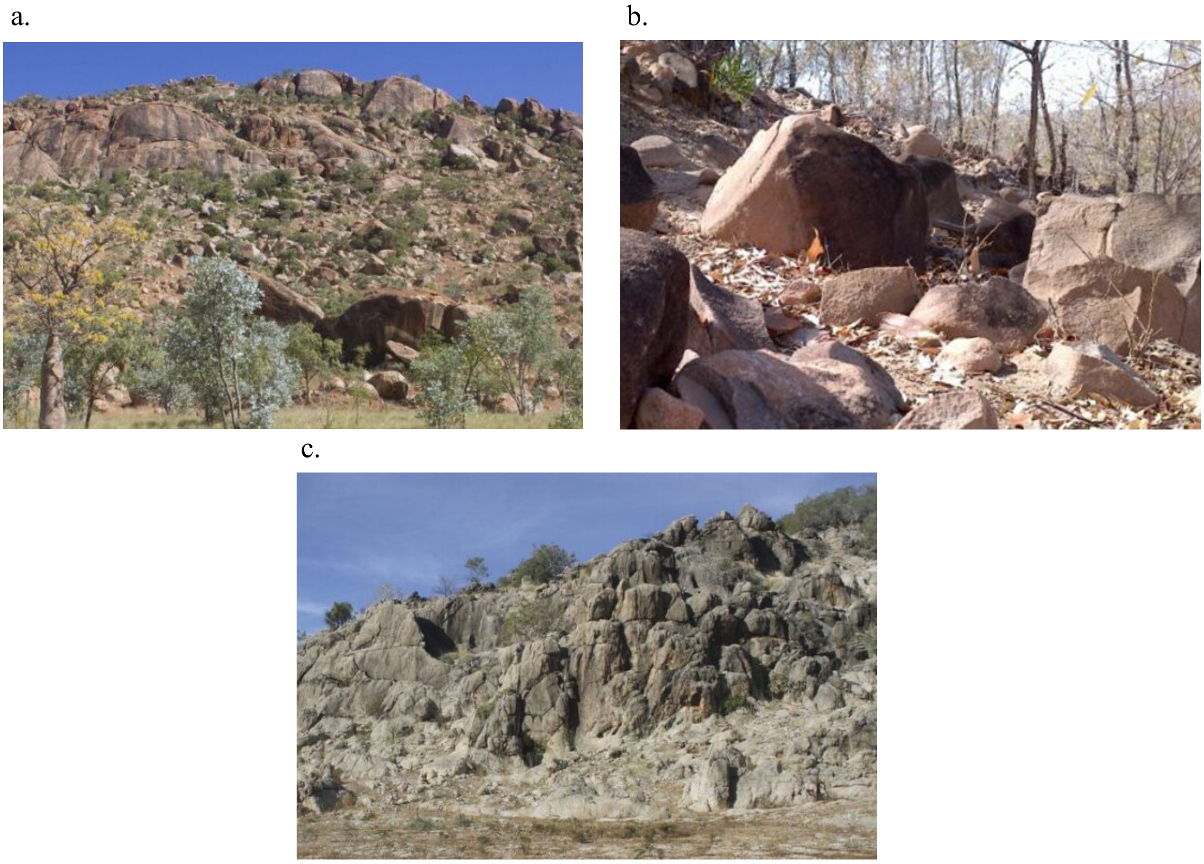

Figure S2. Habitat terrain types of rock-dwelling north Australian *Gehyra*, including **(a)** granite boulders, cliffs (Mt. Nyulasy), **(b)** small, fractured basalt ground rocks (Kidman Springs) and **(c)** limestone outcrops (Gogo Station).

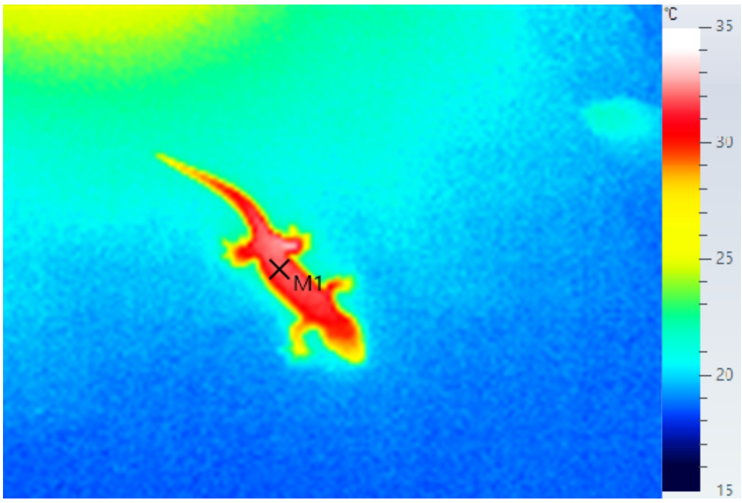

Figure S3. Thermal image of a *Gehyra* showing the temperature sampling site in the lower abdominal region (M1) and the corresponding temperature scale as displayed in the Testo IRSoft thermal imaging software (v4.8) interface. Image taken using a Testo 868 thermal imaging camera (0.08°C thermal sensitivity).

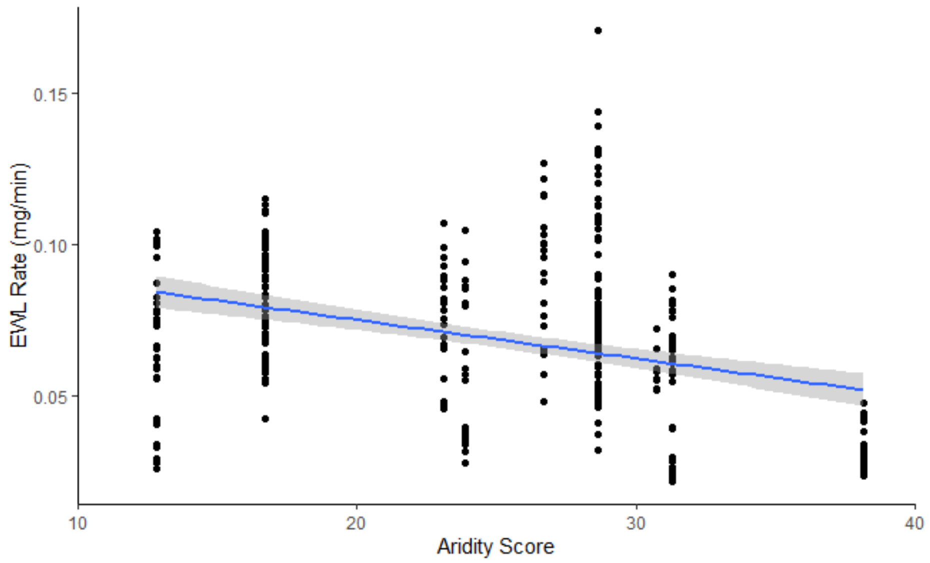

Figure S4. Evaporative water loss (EWL) rates of *Gehyra* species compared to aridity. Aridity score is determined through environmental modelling and is representative of the relative aridity of sampling locations. There was no significant correlation between EWL and aridity when accounting for surface area.

Table S1. Cutaneous resistance values for *Gehyra* species sampled from Western Australia and the Northern Territory in May–June or *September.

Species	Cutaneous Resistance (s/cm)	
	Mean	Standard Deviation
G. australis	990	390
G. calcitectus	1789	1674
G. cf occidentalis	1781	1371

G. chimera	1144	424
G. gemina	1412	458
G. girloorloo	2635	1698
G. ipsa	1377	506
G. kimberleyi	2245	1734
G. koira	1312	658
G. lapistola	2107	1927
*G. minuta**	1280	778
*G. moritzi**	1616	664
G. nana	1704	1398
G. occidentalis	1278	730
G. paranana	1096	305
G. pseudopunctata	1604	886
*G. purpurascens**	1737	592
G. xenopus	1675	926

Table S2. Mean temperature (°C) and absolute humidity (g/m^3) readings from environmental data loggers deployed in crevices and shaded open-air locations across Western Australia and Northern Territory sites.

Location	Measure (Means)		Mean Value	
			Crevice	Open
Buchannan Limestone	*temperature*	*minimum*	28.2	28.4
		mean	30.0	33.0
		maximum	32.2	38.0
		range	4.0	9.6
	absolute humidity	*minimum*	12.1	7.6
		mean	15.7	14.1
		maximum	20.7	25.0
		range	8.6	17.4
Gogo Station	*temperature*	*minimum*	30.7	24.9
		mean	32.7	31.6
		maximum	34.6	38.6
		range	3.9	13.7

	absolute humidity	*minimum*	8.4	5.2
		mean	11.9	11.8
		maximum	16.7	25.5
		range	8.4	20.3
Kidman Springs*	*temperature*	*minimum*	28.1	28.4
		mean	33.5	33.0
		maximum	40.2	38.0
		range	12.1	9.6
	absolute humidity	*minimum*	10.2	7.6
		mean	16.9	14.1
		maximum	29.2	25.0
		range	19.0	17.4
Litchfield	*temperature*	*minimum*	27.1	25.6
		mean	29.2	28.4
		maximum	31.6	32.7
		range	4.5	7.1
	absolute humidity	*minimum*	12.2	12.8
		mean	17.8	19.6
		maximum	24.4	29.3
		range	12.1	16.5

* Open-air values for Kidman Springs were sourced from Buchannan Limestone loggers

Table S3. Post hoc comparisons of mean temperature (°C) and absolute humidity (g/m^3) readings of crevices across Western Australia and Northern Territory locations. * marks a significant difference ($p < 0.05$) between locations. In order per site: blue = mean minimums, black = grand means, red = mean maximums, and green = range.

Mean Values	**Silent Grove**		**Litchfield**		**Kidman Springs**		**Buchannan Limestone**		**Gogo Station**	
	temp	*humidity*	*temp*	*humidity*	*temp*	*humidity*	*temp*	*humidity*	*temp*	*humidity*
Gogo Station				*					30.7	8.4
			*	*		*		*	**32.7**	**11.9**
				*		*			34.6	16.7
					*				3.9	8.4
Buchannan Limestone							28.2	12.1		
				*			**30.0**	**15.7**		
					*	*	32.2	20.7		
					*		4.0	8.6		
Kidman Springs					28.1	10.2				
			*	*	**33.5**	**16.9**				
	*		*		40.2	29.2				
			*		12.1	19.0				
Litchfield			27.1	12.2						
		*	**29.2**	**17.8**						
			31.6	24.4						
			4.5	12.1						
Silent Grove	28.7	12.3								
	29.1	**14.9**								
	29.5	17.9								
	0.9	5.6								