Thermal physiology of Tropical House Geckos (*Hemidactylus mabouia*) in a cool temperate region of South Africa.

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**ABSTRACT**

Temperature profoundly influences the functioning of ectotherms and understanding the thermal biology of invasive species affords valuable insights regarding the suitability of different habitats. Yet, this remains an understudied aspect in the field of invasion biology. Here, we investigated the thermal physiology of the highly invasive Tropical House Gecko (*Hemidactylus mabouia*) in a coastal region of South Africa. The study site is near to the southernmost extent of the species’ distribution and we expected the physiology of individuals at the study site to differ compared to that of individuals inhabiting tropical regions. Relative to tropical geckos, we observed a decrease of 3.4°C in preferred body temperature (T\textsubscript{pref}) to 24.0 °C, which was likely driven by selection for improved functioning within the cooler temperate climate. However, the lower (CT\textsubscript{min}) and upper (CT\textsubscript{max}) critical thermal limits were higher in geckos at the study site. CT\textsubscript{min} was similar between sexes at 11.9 °C, whereas males had a higher CT\textsubscript{max} by ≈1.9 °C reaching 39.7 °C. A broader tolerance range is typical of a highly variable climate, and we presume that the increase in CT\textsubscript{max} allows geckos to better cope with occasional high temperatures. Further, sex-specific differences are uncommon in reptiles, but our study supports claims of improved heat tolerance in male geckos, argued to be related to their aggressive and territorial behaviour. The results also support claims that tropical geckos are more adaptable than previously thought, allowing them to invade new areas. Thereafter, their aggressive behaviour, dietary flexibility and year-round activity likely provides house geckos with a competitive advantage over some native reptiles.

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**Introduction**

Reptiles have a limited capacity for sustained endogenous heat production, coupled with a poor level of insulation to retain any heat produced (Taylor et al. 2021). Therefore, they rely on the thermal heterogeneity within their habitat to thermoregulate behaviourally to maintain operative body temperatures (Kearney and Predavec 2000; Sauer et al. 2016). As with all ectotherms, temperature has a biphasic relationship with organismal functioning in reptiles. For example, they display increased rates in performance (e.g. metabolic rate,
locomotion and digestion) that is positively correlated with temperature until an optimal point, after which further increases in temperature is associated with decreased performance (Huey et al. 2012; Tattersall et al. 2012). Further, the lower (CT<sub>min</sub>) and upper (CT<sub>max</sub>) limits of performance are not symmetrically distributed around the optimal temperature, with a rapid reduction in performance as temperature increases beyond the optimal point. This is of concern as climate change is causing the rapid warming of environmental temperatures to such an extent that the CT<sub>max</sub> of many reptiles is being approached or exceeded (Hoffmann et al. 2013; Dayananda et al. 2021), as seen in several forest dwelling (Diele-Viegas et al. 2018) or desert dwelling (Kirchhof et al. 2017) lizards. However, this is not to say that climate change will be detrimental for all ectotherms (Araújo et al. 2006). Some ectotherms will likely benefit from the warming environmental temperatures as climate change continues because they may currently be experiencing suboptimal temperatures in their respective habitats (Deutsch et al. 2008; Huey et al. 2012). Therefore, the warmer conditions may lead to the displacement of cooler adapted species by their warm adapted counterparts (Araújo et al. 2006). Such displacements are likely to occur on a large spatial scale due to shifting geographic distributions in response to climate change (Dayananda et al. 2021), and range expansions into novel habitats could yield unpredictable changes on a temporal scale and also may change activity patterns (Doody et al. 2019). This would have major implications for the field of invasion biology. For instance, members of the genus Hemidactylus have successfully invaded cooler regions despite their warm tropical origin (Carranza and Arnold 2006; Agarwal et al. 2021). These and other invaders would presumably expand their ranges into colder, currently unsuitable regions, as temperatures continue to warm, potentially causing devastating ecological impacts (Kraus 2015).

In this study, we focused on the nocturnal Tropical House Gecko, also known as the African House Gecko (Hemidactylus mabouia), one of two highly invasive Hemidactylus species. This species is thought to have originated in the Miocene in Zambezia and is native to Central and East Africa (Agarwal et al. 2021) and possibly Madagascar (Carranza and Arnold 2006). It is widely considered to be one of the most invasive reptile species globally, having invaded several of the world’s landmasses, including West Africa, the Caribbean, South and Central America and southern North America. This species commonly associates with humans and their dwellings (Carranza and Arnold 2006), with genetic evidence suggesting that humans served as a significant vector for the dispersal of this species, facilitating its rapid global colonisation (Agarwal et al. 2021). Certainly, H. mabouia (and many other reptile species) benefit from their association with human dwellings as insulated buildings and artificial light sources provide them with various microclimates. The light sources also provide improved feeding opportunities due to insects congregating around them. However, the occurrence of house geckos in high densities in natural areas within invaded regions suggests a high level of adaptability allowing it to establish itself (Rödder et al. 2008).

One of the key factors contributing to the survival of house geckos is their dietary flexibility. When available, they can exploit many human derived non-insect foods such as bread, rice, and pet food (Weterings and Weterings 2019) but there is also evidence of house geckos preying on vertebrates and feeding on other, often native, reptiles (Lamb et al. 2020; Maritz and Maritz 2020). This opportunistic feeding behaviour is however only one aspect contributing to their durability. The other key factor is related
to their physiological tolerance as the successful establishment of house geckos in natural land would require some degree of physiological flexibility to cope with environmental conditions outside of their native range. Thus, studying physiological limits such as thermal tolerance ranges provide valuable insights regarding the suitability of areas for species to inhabit, especially within the context of invasion biology (Rödder et al. 2008; Garner et al. 2020; Lapwong et al. 2020, 2021) and climate change (Gilbert and Miles 2017; Kingsolver and Umbanhowar 2018). Similarly, quantifying the preferred body temperature ($T_{\text{pref}}$) of a reptile, which is the body temperature that individuals select in the absence of ecological constraints, also provides valuable physiological insights regarding the thermal suitability of a habitat. For instance, $T_{\text{pref}}$ serves as a good approximation for the optimal temperature for organismal functioning, including aspects such as locomotory performance and digestion (Angilletta et al. 2002; van Berkel and Clusella-Trullas 2018; Lapwong et al. 2020; Bodenstein et al. 2021). This is because $T_{\text{pref}}$ is generally only a few degrees Celsius lower than the optimal temperature (Crowley 1985).

Theoretically, because ectotherms are reliant on exogenous heat sources to regulate body temperature, a variety of preferences and tolerance ranges should have evolved between species or populations inhabiting contrasting environments or those with contrasting activity patterns; but, support for this notion is equivocal (Lapwong et al. 2020; Bodenstein et al. 2021; Lapwong et al. 2021). For example, diurnal Anolis lizards in the Caribbean inhabit areas with starkly different thermal environments, yet they exhibit similar levels of $CT_{\text{max}}$ but different levels of $CT_{\text{min}}$ (Muñoz et al. 2014). The lack of a distinct evolutionary shift in $CT_{\text{max}}$ amongst diurnal species is due to the varied thermoregulatory opportunities available to them. Individuals that are active during the day can exploit the heterogeneous thermal landscape created by sunlit and shady areas to behaviourally thermoregulate to achieve relatively stable operative body temperatures, resulting in evolutionary inertia; a phenomenon referred to as the “Bogert effect” (sensu Bogert 1949). By contrast, the absence of solar radiation at night creates fewer thermoregulatory opportunities (Tan and Schwanz 2015; but see also Kearney and Predavec 2000; Nordberg and Schwarzkopf 2019), leading to variable selection of $CT_{\text{min}}$. Because nocturnal reptiles are active at night, the Bogert effect should not apply and $CT_{\text{max}}$ should be more variable. Yet, studies such as Clusella-Trullas et al. (2011) and Grigg and Buckley (2013) show that there is a high degree of overlap in $CT_{\text{max}}$ as well as $CT_{\text{min}}$ between nocturnal and diurnal reptiles.

Despite the general overlap in thermal biology of reptiles, Asian House Geckos ($H. \text{frenatus}$) are known to exhibit adaptive shifts in their thermal biology between native tropical populations and introduced populations. For example, $H. \text{frenatus}$ invading the warm temperate regions of south-eastern Australia exhibited lower $T_{\text{pref}}$ and $CT_{\text{min}}$ relative to individuals from their native range, presumably to better cope with the lower temperatures at the introduced site (Lapwong et al. 2020, 2021). Therefore, it is reasonable to also expect to find a change in thermal biology in $H. \text{mabouia}$ across a latitudinal gradient to accommodate the climatic variability. Potential differences in thermal biology should be especially evident between populations that have remained in the tropics and those that have invaded colder temperate regions, such as the eastern parts of South Africa, where nightly temperatures often decrease to less than 10 °C. Thus, we asked the following questions: firstly, has there been a shift in the thermal
preference and tolerance range between *H. mabouia* inhabiting different geographic locations? Secondly, if there has been a shift in these variables, how do the observed values compare to that of other closely related species after accounting for phylogenetic relatedness and size? To address these questions, we attempted to describe key markers of thermal physiology in a population of *H. mabouia* occurring on the fringes of an urban area in the City of Gqeberha (previously known as Port Elizabeth) to compare against previously published data. Given the combination of lower mean temperature, especially at night, and higher daily temperature variability, we hypothesised that individuals in our study would display a higher $CT_{max}$, a lower $CT_{min}$ and a lower $T_{pref}$ compared to geckos found in the tropics (Diele-Viegas et al. 2018). Even though the Amazonian population of *H. frenatus* is also invasive (Agarwal et al. 2021), arguably these individuals would still experience conditions that are relatively similar to their native range, likely retaining the ancestral traits due to phylogenetic inertia.

**Methods**

**Animal capture**

Eighteen geckos (nine males and nine non-gravid females) were captured on a plot in Seaview (34°00'39.8" S, 25°29'29.9" E), Gqeberha, during the autumn months of April and May 2021. Once captured, individuals were sexed, weighed and their morphometric measurements recorded. All geckos were housed individually in glass terraria that were lined with a layer of soil (~5 mm) at the base, topped with a scatter of leaves and small branches for climbing and enrichment. Two live small-sized crickets were released into each gecko’s enclosure as forage, but the consumption of crickets was not guaranteed. Geckos were offered food once but provided with fresh water each morning. This was to ensure that they were fasted at the time of determining thermal preferences. The terraria were kept in a well-ventilated outbuilding without any climate control to mimic natural fluctuations in temperature, but 75 W infrared heating lamps were setup to heat a small section of each enclosure during the evenings, creating a heterogenous thermal landscape for thermoregulatory options.

Mean ($\pm$ SE) day and night ambient temperatures at the study site were 19.7 $\pm$ 0.5 °C and 17.9 $\pm$ 0.4 °C respectively. Ambient temperature was recorded using eight iButtons (DS1923-F5, Hygrochron iButtons, Maxim integrated, Dublin, Ireland) affixed to various exterior surfaces where geckos were regularly seen. These data loggers recorded temperature every 10 minutes and we determined the mean daytime temperature as the arithmetic average of all temperatures recorded between 06:00 and 18:00 corresponding to sunrise and sunset times, whereas nightly temperatures were determined as the arithmetic average of all temperatures recorded between 18:00 and 06:00.

**Thermal preference and critical thermal limits**

The critical thermal limits of geckos were determined using righting response behaviour (Lapwong et al. 2021). Geckos were placed in a round glass container and either heated using a 75 W infrared lamp or cooled by placing the container on crushed ice to achieve heat fluxes of approximately 1 °C min$^{-1}$. The distance between the heating lamp and the
container required to achieve the desired rate of heating was estimated during preliminary trials when we measured the rate of heating within the container at different distances away from the heat lamp using a K-type thermocouple (Digital thermometer VC9808+, ACDC Dynamics, Edenvale, Gauteng, South Africa). The container had holes in the lid for ventilation and to prevent any potential pressure buildup during heating. The container was flipped every minute to assess righting response and the cloacal temperature was taken using the afore-mentioned thermocouple when the individual failed to right itself after five seconds.

We determined preferred body temperature ($T_{\text{pref}}$) at least 24 h after capture, using a cost-free thermal gradient. The experimental setup consisted of a 1.5 m long particle board box with a removable mesh lid. The box was heated on one side using a 100 W infrared heating lamp and cooled on the other side using icepacks. A single gecko was placed in the gradient and allowed a 30 min acclimation period before a cloacal temperature reading was recorded. Thereafter, cloacal temperature was recorded every 30 min for two hours. All trials were performed during the evenings between 19:00 and 00:00 and completed within three days after capture.

**Statistical analysis**

A Levene’s test confirmed that the data had equal variances and we used a Shapiro-Wilk’s test to test for normality and log-transformed the dataset where necessary before any comparisons were made. We used simple t-tests to test for size differences (mass and snout-vent length) between males and females. We also tested whether physiological variables scaled with size using a simple regression analysis and following the positive scaling in one of the variables with body mass (see results), we included body mass as a covariate when testing for sex-specific differences in thermal physiology. Therefore, we used an analysis of covariance (ANCOVA) to compare $CT_{\text{max}}$, $CT_{\text{min}}$ and $T_{\text{pref}}$ between males and females. We also pooled the data across sexes to compare to values reported in an Amazonian population (Diele-Viegas et al. 2018) using a one-sample t-test.

To determine whether any observed shift in thermal physiology of the current study population could be due to an evolutionary change or simply the result of phenotypic plasticity, we attempted to place our data within a phylogenetic context. Although the influence of body size is often overlooked in studies of critical thermal limits, size could be a significant factor (Claunch et al. 2021). As such, we decided to perform a phylogenetic generalised least squares (PGLS) regression analysis to determine if the results of our study deviated significantly from what can be expected based on size while accounting for the influence of phylogenetic relatedness. Firstly, to compile our dataset we extracted from the GlobTherm database (https://doi.org/10.5061/dryad.1cv08) data for all individuals from Order Squamata that had available both the upper and lower critical thermal limits; yielding a total of 163 candidate species. Thereafter, we reviewed the original sources and performed literature searches using Google Scholar and ISI Web of Science to obtain information on body mass and thermal preference (or selected temperature) of each species. Unfortunately, a large number of studies did not report concurrent measurements of body mass and thermal preference or reported only a mass range. All candidates for which we could not obtain a complete dataset of information
(concurrent measurements of body mass, $\text{CT}_{\text{max}}$, $\text{CT}_{\text{min}}$ and $\text{T}_{\text{pref}}$) were excluded. The final dataset included only 31 species from families most closely related to the study species, of which 18 were from Scincidae, 6 were from Gekkota (including data from the current study), 4 were from Lacertoidae and 3 from Iguania (Supplementary Table 1).

Once the dataset was compiled, we generated a phylogenetic tree using the species-level squamate phylogeny of Tonini et al. (2016) obtained from the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.db005). The original phylogeny containing over 9000 species was pruned to include only the species we used using the R package “ape” (Paradis et al. 2004). We then tested for evidence of phylogenetic signal using Blomberg et al.’s (Blomberg et al. 2003) $K$-statistic and $p$-values using the R package “picante” (Kembel et al. 2010), where $k$-values less than one indicates that closely related species resemble each other less than expected under a Brownian motion evolutionary model. $K$-values greater than one were taken to indicate that closely related species resemble each other more than expected. Thereafter, we conducted a PGLS analysis using the R package “caper” (Orme et al. 2013). All statistical procedures were performed using R version 3.6.1. (R Core Team 2019), and the data are presented as mean ± standard error, unless stated otherwise.

**Results**

Males ($6.7 \pm 0.6$ g) were significantly heavier than females ($4.6 \pm 0.4$ g; $t_{\text{stat}} = 2.77, df = 16, p = 0.014$) but there was no difference in snout-vent length between sexes ($\delta$: $64 \pm 2$ mm vs $\varphi$: $60 \pm 3$ mm; $t_{\text{stat}} = -1.16, df = 16, p = 0.131$). There was a significant relationship between body mass and $\text{CT}_{\text{max}}$ ($F_{(1,17)} = 4.98, p = 0.040$), but not between body mass and $\text{CT}_{\text{min}}$ ($F_{(1,17)} = 0.69, p = 0.419$) or body mass and $\text{T}_{\text{pref}}$ ($F_{(1,17)} = 0.04, p = 0.851$). Although there was a significant relationship between body mass and $\text{CT}_{\text{max}}$ ($F_{(1,17)} = 0.18, p = 0.674, \text{CT}_{\text{min}}: F_{(1,17)} = 0.76, p = 0.40, \text{T}_{\text{pref}}: F_{(1,17)} = 2.57, p = 0.129$). Accounting for the potential effect of mass, males had a significantly higher $\text{CT}_{\text{max}}$ compared to females ($\delta$: $39.7 \pm 0.3$ °C vs $\varphi$: $37.8 \pm 0.5$ °C; $F_{(1,15)} = 4.88, p = 0.043$), but there was no sex-specific differences in $\text{CT}_{\text{min}}$ ($\delta$: $12.1 \pm 0.4$ °C vs $\varphi$: $11.8 \pm 0.4$ °C; $F_{(1,15)} = 1.55, p = 0.232$) or in $\text{T}_{\text{pref}}$ ($\delta$: $23.4 \pm 1.0$ °C vs $\varphi$: $24.7 \pm 1.1$ °C; $F_{(1,15)} = 1.29, p = 0.274$) (Figure 1).

The $\text{CT}_{\text{max}}$ of the study population was significantly higher than that of the Amazonian population ($\text{CT}_{\text{max}} = 36.1$ °C), irrespective of whether the data were compared using males only ($t_{\text{stat}} = 12.355, df = 8, p < 0.001$), females only ($t_{\text{stat}} = 3.398, df = 8, p = 0.009$) or pooled across sexes ($\text{CT}_{\text{max}} = 38.7$ °C; $t_{\text{stat}} = 7.288, df = 17, p < 0.001$). Similarly, the $\text{CT}_{\text{min}}$ ($= 11.9$ °C) of the study population was significantly higher than that of the Amazonian population ($\text{CT}_{\text{min}} = 10.6$ °C; $t_{\text{stat}} = 4.371, df = 17, p < 0.001$), whereas $\text{T}_{\text{pref}}$ ($= 24.0$ °C) of the study population was significantly lower than that of the Amazonian population ($\text{T}_{\text{pref}} = 27.4$; $t_{\text{stat}} = -4.246, df = 17, p < 0.001$).

A phylogenetic signal was detected in the dataset for $\text{CT}_{\text{max}}$ ($k = 0.49, p = 0.004$), $\text{CT}_{\text{min}}$ ($k = 0.38, p = 0.021$) and $\text{T}_{\text{pref}}$ ($k = 0.40, p = 0.012$). However, the PGLS regression analysis showed that there was no relationship between body mass and any of the thermal physiological variables among the 31 species analysed (Table 1, Figure 2) and the large scatter in the dataset prevented further phylogenetic comparison.
Discussion

Although the thermal suitability of an area may not be the main factor governing the success of an invading species, invaders cannot survive in an area that does not have a high overlap between the environmental conditions experienced and their tolerable temperatures. We hypothesised that individuals in our study would have higher $CT_{\text{max}}$ and lower $CT_{\text{min}}$ compared to their tropical counterparts, to accommodate the cooler temperate

Table 1. Regression statistics of the phylogenetic generalised least squares (PGLS) regression analyses describing the relationship between body mass and thermal physiological variables for 31 squamate species. Critical thermal maximum = $CT_{\text{max}}$, critical thermal minimum = $CT_{\text{min}}$, and preferred body temperature = $T_{\text{pref}}$

| Variable | Value  | SE   | $t$ statistic | $p$-value |
|----------|--------|------|---------------|-----------|
| $CT_{\text{max}}$ | Intercept | 40.87 | 1.59 | 25.66 | 0.000 |
| | Slope | 0.06 | 0.04 | 1.48 | 0.151 |
| $CT_{\text{min}}$ | Intercept | 7.45 | 2.05 | 3.64 | 0.001 |
| | Slope | 0.03 | 0.05 | 0.53 | 0.603 |
| $T_{\text{pref}}$ | Intercept | 31.06 | 2.91 | 10.67 | 0.000 |
| | Slope | -0.01 | 0.07 | -0.12 | 0.904 |

Figure 1. Critical thermal limits and preferred body temperature in *Hemidactylus mabouia* from the temperate region of Gqeberha (formerly Port Elizabeth), South Africa. The horizontal line in each box plot is the median value, the boxes define the 25th–75th percentiles, the whiskers define 10th–90th percentiles and black circles represent values beyond those percentiles ($N = 9$ per sex and significant differences are indicated above the plots)
climate. By comparison to individuals from the Amazon (Diele-Viegas et al. 2018), where environmental conditions would have been similar to their native range, the results supported the former but not the latter hypothesis. Relative to the Amazonian population, *H. mabouia* in the current study displayed a CT_{min} that was 1.3 °C higher on average and CT_{max} in females and males was 1.7 °C and 3.6 °C higher on average, respectively. Despite the increase in CT_{min}, the overall observation aligns with the generalisation that reptiles inhabiting environments with high temperature variability usually exhibit broader tolerance ranges, representative of a more generalist thermal strategy (Cameron et al. 2018). We also hypothesised that individuals in our study would have a lower T_{pref} than individuals from the Amazonian population. This was based on the link between T_{pref} and performance. Indeed, nocturnal reptiles do show adaptive responses to cooler climates by increasing performance at lower temperatures (Cowles and Boger 1944; Autumn

Figure 2. Scatterplots of thermal physiological variables versus body mass for 31 squamate species. (a) Scatterplot of the upper critical limits, (b) scatterplot of the lower critical limit, and (c) scatterplot of the preferred body temperatures. Open circles represent diurnal species, black circles represent nocturnal species and grey circles represent cathemeral species.
et al. 1994), and the results supported the hypothesis. The preferred body temperature in *H. mabouia* in our study was, on average, 3.4 °C lower than the Amazonian population.

It should be noted that two of the three observations made in our study contradicts the observations made by Clusella-Trullas et al. (2011). The aforementioned study found that CT_{min} was positively related to the mean temperatures experienced, while T_{pref} was more closely related to precipitation, and decreased as precipitation increased. In general, tropical regions are warmer and wetter than temperate regions, and in the context of our study, the difference in precipitation would have been exacerbated during the past few decades as South Africa has faced multiple droughts. The Eastern Cape region of South Africa is currently facing an ongoing drought since 2015 (Mahlalela et al. 2020). Thus, if precipitation was the dominant driver of T_{pref} in *H. mabouia* it should have been detected in our study. The discrepancies between our study and that of Clusella-Trullas et al. (2011) reinforces the idea that T_{pref} and CT_{min} are labile, whereas CT_{max} is less so (Araújo et al. 2013; Grigg and Buckley 2013; Muñoz et al. 2014); a phenomenon observed even at an individual-level during the course of its lifetime (Dominguez-Guerrero et al. 2021).

The interpretation of the data presented above hinges on two major assumptions. The first is that the methodology used yielded comparable data and secondly that the comparison was made using the same species. With regards to the first assumption, the details provided for the temperature sensing equipment used by Diele-Viegas et al. (2018) is very limited. We therefore cannot rule out that methodological differences may have biased our comparison. As for the second assumption, it could be argued that the individuals in the current study and those in the study by Diele-Viegas et al. (2018) are not the same. Certainly, *H. mabouia* represents a species complex that could include 20 species-level lineages, with South African hosting at least three genetically distinct populations (Agarwal et al. 2021). If they are not the same species, the interpretation of the results would change from one of high adaptability in an Asian species facilitating large-scale invasion to, independently derived traits with individuals in our study possibly inheriting their traits from an ancestor that may have been indigenous to southern African. In support of our view, we argue that even though specimens from our study site or that of Diele-Viegas et al. (2018)’s were not included in the phylogenetic analyses of Agarwal et al. (2021), based on where they collected specimens, the comparison we make here likely involved what Agarwal et al. (2021) referred to as *H. mabouia sensu stricto*. At a minimum, the distribution map presented as Figure 1 in Agarwal et al. (2021) confirms the presence of *H. mabouia ss* within the Eastern Cape province. The corresponding collection site is approximately 400 km away from our study site, connected by a major national roadway. Other sample localities within South Africa that house genetically distinct populations are much further away. Nevertheless, it is necessary for future studies to validate our assumptions.

Given the uncertainty discussed above, our study cannot strictly address whether the changes in thermal physiology are representative of true evolutionary changes in response to the conditions at lower latitudes. However, there is evidence of tropical reptiles being adaptive to new conditions (Leal and Gunderson 2012; Lapwong et al. 2020, 2021). For example, Leal and Gunderson (2012) argued that the Crested Anole (*Anolis cristatellus*), a diurnal species native to Puerto Rico, evolved an improved cold tolerance within approximately 35 generations after invading Miami in response to the generally lower temperatures experienced at the latter site. Therefore, in future, once more is known about the
origin of *H. mabouia* in South Africa, it would be possible to revisit the current study to state whether a similar evolutionary process has occurred in the study population.

The current study also highlights a difference in CT_{max} between male and female *H. mabouia*. Sex-specific differences in thermal biology among reptiles tend to be rare and the differences are often very small (Huey and Pianka 2007), so it remains a largely overlooked aspect. An argument could be made that males were larger than females, therefore they benefited from a higher level of thermal inertia, which may lead to a larger thermal gradient between cloacal temperature and brain temperature (Claunch et al. 2021). This argument is supported by the relationship we observed between CT_{max} and body mass. As a counter argument, we offer that if size alone was the determining factor, we should have also seen a sex-specific difference in CT_{min} as males would still have benefited from a higher level of thermal inertia, resulting in the opposite effect whereby cloacal temperatures should have been lower in males. Furthermore, the interspecific analyses found no relationship between mass and the thermal variables studied. While it is true that larger-bodied individuals have slower rates of heat exchange, the results suggest that the effect was negligible for the 31 squamates (all < 60 g) included in the analyses. Thus, our observation seems to support previous reports of sex-specific differences in the closely related species *H. frenatus* (Cameron et al. 2018).

Male *H. frenatus* had a broader thermal activity range, greater bite force and faster sprint speeds compared to females. The explanation provided by the authors for the disparity between sexes was that males are more aggressive and often engage in combat for territory, protection, and mate acquisition so they gain an advantage for maintaining activity over a large range of temperatures (Cameron et al. 2018). On the other hand, females may be restricted by physiological requirements related to the temperature sensitivity of development and ovipositing (Cameron et al. 2018). The same argument can be presented to explain the results of the current study. Furthermore, given that previous studies on sex-specific differences in thermal biology focused on diurnal species, it is possible that sex-specific differences may be more common among nocturnal species. Thus, we encourage future research on the topic, especially in other nocturnal species or species where males display aggression and territorial behaviour.

Overall, the current study supports the argument that the thermal physiology of invasive house geckos varies latitudinally, allowing them to survive in areas outside of their native land and affording them the opportunity to compete with local species. Physiological flexibility is certainly a major contributor to the global invasion by house geckos (Romero-Báez et al. 2020), but local reptile species are likely to be better suited to their native environment (Garner et al. 2020). Thus, once house geckos reach suitable habitat, their successful establishment is ultimately due to a combination of physiological and dietary flexibility (Weterings and Weterings 2019), their aggressive behaviour (Lamb et al. 2020; Agarwal et al. 2021) and their tendency to remain reproductively active throughout the year (Anjos and Rocha 2008). Together, these mechanisms provide them with a competitive edge, often displacing and forcing local species into suboptimal habitats.

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