THERMAL PHYSIOLOGY OF THE INVASIVE TROPICAL HOUSE GECKO, Hemidactylus maboula (Squamata, Gekkonidae)

JULIANA LUZETE^{1,2}, LORENA O. PINHO¹, ISABELA F. OLIVEIRA¹, AND JULIA KLACZKO^{1,3,4}

¹Laboratory of Comparative Vertebrate Anatomy, Department of Physiological Sciences, Institute of Biological Sciences, University of Brasilia, Brasilia, DF, 70910-900, Brazil

2Laboratory of Evolution and Integrative Biology, Department of Biology, Faculty of Philosophy,

Science and Letters of Ribeirão Preto, University of São Paulo, Ribeirão Preto, SP, 14040-900, Brazil

3Department of Life Sciences, Natural History Museum, London SW7 5BD, UK

4*Corresponding author, e-mail: jklaczko@unb.br*

Abstract.—Thermal physiological traits are ecologically important to ectotherms and seem to be under natural selection in lizards. Therefore, thermal physiology studies are particularly helpful in understanding biological invasions and may provide insights into what makes an invader successful and distribution patterns. Among invasive vertebrates, the Tropical House Gecko (*Hemidactylus mabouia*) is noticeable for being an extremely successful invader that colonized a wide range of habitats with different climatic conditions. We described the $T_{pref'}$ CT_{min}, CT_{max}, and thermal tolerance of an urban population of *H. mabouia* in the Cerrado savanna region of Brazil and tested for differences between sexes and ontogenetic stages. Juvenile *H. mabouia* exhibited higher CT_{min}, lower CT_{max}, and a narrower thermal tolerance range than adults. This result could be explained by the effects of body size in the thermoregulation capacity or related with differences in microhabitat usage. We also tested two methods to measure body temperature: a thermocouple sensor inserted in the cloaca versus in the abdomen surface. Our study provides new information regarding the thermal physiology of *H. mabouia* and a detailed methodology for handling these geckos in the laboratory and measuring thermal physiology traits, which will be useful for future studies in this species.

Key Words.—ecophysiology; exotic; lizard; non-native; reptile; thermoregulation

INTRODUCTION

Temperature is one of the major factors affecting the physiology of living organisms and is consequently related to fitness (Brown et al. 2004; Angilletta 2009). Ectotherms are especially susceptible to environmental temperature because they depend on external heat sources to regulate body temperature (Tb; Vitt and Caldwell 2013). Lizards, well-known vertebrate ectotherms, are active only in a narrow temperature range, in which their performance is optimized (Angilletta 2009; Huey et al. 2010). They coordinate behavioral (e.g., microhabitat choice, posture, and panting) and physiological (e.g., evaporative water loss and cardiovascular alterations) mechanisms to thermoregulate and maintain body temperatures inside their active range (Seebacher and Franklin 2005; Vitt and Caldwell 2013). Thermoregulation can be studied through thermal physiological traits such as preferred (T_{pref}), critical thermal minimum (CT_{min}), and critical thermal maximum (CT_{max}) temperatures (Angilletta 2009; Vitt and Caldwell 2013). These traits are ecologically important because they are related to performance in different physiological processes

directly related to the fitness of an organism (Dawson 1975). In addition, studies have shown that thermal physiological traits of some species are under natural selection (e.g., Gilbert and Miles 2017).

Understanding the ecophysiology of an organism helps better comprehend species distribution patterns, life-history traits, and allows researchers to predict the impacts of environmental changes on the persistence and spread of a population (Rato and Carretero 2015). For example, during the colonization of novel habitats, climate matching between origin and introduction sites dramatically increases the likelihood of establishment success of non-native species (Bomford et al. 2009). Non-native populations facing environmental conditions different from that to which it is adapted often experience physiological or behavioral changes, enabling their spread beyond the ancestral predicted range (e.g., Leal and Gunderson 2012: Kolbe et al. 2014: Lapwong et al. 2020, 2021). Thus, ecophysiology studies are critical to understanding biological invasions. Specifically, due to the importance of temperature regimes, understanding the thermal biology of exotic lizards may help elucidate invasion processes and patterns (Kelley 2014). Moreover, as invaders can drive native species to extinction and disturb the whole ecosystem (Lockwood et al. 2013), the study of invasive species is indispensable to biodiversity conservation.

Among invasive lizards, the Tropical House Gecko (Hemidactvlus mabouia) has the highest establishment success rate (Bomford et al. 2009) and is one of the most broadly distributed and prevalent species globally (Kluge 1969; Powell et al. 1998; Agarwal et al. 2021). Hemidactylus mabouia is native to sub-Saharan Africa and is invasive from South America through North America, where it has become established in areas with climatic conditions different from its native distribution range and with seemingly low suitability (Agarwal et al. 2021). Usually, this species invades human environments; however, it also colonizes natural habitats (Kluge 1969; Powell et al. 1998; Rocha et al. 2011). Studies have shown that H. mabouia can cause the complete displacement of resident species from urban habitats via competition and predation in less than a decade, posing a risk to native geckos (Short and Petren 2012; Hughes et al. 2015; Lamb et al. 2021). Despite its abundance in various countries and ecological importance, there is still a lack of knowledge about the thermal physiology of H. mabouia. Hypotheses that explain the success of H. mabouia invoke thermoregulation as a critical aspect in its invasion process (Agarwal et al. 2021), reinforcing the need for thermal physiology studies in the species. In an attempt to better determine the thermal biology of Hemidactylus mabouia, the objectives of our study were: (1) to describe T_{pref} , CT_{min} , CT_{max} , and thermal tolerance (i.e., the temperature range in which activity is possible) for an invasive population occupying urban areas in the Cerrado savanna region; (2) to analyze if these traits differ between sexes or ontogenetic stages; and (3) to compare surface temperature measured in the abdomen to internal body temperature measured in the cloaca to obtain Tb measures. These data can help to understand the ability of *H. mabouia* to invade habitats, and provide information for further studies of the thermal physiology of *H. mabouia* in other populations

MATERIAL AND METHODS

Collection and animal handling.—We collected individual *Hemidactylus mabouia* by active search and captured them by hand in urban areas of Distrito Federal, Brazil (-15.7801, -47.9292), between March 2019 and February 2021. The Distrito Federal is localized in a region of Cerrado savanna, characterized by a dry season between May and September, with a mean air temperature of 20° C (range, 13° –25° C) and relative air humidity of 55% (range, 47–66%), and a wet season between October and April, with a mean temperature of 22° C (range, 18° –28° C) and relative humidity of 74% (range, 75–78%; https://clima. inmet.gov.br/GraficosClimatologicos/DF/83377). We captured lizards on outside walls between 1800 and 2300 and then took them to the laboratory at the Institute of Biological Sciences of the University of Brasilia, where we kept them in captivity. We kept the geckos in black plastic containers (44 \times 32 \times 25 cm) covered with thin mesh fabric, with sand and vermiculite as the substrate, and bricks as refuges. We kept a maximum of five animals per container, but never more than one male in a group. We humidified terrariums daily and used heating plates suitable for reptile care to keep the ideal temperature for lizards, around 32° C (LLL Reptile and Supply Co., Inc. 2021. House Gecko. Available from https://www.lllreptile.com/articles/25-house-gecko/ [Accessed 7 May 2021]). The room temperature ranged between 22°-30° C and was naturally illuminated, following a natural photoperiod cycle. We fed geckos everyday with live Cockroaches (Nauphoeta cinerea), Mealworms (Tenebrio molitor), or Peanut Beetle (Palembus dermestoides) larvae to which we added calcium, phosphorus, and vitamin D supplements. All individuals had water at their disposal.

Experimental procedure.—We described the thermal physiology of 91 H. mabouia of both sexes and including juveniles and adults, using four measurements: T_{pref} , CT_{min} , CT_{max} , and thermal tolerance (Table 1). We kept lizards in captivity for at least one week before performing experimental procedures (Taylor et al. 2020). Before experimental procedures, we weighed lizards on a precision balance and measured their body temperature at ambient conditions. We performed all experiments at night (i.e., after 1800) during the activity period of H. mabouia (Howard et al. 2001; Albuquerque et al. 2013). We used a thermocouple Tp-01 type K sensor connected to a digital thermometer to measure all body temperatures. We only fixed the sensor to the abdomen of the lizard with micropore surgical tape when measuring the temperature. We tried to minimize handling time as much as possible to not influence the body temperature of the animal. We did not measure cloacal temperature of small juveniles because the sensor was too big. Also, we positioned the thermocouple sensor only at the moment of measurement because the skin of this gecko is fragile and maintaining the sensor fixed during the entire duration of the trial, as commonly done in other species, could hurt them.

To measure T_{prep} we placed lizards individually in glass aquariums with a heating lamp on one end and ice on the other. The dimensions of the aquarium varied between 21.5×44.5 cm and 34×80 cm long, creating a photothermal gradient ranging from 24° -55° C in the smaller and from 16° -55° C in the larger. We kept the lizard in the thermal gradient for 2 h and measured its body temperature every 20 min. We used the first 20

min for the acclimatization of lizards to the thermal gradient, which resulted in six measurements. Finally, we used the mean of the six measurements to estimate the T_{pref} . We used a photothermal gradient following the previous study method with *H. mabouia* (Diele-Viegas et al. 2018), and because the species is frequently found near artificial lights in urban environments, the lamplight does not drive off the animals (Howard et al. 2001; Hughes et al. 2015).

To obtain the CT_{min}, we placed the lizards in a perforated plastic container positioned inside a foam container cooled with ice. The temperature inside the cool chamber remained nearly constant at approximately 0.2° C during the trials. Next, we turned the animals on their backs, and when they lost their righting response, we measured their body temperature. Loss of righting response is the most used parameter to measure critical thermal limits in reptiles (Taylor et al. 2020). To obtain CT_{max}, we positioned the animal in the perforated plastic container inside a foam container heated with boiling water. The heating chamber temperature was kept around 50° C during the trial, and we also kept lizards inside the container until the loss of the righting response. Each lizard spent between 5-10 min inside the container during CT_{min} and CT_{max} trials, depending on how long it took for them to lose their righting response. We measured CT_{max} 2–4 d after CT_{min} so that animals could recover, and we always chose to measure CT_{min} before CT_{max} because the latter might impair the animals more. Thermal tolerance was measured as the difference between CT_{max} and CT_{min}.

After experimental procedures, we euthanized animals via intraperitoneal injection of lethal doses of Neocaine anesthetic, as suggested by the National Council for Animal Experimentation Control (CONCEA; Conselho Nacional de Controle de Experimentação Animal. 2021. Guia Brasileiro de Produção, Manutenção ou Utilização de Animais para Atividade de Ensino ou Pesquisa Científica. Available from https://www.gov.br/mcti/ptbr/composicao/conselhos/concea/paginas/publicacoeslegislacao-e-guia/guia-brasileiro-de-producaomanutencao-ou-utilizacao-de-animais-para-atividadesde-ensino-ou-pesquisa-cientifica [Accessed 6 October 2022]). We fixed lizards in 10% formalin buffered with sodium chloride (NaCl) for 2-3 d and stored them in a 70% alcohol solution. We determined sex by hemipenis eversion and gonad observation. Specimens with snoutvent length (SVL) over 46 mm were considered adults, following Anjos and Rocha (2008).

Comparison between methodologies.—To analyze if the surface temperature of the body measured with the thermometer placed on the abdomen of the lizard corresponds to internal body temperature measured in the cloaca, we performed CT_{min} and CT_{max} experiments

with 14 adult *H. mabouia*. We performed two trials for each parameter: one with the thermocouple sensor fixed on the abdomen with micropore surgical tape and another with the thermocouple sensor inserted in the cloaca of larger lizards. Each trial was separated by one week to recover the lizards fully. All other experimental conditions were the same as described above.

Data analyses.--We used the statistical software environment R 3.6.3 (R Core Team 2013) and RStudio 1.2.5019 (RStudio Team 2015) for all analyses. In addition, we log-transformed all trait values for all subsequent analyses to assure normality. To assess the effects of mass and sex on the T_{pref}, CT_{min}, CT_{max}, and thermal tolerance, we performed Analyses of CoVariance (ANCOVA) using sex as a factor and mass as a covariate for each trait separately. A few individuals were damaged, and we were not able to include their snout-vent length (SVL) into the analysis, therefore, we chose to use mass as a measure of size because both were highly correlated (r = 0.97, P < 0.001) in geckos for which we had data on mass and SVL. Also, mass is directly related to metabolic rate (Andrews and Pough 1985; Brown et al. 2004) and might influence thermal physiology. Because sex did not affect the traits (Table 2), we performed Analyses of Variance (ANOVA) to test for differences in the T_{pref}, CT_{min}, CT_{max}, and thermal tolerance between adults and juveniles. To compare CT_{min} and CT_{max} measured on the abdomen and in the cloaca, we used paired t-tests.

RESULTS

The mean weight of adult males was 4.26 ± 1.30 (standard deviation) g (range, 2.36–6.53 g), adult females was 3.44 ± 0.84 g (range, 1.66–4.95 g), and juveniles was 0.80 ± 0.48 g (range, 0.25–1.70 g). Mean body temperature of *H. mabouia* in ambient conditions at the laboratory was $28.92^{\circ} \pm 2.88^{\circ}$ C (range, 22.0° – 33.6° C; Table 1). The lowest value of CT_{min} was 10.4° C and the highest CT_{max} was 44.8° C. T_{pref}, CT_{min}, and CT_{max} had similar variation breadth (10° – 11° C), but thermal tolerance showed broader variation (Table 1). Only five individuals among 52 had T_{pref} below 30° C, however.

Mass and sex had no significant effect on T_{pref} and CT_{max} when temperature was measured in the abdomen (Table 2; Appendix Fig. 1). T_{pref} did not differ significantly between adults and juveniles (*F*1,50 = 0.055, *P* = 0.815; Fig. 1) but CT_{max} showed a marginally significant difference between stages (*F*1,59 = 3.89, *P* = 0.053; Fig. 1). The CT_{min} and thermal tolerance were not significantly affected by sex but were significantly affected by mass (Table 2; Appendix Fig. 1) and both differed significantly between adults and juveniles

TABLE 1. Mean values of thermal physiological traits for the Tropical House Gecko (*Hemidactylus mabouia*) in an urban population in the Cerrado savanna region of Brazil. Abbreviations are n = number of individuals analyzed, M = males, F = females, J = juveniles, A = adults, SD = standard deviation, T_{pref} = preferred temperature, CT_{min} = critical thermal minimum, CT_{max} = critical thermal maximum.

	Mean ± SD	Range	n		
Trait	(°C)	(°C)	M/F	J/A	
T _{pref}	32.7 ± 2.3	26.8-36.8	21/20	24/28	
CT	15.4 ± 2.9	10.4-22.8	28/33	18/51	
CT _{max}	39.7 ± 2.0	34.1-44.8	27/27	12/49	
Thermal tolerance	24.22 ± 3.7	14.9–29.9	24/24	12/43	

(CT_{min}: $F_{1,67} = 17.56$, P < 0.001; Thermal tolerance: $F_{1,53} = 17.47$, P < 0.001; Fig. 1). Both CT_{min} and CT_{max} measured on the abdomen were significantly higher than cloacal temperatures (CT_{min}: t = 3.198, df = 13, P< 0.010; CT_{max}: t = 2.193, df = 13, P = 0.047; Appendix Fig. 2).

DISCUSSION

We tested whether sexes and ontogenetic stages of Hemidactvlus mabouia differed in thermal physiology to evaluate intrapopulation variation. Our results showed no difference between males and females in any of the analyzed traits. Sexual differentiation in thermal physiology is usually related to temporal or spatial niche segregation between sexes (Paranjpe et al. 2013). Consistent with our results, male and female H. mabouia show no difference in refuge choice or trophic niche, indicating that both use the same microhabitats (Rocha and Anjos 2007; Williams et al. 2016). Studies with other species of Hemidactylus also found no intersexual variation in T_{pref} (Hitchcock and McBrayer 2006; Romero-Báez et al. 2020). Accordingly, Huey and Pianka (2007), in a broad-scale analysis of the thermal biology of desert lizards, suggested that differences between males and females in thermal biology should be rare in lizards.

When comparing the thermal physiological traits between ontogenetic stages, we found that juvenile *H*.



FIGURE 1. Boxplots showing the variation of the four thermal physiological traits analyzed between adult and juvenile Tropical House Geckos (*Hemidactylus mabouia*) in an urban population in the Cerrado savanna region of Brazil. (A) preferred temperature; (B) critical thermal minimum; (C) critical thermal maximum; and (D) thermal tolerance. Lower and upper box limits represent, respectively, first and third quartiles, internal bar the median, internal point the mean, and whisks the minimum and maximal values inside the 99% interval. Ontogenetic stages differ in the critical thermal minimum, critical thermal maximum, and thermal tolerance (* P = 0.05, ** P < 0.01; **** P < 0.001).

mabouia exhibited higher CT_{min} and lower CT_{max} , resulting in a narrower thermal tolerance breadth than adults. The ontogenetic variation in the CT_{min} and thermal tolerance is explained by mass, but not in the CT_{max} . Body size can affect the thermoregulation capacity of lizards by influencing thermal inertia (e.g., Zamora-Camacho et al. 2014; Claunch et al. 2020). Smaller animals have a larger surface area to volume ratio, which increases their cooling and heating rates (e.g., Martín and López 2003; Zamora-Camacho et al. 2014). Accordingly, juvenile *H. mabouia* have a higher water-loss rate than adults (Johnson et al. 2013), which could also protect them from overheating (Tattersall et al. 2006).

It has been reported that juvenile *Hemidactylus mabouia* prefer hotter substrates and are more active earlier in the evening when ambient temperatures were

TABLE 2. *F* and *P* values from ANCOVA testing of the effects of mass and sex on the thermal physiology of the Tropical House Gecko (*Hemidactylus mabouia*) in an urban population in the Cerrado savanna region of Brazil. The abbreviation df = degrees of freedom, T_{pref} = preferred temperature, CT_{min} = critical thermal minimum, CT_{max} = critical thermal maximum.

	Mass		Sez	Sex		Mass:Sex	
Trait	F	Р	F	Р	F	Р	df
T _{pref}	2.71	0.108	3.16	0.083	0.197	0.659	37
CT _{min}	25.4	< 0.001	0.182	0.671	0.009	0.923	56
CT _{max}	2.08	0.155	0.106	0.746	1.07	0.306	50
Thermal tolerance	30.0	< 0.001	< 0.001	0.988	2.53	0.119	44

higher (Howard et al. 2001). The different microhabitats used by adults and juveniles could be related to the CT_{min} differences and a possible mechanism of resource partitioning to reduce competition between adults and juveniles. When comparing the feeding similarity (i.e., number of prey groups) between classes, one study found more similarity between adult males and females compared to either sex and juveniles (Bonfiglio et al. 2006); while another study found more similarity between adult females and juveniles compared to adult males and juveniles (Iturriaga and Marrero 2013). Still, feeding ecology studies show that adults and juveniles do not differ in the overall diet composition and suggest low intraspecific competition (Albuquerque and Anjos 2007; Iturriaga and Marrero 2013). On the other hand, this difference in microhabitat use could be a mechanism for juveniles to avoid aggressive behaviors and predation by adult males (Bonfiglio et al. 2006; Iturriaga and Marrero 2013). Additionally, a third explanation could be that the lower capacity to conserve heat drives a different microhabitat use by juveniles, as seen in other lizard species (e.g., Middendorf and Simon 1988; Vasconcelos et al. 2012). Under this third scenario, the greater sensitivity of juveniles to low temperatures would constrain their activity to earlier in the evening and drive the choice for hotter substrates.

In species exhibiting variation in the critical thermal limits between stages, juveniles usually show narrower thermal tolerance breadth (e.g., Xu and Ji 2006; Tang et al. 2013; Gilbert and Lattanzio 2016). Ontogenetic variations could cause differential survival rates between adults and juveniles in the case of temperature changes, thus, influencing the ability of individuals in a population to respond to climate change (Gilbert and Lattanzio 2016). Furthermore, the higher sensitivity of juveniles to extreme temperatures can drive some populations to local extinction (Diele-Viegas et al. 2019). The invasive Mediterranean House Gecko (H. turcicus), Moorish Gecko (Tarentola mauritanica), and Italian Wall Lizard (Podarcis siculus) also show ontogenetic variation in thermal physiology (Hitchcock and McBrayer 2006; Carretero 2008; Liwanag et al. 2018) and have colonized regions with climatic conditions different from their native habitat (Gomez-Zlatar et al. 2006; Baldo et al. 2008; Kolbe et al. 2013). Therefore, the presence of ontogenetic variation in invasive species suggests that this characteristic does not necessarily have a negative impact on the persistence of populations facing stressful temperatures.

Body size greatly influences the thermal biology of lizards and has important implications for experimental procedures (Camacho and Rusch 2017; Claunch et al. 2020). Some authors argue that differences between internal and surface temperature are negligible in small size lizards because blood flow should equilibrate temperature rapidly throughout the body (e.g., Porter et al. 1973). Our results, however, indicate that this might not be true for all thermal physiological traits or for all species. When comparing critical thermal limits measured in different body parts of *H. mabouia*, we found that temperatures measured in the abdomen surface were higher than internal cloacal temperatures. These results reinforce other studies that highlight the importance of standardized methods in thermal biology so that different works are comparable (e.g., Camacho and Rusch 2017).

In natural environments, H. mabouia occurs primarily in open vegetation areas with a high incidence of solar radiation (Rocha et al. 2011). There are no records of this species invasion in tropical rainforests (i.e., Amazon and Atlantic forests), occurring only in anthropogenically modified places (Vitt et al. 2008; Rocha and Bergallo 2011; Rocha et al. 2011; Telles et al. 2015). It has been suggested that the high humidity of forests imposes thermal restrictions on the nocturnal activity of H. mabouia, hampering their establishment in these areas (Rocha and Bergallo 2011; Rocha et al. 2011; Telles et al. 2015). A study by Diele-Viegas et al. (2018) reported a T_{pref} of 27.4° C, a CT_{min} of 10.6° C, and CT_{max} of 36.1° C for individuals of *H. mabouia* in the Amazon region. Compared with our sample collected in the Cerrado, these lower values in the Amazon region would corroborate the previous hypothesis. Accordingly, many lizards inhabiting areas of dense forests have lower values of thermal physiological traits compared to conspecifics or closely related species from areas of open vegetation due to the cooler environment below the canopy caused by the low incidence of solar radiation (Kohlsdorf and Navas 2006; Pontes-da-Silva et al. 2018; Yuan et al. 2018). Comparisons between our data and the data provided by Diele-Viegas et al. (2018) must be made with caution, however. Although our study and Diele-Viegas et al. (2018) used similar methodologies, the two differ in the type of thermometer used, which may make comparisons unreliable. Further studies comparing different populations of *H. mabouia* will be critical to understanding its current distribution range, predicting future patterns, and evaluating the role of physiological adaptation in its establishment success.

Another possible explanation for the lower establishment success rate of *H. mabouia* in the Amazon rainforest could be its competitive ability against native species. It has been suggested that biotic interactions might be a limiting factor during the colonization process of *H. mabouia* (Agarwal et al. 2021). In the Amazon, *H. mabouia* and the native Turnip-Tailed Gecko (*Thecadactylus rapicauda*) exhibit similar habits and it appears to occur competitive exclusion between the two in urban areas (Vitt and Zani 1997). *Hemidactylus mabouia* and *T. rapicauda* show similar T_{pref} and CT_{max}, but the latter shows a much lower CT_{min} (Diele-Viegas et

al. 2018). Less suitable climatic conditions and a limited capacity of physiological adaptation could cause fitness disadvantages to H. mabouia. Influences of climatic conditions on the competitive ability were described for the Mourning Gecko (Lepidodactvlus lugubris) and the Asian House Gecko (H. frenatus; Case et al. 1994). In the Pacific islands, L. lugubris is displaced from urban areas by H. frenatus, but the former remains the most abundant gecko in forested environments, where H. frenatus cannot invade (Case et al. 1994). The competitive superiority of L. lugubris in forests appears to be related to its thermal physiology better adapted to the cooler and wetter environment, allowing L. lugubris to resist the competitive displacement by H. frenatus (Case et al. 1994). In the Atlantic Forest, H. mabouia competes with Gymnodactylus darwinii (no common name; Texeira 2002); however, there is no information about the T_{nref} or critical thermal limits for the former species. There are no records of competition between H. mabouia and native species in other biomes, but it may compete with other sympatric geckos sharing similar habits and diet, such as Gymnodactylus amarali (no common name; Colli et al. 2003), the Country Leaf-Toed Gecko (Hemidactylus agrius; Passos et al. 2015), and the Brazilian Gecko (Phyllopezus pollicaris; Albuquerque et al. 2013). Thus, future studies comparing the thermal physiology of H. mabouia and native species with whom it may compete will also be important to understand its invasion process.

In the Americas, H. mabouia occurs from southern Paraguay north to southern Texas (Powell et al. 1998; Fierro-Cabo and Rentfro 2014), and its potential distribution encompasses a large portion of the tropical region (Rödder et al. 2008; Agarwal et al. 2021). Cold temperatures appear to be one of the main abiotic factors limiting the dispersal of H. mabouia both beyond and within the tropical region. Our results suggest that low temperatures are probably an important factor limiting juvenile activity. Temperature increases caused by global warming could favor the invasion of H. mabouia in some areas that are currently too cold for its survival (Rödder et al. 2008), transforming H. mabouia into an additional threat to native geckos besides the temperature increase. Our results clarify the urgency of more in-depth studies concerning the thermal physiology of H. mabouia, particularly those evaluating the capacity of adaptation (either through evolutionary genetic change or phenotypic plasticity) of related traits, which will have important implications for the conservation of native species.

Acknowledgments.—We are grateful to Luisa M. Diele-Viegas for comments on the first version of the manuscript. We thank all laboratory colleagues (LACV/ UnB) who helped with fieldwork and animal care. Animal collection and experiments were approved by Chico Mendes Institute for Biodiversity Conservation (ICMBio, n° 0632260220190624) and University of Brasilia Ethics Committee for Animal Use (CEUA-UNB, n° 116/2017), respectively. Funding for this study was provided by Research Support Foundation of the Federal District (FAPDF, n° 0193.001637/2017) and Juliana Luzete was funded by a scholarship from Coordination of Superior Level Staff Improvement (CAPES, n° 88882.384444/2019-01).

LITERATURE CITED

- Agarwal, I., L.M.P. Ceríaco, M. Metallinou, T.R. Jackman, and A.M. Bauer. 2021. How the African House Gecko (*Hemidactylus mabouia*) conquered the world. Proceedings of the Royal Society B: Biological Sciences 8:210749. https://doi.org/10.1098/ rsos.210749.
- Albuquerque, N.R., M.P. Soares, and L.S. Alves. 2013. Diet of two sit-and-wait lizards, *Phyllopezus pollicaris* (Spix, 1825) (Phyllodactylidae) and *Hemidactylus mabouia* (Moreau de Jonnès, 1818) (Gekkonidae) in a perianthropic area of Mato Grosso do Sul, western Brazil. Biota Neotropica 13:376–381.
- Andrews, R.M., and F.H. Pough. 1985. Metabolism of squamate reptiles: allometric and ecological relationships. Physiological Zoology 58:214–231.
- Angilletta, M. 2009. Thermal Adaptation: A Theoretical and Empirical Synthesis. Oxford University Press, New York, New York, USA.
- Anjos, L.A., and C.F.D. Rocha. 2008. Reproductive ecology of the invader species gekkonid lizard *Hemidactylus mabouia* in an area of southeastern Brazil. Iheringia. Série Zoologia 98:205–209.
- Baldo, D., C. Borteiro, F. Brusquetti, J.E. García, and C. Prigioni. 2008. Reptilia, Gekkonidae, *Hemidactylus mabouia*, *Tarentola mauritanica*: distribution extension and anthropogenic dispersal. Check List 4:434–438.
- Bomford, M., F. Kraus, S.C. Barry, and E. Lawrence. 2009. Predicting establishment success for alien reptiles and amphibians: a role for climate matching. Biological Invasions 11:713–724.
- Bonfiglio, F., R.L. Balestrin, and L.H. Cappellari. 2006. Diet of *Hemidactylus mabouia* (Sauria, Gekkonidae) in urban area of Southern Brazil. Biociencias 14:107– 111.
- Brown, J.H., J.F. Gillooly, A.P. Allen, V.M. Savage, and G.B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.
- Camacho, A., and T.W. Rusch. 2017. Methods and pitfalls of measuring thermal preference and tolerance in lizards. Journal of Thermal Biology 68:63–72.
- Carretero, M.A. 2008. Preferred temperatures of *Tarentola mauritanica* in spring. Acta Herpetologica 3:57–64.
- Case, T.J., D.T. Bolger, and K. Petren. 1994. Invasions

and competitive displacement among house geckos in the tropical Pacific. Ecology 75:464–477.

- Claunch, N.M., E. Nix, A.E. Royal, L.P. Burgos, M. Corn, P.M. DuBois, K.N. Ivey, E.C. King, K.A. Rucker, T.K. Shea, et al. 2020. Body size impacts critical thermal maximum measurements in lizards. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology 335:96–107.
- Colli, G.R., D.O. Mesquita, P.V. Rodrigues, and K. Kitayama. 2003. Ecology of the gecko *Gymnodactylus* geckoides amarali in a Neotropical savanna. Journal of Herpetology 37:694–706.
- Dawson, W.R. 1975. On the physiological significance of the preferred body temperatures of reptiles. Pp. 443– 473 *In* Perspectives of Biophysical Ecology. Gates, D.M., and R.B. Schmerl (Eds.). Springer-Verlag, New York, New York, USA.
- Diele-Viegas, L.M., L.J. Vitt, B. Sinervo, G.R Colli, F.P. Werneck, D.B. Miles, W.E. Magnusson, J.C. Santos, C.M. Sette, G.H.O. Caetano, et al. 2018. Thermal physiology of Amazonian lizards (Reptilia: Squamata). PLoS ONE 13:e0192834. https://doi. org/10.1371/journal.pone.0192834
- Diele-Viegas, L.M., F.P. Werneck, and C.F.D. Rocha. 2019. Climate change effects on population dynamics of three species of Amazonian lizards. Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 236:110530. https://doi. org/10.1016/j.cbpa.2019.110530.
- Fierro-Cabo, A., and A. Rentfro. 2014. First record of the Tropical House Gecko *Hemidactylus mabouia* (Moreau de Jonnès, 1818) in Texas. BioInvasions Records 3:309–312.
- Gilbert, A.L., and M.S. Lattanzio. 2016. Ontogenetic variation in the thermal biology of Yarrow's Spiny Lizard, *Sceloporus jarrovii*. PLoS ONE 11:e0146904. https://doi.org/10.1371/journal.pone.0146904.
- Gilbert, A.L., and D.B. Miles. 2017. Natural selection on thermal preference, critical thermal maxima and locomotor performance. Proceedings of the Royal Society B: Biological Sciences 284:20170536. https:// doi.org/10.1098/rspb.2017.0536.
- Gomez-Zlatar, P., M.P. Moulton, and R. Franz. 2006. Microhabitat use by introduced *Hemidactylus turcicus* (Mediterranean Geckos) in north central Florida. Southeastern Naturalist 5:425–434.
- Hitchcock, M.A., and L.D. McBrayer. 2006. Thermoregulation in nocturnal ecthotherms: seasonal and intraspecific variation in the Mediterranean Gecko (*Hemidactylus turcicus*). Journal of Herpetology 40:185–195.
- Howard, K.G., J. Parmerlee, and R. Powell. 2001. Natural history of the edificarian geckos *Hemidactylus mabouia*, *Thecadactylus rapicauda*, and *Sphaerodactylus sputator* on Anguilla. Caribbean

Journal of Science 37:285-288.

- Huey, R.B., and E.R. Pianka. 2007. Lizard thermal biology: do genders differ? American Naturalist 170:473–478.
- Huey, R.B., J.B. Losos, and C. Moritz. 2010. Are lizards toast? Science 328:832–833.
- Hughes, D.F., W.E. Meshaka, and G. van Buurt. 2015. The superior colonizing gecko *Hemidactylus mabouia* on Curaçao: conservation implications for the native gecko *Phyllodactylus martini*. Journal of Herpetology 49:60–63.
- Iturriaga, M., and R. Marrero. 2013. Feeding ecology of the Tropical House Gecko *Hemidactylus mabouia* (Sauria: Gekkonidae) during the dry season in Havana, Cuba. Herpetology Notes 6:11–17.
- Johnson, S.K., J.S. Parmerlee, D.A. Eifler, and R. Powell. 2013. Comparative water-loss rates of *Hemidactylus mabouia* and *Sphaerodactylus notatus* on Eleuthera Island, Commonwealth of the Bahamas. Herpetology Notes 6:471–475.
- Kelley, A.L. 2014. The role thermal physiology plays in species invasion. Conservation Physiology 2:cou045. https://doi.org/10.1093/conphys/cou045.
- Kluge, A.G. 1969. The evolution and geographical origin of the New World *Hemidactylus mabouiabrookii* complex (Gekkonidae, Sauria). Miscellaneous Publications of the Museum of Zoology, University of Michigan 138:1–78.
- Kolbe, J.J., J.C. Ehrenberger, H.A. Moniz, and M.J. Angilletta. 2014. Physiological variation among invasive populations of the Brown Anole (*Anolis* sagrei). Physiological and Biochemical Zoology 87:92–104.
- Kolbe, J.J., B.R. Lavin, R.L. Burke, L. Rugiero, M. Capula, and L. Luiselli. 2013. The desire for variety: Italian Wall Lizard (*Podarcis siculus*) populations introduced to the United States via the pet trade are derived from multiple native-range sources. Biological Invasions 15:775–783.
- Kohlsdorf, T., and C.A. Navas. 2006. Ecological constraints on the evolutionary association between field and preferred temperatures in Tropidurinae lizards. Evolutionary Ecology 20:549–564.
- Lamb, A.D., C.A Lippi, G.J. Watkins-Colwell, A. Jones, D.L. Warren, T.L. Iglesias, M.C. Brandley, and A. Dornburg. 2021. Comparing the dietary niche overlap and ecomorphological differences between invasive *Hemidactylus mabouia* geckos and a native gecko competitor. Ecology and Evolution 11:18719–18732.
- Lapwong, Y., A. Dejtaradol, and J.K. Webb. 2020. Shifts in thermal preference of introduced Asian House Geckos (*Hemidactylus frenatus*) in temperate regions of southeastern Australia. Journal of Thermal Biology 91:102625. https://doi.org/10.1016/j. jtherbio.2020.102625.

- Lapwong, Y., A. Dejtaradol, and J.K. Webb. 2021. Shifts in thermal tolerance of the invasive Asian House Gecko (*Hemidactylus frenatus*) across native and introduced ranges. Biological Invasions 23:989–996.
- Leal, M., and A.R. Gunderson. 2012. Rapid change in the thermal tolerance of a tropical lizard. American Naturalist 180:815–822.
- Liwanag, H.E.M., D. Haro, B. Callejas, G. Labib, and G.B. Pauly. 2018. Thermal tolerance varies with age and sex for the nonnative Italian Wall Lizard (*Podarcis siculus*) in southern California. Journal of Thermal Biology 78:263–269.
- Lockwood, J.L., M.F. Hoopes, and M.P. Marchetti. 2013. Invasion Ecology. 2nd Edition. Wiley-Blackwell, Malden, Massachusetts, USA.
- Martín, J., and P. López. 2003. Ontogenetic variation in antipredator behavior of Iberian Rock Lizards (*Lacerta monticola*): effects of body-size-dependent thermal-exchange rates and costs of refuge use. Canadian Journal of Zoology 81:1131–1137.
- Middendorf, G.A., and C.A. Simon. 1988. Thermoregulation in the iguanid lizard *Sceloporus jarrovi*: the influences of age, time, and light condition on body temperature and thermoregulatory behaviors. Southwestern Naturalist 33:347–356.
- Paranjpe, D.A., E. Bastiaans, A. Patten, R.D. Cooper, and B. Sinervo. 2013. Evidence of maternal effects on temperature preference in Side-blotched Lizards: implications for evolutionary response to climate change. Ecology and Evolution 3:1977–1991.
- Passos, D.C., C.A.B. Galdino, C.H. Bezerra, and D. Zanchi-Silva. 2015. On the natural history of the poorly known Neotropical lizard *Hemidactylus agrius* (Squamata: Gekkonidae). North-Western Journal of Zoology 11:133–137.
- Pontes-da-Silva, E., W.E. Magnusson, B. Sinervo, G.H. Caetano, D.B. Miles, G.R. Colli, L.M. Diele-Viegas, J. Fenker, J.C. Santos, and F.P. Werneck. 2018. Extinction risks forced by climatic change and intraspecific variation in the thermal physiology of a tropical lizard. Journal of Thermal Biology 73:50–60.
- Porter, W.P., J.W. Mitchell, W.A. Beckman, and C.B. Dewitt. 1973. Behavioral implications of mechanistic ecology. Oecologia 13:1–54.
- Powell, R., R.I. Crombie, and H.E.A. Boos. 1998. *Hemidactylus mabouia*. Catalog of American Amphibians and Reptiles 674:1–11.
- R Development Core Team. 2013. R: A Language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http:// www.R-project.org/.
- Rato, C., and M.A. Carretero. 2015. Ecophysiology tracks phylogeny and meets ecological models in an Iberian gecko. Physiological and Biochemical Zoology 88:564–575.

- Rocha, C.F.D., and L.A. Anjos. 2007. Feeding ecology of a nocturnal invasive alien lizard species, *Hemidactylus mabouia* Moreau de Jonnès, 1818 (Gekkonidae), living in an outcrop rocky area in southeastern Brazil. Brazilian Journal of Biology 67:485–491.
- Rocha, C.F.D., and H.G. Bergallo. 2011. Occurrence and distribution of the exotic lizard *Hemidactylus mabouia* Moreau de Jonnès, 1818 in Ilha Grande, RJ, Brazil. Brazilian Journal of Biology 71:447–450.
- Rocha, C.F.D., L.A. Anjos, and H.G. Bergallo. 2011. Conquering Brazil: the invasion by the exotic gekkonid lizard *Hemidactylus mabouia* (Squamata) in Brazilian natural environments. Série Zoologia 28:747–754.
- Rödder, D., M. Solé, and W. Böhme. 2008. Predicting the potential distributions of two alien invasive house geckos (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). North-Western Journal of Zoology 4:236–246.
- Romero-Báez, Ó., R. Santos-Bibiano, M.A. Domínguez-Godoy, D.B. Miles, and F.J. Muñoz-Nolasco. 2020. Thermal ecophysiology of a native and an invasive gecko species in a tropical dry forest of Mexico. Journal of Thermal Biology 90:102607. https://doi. org/10.1016/j.jtherbio.2020.102607.
- RStudio Team. 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, Massachusetts, USA. http://rstudio.com/.
- Seebacher, F., and C.E. Franklin. 2005. Physiological mechanisms of thermoregulation in reptiles: a review. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 175:533– 541.
- Short, K.H., and K. Petren. 2012. Rapid species displacement during the invasion of Florida by the Tropical House Gecko *Hemidactylus mabouia*. Biological Invasions 14:1177–1186.
- Tang, X.L., F. Yue, J.Z. He, N.B. Wang, M. Ma, J.R. Mo, and Q. Chen. 2013. Ontogenetic and sexual differences of thermal biology and locomotor performance in a lacertid lizard, *Eremias multiocellata*. Zoology 116:331–335.
- Tattersall, G.J., V. Cadena, and M.C. Skinner. 2006. Respiratory cooling and thermoregulatory coupling in reptiles. Respiratory Physiology and Neurobiology 154:302–318.
- Taylor, E.N., L.M. Diele-Viegas, E.J. Gangloff, J.M. Hall, B. Halpern, M.D. Massey, D. Rödder, N. Rollinson, S. Spears, B. Sun, et al. 2020. The thermal ecology and physiology of reptiles and amphibians: a user's guide. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology 335:13–44.
- Telles, F.B.S., C.M. Militão, H.G. Bergallo, and C.F.D. Rocha. 2015. Invasion of the alien gecko *Hemidactylus mabouia* (Moureau de Jonnès, 1818) in a natural habitat at Praia do Sul Biological Reserve,

Ilha Grande, RJ, Brazil. Brazilian Journal of Biology 75:768–770.

- Texeira, R.L. 2002. Aspectos ecológicos de *Gymnodactylus darwinii* (Sauria: Gekkonidae) em Pontal do Ipiranga, Linhares, Espírito Santo, Sudeste do Brasil. Boletim do Museu de Biologia Mello Leitão 14:21–31.
- Vasconcelos, R., X. Santos, and M.A. Carretero. 2012. High temperatures constrain microhabitat selection and activity patterns of the insular Cape Verde Wall Gecko. Journal of Arid Environments 81:18–25.
- Vitt, L.J., and J.P. Caldwell. 2013. Herpetology: An Introductory Biology of Amphibians and Reptiles. 4th Edition. Academic Press, San Diego, California, USA.
- Vitt, L.J., and P.A. Zani. 1997. Ecology of the nocturnal lizard *Thecadactylus rapicauda* (Sauria: Gekkonidae) in the Amazon Region. Hepertologica 53:165–179.
- Vitt, L., W.E. Magnusson, T.C. Ávila-Pires, and A.P. Lima. 2008. Guide to the Lizards of Reserva Adolpho Ducke, Central Amazonia. Áttema, Manaus, Amazonas, Brazil.

Williams, R., A.P. Pernetta, and J.A. Horrocks. 2016.

Outcompeted by an invader? Interference and exploitative competition between Tropical House Gecko (*Hemidactylus mabouia*) and Barbados Leaf-toed Gecko (*Phyllodactylus pulcher*) for diurnal refuges in anthropogenic coastal habitats. Integrative Zoology 11:229–238.

- Xu, X.F., and X. Ji. 2006. Ontogenetic shifts in thermal tolerance, selected body temperature and thermal dependence of food assimilation and locomotor performance in a lacertid lizard, *Eremias brenchleyi*. Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology 143:118–124.
- Yuan, F.L., A.H. Freedman, L. Chirio, M. LeBreton, and T.C. Bonebrake. 2018. Ecophysiological variation across a forest-ecotone gradient produces divergent climate change vulnerability within species. Ecography 41:1627–1637.
- Zamora-Camacho, F.J., S. Reguera, and G. Moreno-Rueda. 2014. Bergmann's rule rules body size in an ectotherm: heat conservation in a lizard along a 2200-metre elevational gradient. Journal of Evolutionary Biology 27:2820–2828.



JULIANA LUZETE received a Master's degree in Zoology and a B.S. in Biology from the University of Brasilia, Brazil. She is currently an Ph.D. candidate at University of São Paulo, Faculty of Philosophy, Science and Letters of Ribeirão Preto. Juliana is interested in phenotypic diversification in reptiles and how it arises. Currently, she is studying phenotypic variation and development of *Hemidactylus mabouia*. (Photographed by Juliana Luzete).



LORENA O. PINHO received a B.S. degree in Biology from the University of Brasilia, Brazil. In her undergraduate research project at the Laboratory of Comparative Vertebrate Anatomy, she worked on lizard development and lizard thermal physiology. (Photographed by Premium Evento).



ISABELA F. OLIVEIRA is a Biology undergraduate student at the University of Brasilia, Brazil. In her undergraduate research project at the Laboratory of Comparative Vertebrate Anatomy, she has been working on developmental phenotypic plasticity in lizards. (Photographed by Isabela F. Oliveira).



JULIA KLACZKO is currently an Adjunct Professor of the Institute of Biological Sciences at University of Brasilia, Brazil. She received a B.S. in Biology from the Federal University of São Carlos, a Ph.D. in Zoology from the University of São Paulo. Julia was a postdoctoral fellow at Harvard University, Cambridge, Massachusetts, USA, and the University of Campinas, São Paulo, Brazil. Her research focuses on morphology of extant groups in particular reptile macroevolution, genitalia evolution, and skull shape evolution in vertebrates. (Photographed by Julia Klaczko).



APPENDIX FIGURE 1. Boxplots showing the similarity of the four thermal physiological traits analyzed between male and female Tropical House Geckos (*Hemidactylus mabouia*) in Brasilia, Brazil. (A) preferred temperature; (B) critical thermal minimum; (C) critical thermal maximum; and (D) thermal tolerance. Lower and upper box limits represent, respectively, first and third quartiles, internal bar the median, internal point the mean, and whisks the minimum and maximal values inside the 99% interval.



APPENDIX FIGURE 2. Boxplots showing variation between body temperature of Tropical House Geckos (*Hemidactylus mabouia*) measured with the thermocouple sensor fixed on the abdomen and inserted in the cloaca. (A) Critical thermal minimum and (B) critical thermal maximum. Lower and upper box limits represent, respectively, first and third quartiles, internal bar the median, internal point the mean, and whisks the minimum and maximal values inside the 99% interval. The two differ in the measures of critical thermal minimum (** P < 0.01) and critical thermal maximum (*P < 0.05).