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UPPER THERMAL LIMITS IN THE EXOTIC GECKO *HEMIDACTYLUS MABOUIA* FROM FLORIDA

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Abstract.— As climate change continues to threaten biodiversity around the world, time is running out to protect many species from extinction. Lizards are among the most threatened species, and over twenty percent of all lizard species are expected to face extinction as temperatures increase globally. An open question is whether invasive species will suffer the same consequences of climate warming as endemic species. *Hemidactylus mabouia*, the Tropical House Gecko, is an exotic and highly abundant species of gecko in Florida and limited information is available on their thermal tolerance in the invaded range. We collected *H. mabouia* in Sarasota, Florida, where we measured critical thermal maximum (CT_{max}) by two commonly employed methods to determine the loss of normal function: pants and muscular spasms. We hypothesized that the two methods of measuring CT_{max} would produce similar results in *H. mabouia*. We found that the mean for CT_{max} (pant = 38.5 °C) was significantly different than the mean for CT_{max} (spasm = 41.9 °C). *Hemidactylus mabouia* had high CT_{max} estimates, higher than temperatures predicted from global warming. Based on these findings, climate warming is not likely to contribute to the population decline of *H. mabouia* in Florida in the near future, and there is a strong relationship between CT_{max} and method of measurement.

INTRODUCTION

Climate change is one of the leading causes of global biodiversity loss and has contributed to the extinction of a variety of species from many different categories of life (Taylor et al. 2021; Agarwal et al. 2021). Ectothermic species such as squamates are particularly vulnerable to the gradual increase in temperature of our Earth, and their populations are expected to decline at a much faster rate than other organisms (Sinervo et al. 2010; Huey and Kingsolver 2019).

Small changes to an environmental characteristic such as temperature or precipitation often result in irreversible ecological impacts on ecosystems (Binita et al. 2020). A primary example of this is the state of Florida, a peninsula almost entirely surrounded by water, making it highly susceptible both to rising sea levels as well as rising temperatures (Binita et al. 2020). Despite the fact that the average temperature in Florida has only increased by 0.55 °C in the past century, the average temperature of southern Florida has increased by 1.94 °C and will likely continue to rise into the future (US EPA 2016). Although this may not seem like a noticeable increase, other recent statistics put it into perspective. As of 2016, approximately 15 days out of the year reached a maximum temperature of 35 °C, whereas seventy years from now, an estimated 45–90 days out of a year will reach a maximum temperature this high (US EPA 2016). Florida is also prone to heat waves, which have increased in frequency and intensity (4–6 °C hotter) over the last fifteen years, with even more increases predicted for the near future (US EPA 2016; Raghavendra et al. 2019). Heat waves are of particular concern to urban wildlife, as the urban heat island effect exacerbates the already-harmful effects caused by heat waves (Binita et al. 2020).

Our species of interest is the exotic Tropical House Gecko, *Hemidactylus mabouia*, a gekkonid native to the south-central region of Africa (Agarwal et al. 2021). This species is thought to have the widest population distribution of all *Hemidactylus* species (Agarwal et al. 2021), ranging now from Africa to South America to the United States and beyond (Hughes et al. 2015). Most relevant to this study, *H. mabouia* has successfully and prominently colonized the state of Florida. Though it is not the first *Hemidactylus* species to invade this region of the United States, it has successfully outcompeted all other introduced geckos in Florida, including the Common House Gecko (*H. frenatus*); the Indo-Pacific Gecko (*H. garnotii*); and the Mediterranean House Gecko (*H. turcicus*) (Meshaka 2000). Although there are many factors that have contributed to the expansion of *H. mabouia* into other

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regions, one cause may be their ability to tolerate high temperatures in sub-tropical environments, especially in urban heat islands that have higher average temperatures than natural habitats (Agarwal et al. 2021). As Lapwong et al. (2021) determined, *Hemidactylus* species in their native range of south-central Africa have been shown to rapidly adjust their thermal tolerance in order to adapt to ecosystems with more variable climates, however, there are no data available on the thermal tolerance of *H. mabouia* populations in Florida.

In thermal ecology, one of the most important values obtained when determining the overall effects of global warming on a species is their critical thermal maximum (CT_{max}), defined as the lower thermal limit at which an organism loses the ability to function (Taylor et al. 2021). CT_{max} can be tested in squamates using a variety of different behavioral endpoints, however, it remains unclear whether these endpoints produce similar results or if one method is more accurate or precise. In a study by Brusch et al. (2016) conducted in La Selva, Costa Rica, CT_{max} was determined for ten different squamate species by the temperature at which an organism could no longer perform a righting reflex after being flipped on its back. Carothers et al. (1997) identified the thermal tolerance of *Liolaemus* lizards in the Andes mountains of Chile by using panting as an endpoint. Most recently, and most relevant to this study, Doan et al. (2022) adopted an uncommon endpoint for determining CT_{max}, derived from Lutterschmidt and Hutchison's (1997) study, which used full-body spasms as the endpoint of normal functioning for several species of fish, amphibians, and reptiles. Although the righting response endpoint described in Brusch et al. (2016) is one of the more popular methods for testing thermal tolerance, Doan et al. (2022) found this method to be unreliable for the species they tested, because some lizard species become so stressed by being flipped over that getting an accurate CT_{max} estimate was impossible. It is better to use a method where the animal is not physically manipulated. Additionally, because the panting and spasm endpoints are not as widely used in CT_{max} studies, we chose to measure CT_{max} using both endpoints comparatively in an effort to determine if they produced similar results.

Through measuring the CT_{max} of *H. mabouia* specimens, which are highly abundant throughout Florida (Meshaka 2000; Agarawal et al. 2021), this study attempted to answer the following questions: a) Is *Hemidactylus mabouia* at risk of population decline due to rising temperatures in Florida?; b) Is measuring CT_{max} using involuntary spasms as an endpoint (Doan et al. 2022) more precise for determining the CT_{max} of squamates than using pants (Carothers et al. 1997)? Because both endpoints have been used interchangeably in CT_{max} studies for a variety of species, we also tested to determine if they produced the same CT_{max}. We tested both endpoints at the same time so that they would be directly comparable. In addition to these questions, we also examined the relationship between CT_{max} and sex (male vs female), as well as CT_{max} and age class (adult vs. juvenile) for *H. mabouia*, as previous research has indicated that these characteristics may have an impact on thermal tolerance (Carothers et al. 1997; Rock and Cree 2008). The results of this study shed light on how exotic species will continue to affect communities as temperatures rise with the advance of global warming.

MATERIALS AND METHODS

Field Methods

Hemidactylus mabouia were collected in the spring of 2022 in Sarasota County at several different locations around the New College of Florida campus (27.38528° N, -82.56204° W), between the hours of 21:30 and 23:30. Specimens were caught using nets and by hand on concrete buildings and ceilings, underneath wooden benches, and in the grass. After capture, each lizard was placed in a 17.7 x 18.8 cm bag. Specimens were then transferred back to the laboratory and remained in their bags for a period of 20–24 h to acclimate to laboratory temperature. Foliage was added to each bag at the site of capture and bags were misted upon return to the laboratory in order to reduce the stress of the animals.

Laboratory Methods

There has been extensive literature published regarding many different methods to determine the endpoint at which to define CT_{max} (Taylor et al., 2021). In this study, we wished to compare two methods for determining endpoints. We originally planned to compare righting response (e.g., Brusch et al. 2016) with full body spasms (Doan et al. 2022), but after attempts to verify righting response as a valid endpoint for *H. mabouia* (Phillips et al. 2016), we found the righting response to be unreliable for this species because the lizards clung to the researcher or lid of the container when they were flipped. Therefore, we decided to measure the thermal tolerance using full body spasms and panting (e.g. Carothers et al. 1997) as two endpoints for cessation of normal bodily function, defined as organized locomotory function that can help lizards to escape deadly thermal environments (Doan et al. 2022).

After the 20–24 h acclimation period in the laboratory, each *H. mabouia* specimen was tested to determine its CT_{max}. Similar to Doan et al. (2022), a large plastic tub (59.7 cm length x 42.9 cm width x 14.9 cm height) was filled to ~1.5 cm with water starting at ~26 °C (Max: 33.5 °C; Min: 22.2 °C). Each lizard was removed from its respective bag and placed into a rectangular plastic container (17 cm length x 10 cm width x 3.5 cm height) floating within the larger container. During the experiment, water temperature was measured with a floating bath thermometer, and ambient and specimen temperatures were measured using an infrared thermometer. Because the geckos are relatively small and have thin skin, their body temperatures are well measured with infrared thermometers (Taylor et al. 2021). Testing began after verifying that the temperature of each lizard matched that of the starting temperature of the water.

Once each specimen had acclimated, the start time was recorded, and hot water was added gradually to the tub via an electric kettle every 2 min to increase the temperature by approximately 0.5 °C. Each time more water was added to the bath, the timer was paused until it had increased to the new desired temperature, after which testing continued. Lizards that attempted to climb up the walls of the container or the mesh to avoid the rising temperature were gently pushed back by tapping along the sides of the container and the top of the lid in order to return them to the center of the container. If a new desired water temperature was reached prematurely, testing proceeded without the addition of more water until a higher temperature was needed. By contrast, given that the ambient temperature of the laboratory was usually cooler than the water temperature, the temperature of the water bath could decrease in between sampling periods. If the water temperature decreased more than 1 °C below the desired temperature, additional hot water was added into the tub to raise it back up to the necessary testing temperature.

In order for testing to conclude, each lizard was required to perform two necessary behaviors: panting and muscular spasms, both of which were used as endpoints to determine the CT_{max} of the specimens. If and when a specimen demonstrated panting, the temperature of the lizard was recorded using an infrared thermometer as well as the time elapsed since the start of the test, denoted as CT_{max} (pant). Testing then proceeded, continuously raising the water temperature ~0.5 °C every 2 minutes until the lizard exhibited distress in the form of a muscular spasm, defined as an involuntary twitch of the body (Doan et al. 2022). When this occurred, the temperature of the lizard, as well as the time elapsed, were once again recorded. The experiment continued until the specimen had expressed five individual occurrences of spasms. When 5 spasms were observed, the body temperature of the lizard at the time of the fifth spasm was recorded and was defined as CT_{max} (spasm) for that lizard, as recommended by Doan et al. (2022). If a lizard did not pant during the experiment, the CT_{max} value was not reported for this endpoint. Similarly, if a lizard did not spasm 5 times and instead stopped all movement within its container for a period of more than 5 minutes, a CT_{max} value was not recorded for the spasm endpoint and the specimen was removed from the tub. Once a specimen met the criteria of both panting and experiencing 5 uncontrolled spasms, the container within which it was held was promptly removed from the tub of hot water and placed on a nearby laboratory table in order to return it to a non-critical temperature, ensuring its survival. If a lizard failed to reach either endpoint and was no longer attempting to escape containment, its container was removed from the water in order to prevent the animal from lethally overheating. After all the lizards in the current testing period had reached their CT_{max} estimates, observations and measurements were recorded for each specimen.

Sex was determined in adult and sub-adult specimens by examining the base of the tail to observe the presence of a hemipenal bulge (Das and Purkayastha 2012). Sex was not determined for juvenile specimens, and sub-adults were not classified. The snout-vent length (SVL) and tail length were measured for each specimen using calipers and the condition of the tail was reported as either entire or regenerated. All specimens survived the procedure and were promptly euthanized by administering sodium pentobarbital and placing them in a laboratory freezer, as per guidelines of the Florida Fish and Wildlife Conservation Commission, given that *H. mabouia* is recognized as an exotic species in Florida.

Statistical Analysis

We tested differences between the two CT_{max} endpoints using a Wilcoxon signed-rank test. A Levene's test was also run to test the difference in variance between the endpoints. In addition to testing these differences, we also compared the CT_{max} between adults and juveniles, as well as the CT_{max} of each sex for adults for both endpoints, using Welch's t-tests for each endpoint (panting or spasms) separately. Spearman correlation coefficients were used to compare the CT_{max} and SVL of each lizard for the two endpoints. All statistical analyses were conducted using IBM SPSS version 29. Statistical significance was defined at $P \leq 0.05$ and means are presented +/- SD.

RESULTS

Forty-two Tropical House Geckos (*Hemidactylus mabouia*) were collected (18 juveniles, 14 adult males, and 10 adult females). Thirty-five lizards were included in the panting study (11 juveniles, 14 males, and 10 females), while 34 lizards were used in the spasm study (15 juveniles, 12 males, and 7 females). Eight lizards failed to meet the criteria of spasming 5 times. One lizard failed to pant and a CT_{max} value was not reported for this endpoint. Twenty-eight lizards met the criteria for both the panting and spasm endpoints.

CT_{max} by Method

The average CT_{max} for lizards measured by panting was 38.5 ± 2.6 °C, while the average measured by spasms was 41.9 ± 0.92 °C. We found a significant relationship between CT_{max} and the method of measurement ($S = 6.0$, $n = 28$, $P = < 0.001$). Panting ($s^2 = 6.998$) had a significantly higher variance than spasms ($s^2 = 0.853$) (Levene's = 23.563, df = 54, $P = < 0.0001$) (Fig. 1).

CT_{max} and Sex

The mean CT_{max} (pant) for males was 38.4 ± 2.5 °C and 38.5 ± 2.5 °C for females. For CT_{max} (spasm), the average male CT_{max} was 41.6 ± 0.79 °C, and 42.4 ± 0.57 °C for females. There was no significant relationship between sex and CT_{max} (pant) (Welch's $t = 0.06$, df = 19.35, $P = 0.954$), however, there was a significant relationship between sex and CT_{max} (spasm) (Welch's $t = 2.6$, df = 15.97, $P = 0.020$).

CT_{max} and Age Class (Adult vs Juvenile)

The mean CT_{max} (pant) for adults was 38.5 ± 2.5 °C, whereas the average CT_{max} for juveniles was 37.7 ± 3.2 °C. For CT_{max} (spasm), adults averaged 41.9 ± 0.81 °C, whereas the juvenile average was 42.0 ± 1.4 °C. There was no significant relationship between age class and CT_{max} for either testing method (pants: Welch's $t = 0.70$, df = 15.73, $P = 0.496$; spasms: Welch's $t = -0.28$, df = 21.16, $P = 0.783$).

CT_{max} and Snout-Vent Length (SVL)

The mean SVL for juveniles was 28.2 mm, 52.6 mm for males, and 49.8 mm for females. There were no significant linear relationships between CT_{max} (pant) or CT_{max} (spasm) and SVL (pants: $r = 0.2$, $n = 33$, $P = 0.343$; spasms: $r = -0.05$, $n = 35$, $P = 0.782$.

DISCUSSION

With a mean CT_{max} (pant) of 38.5 °C and CT_{max} (spasm) of 41.9 °C, it was determined that *Hemidactylus mabouia* is not at immediate risk of population decline in Florida caused by increased temperatures associated with climate change. Because these values are both higher than the predicted 35 °C temperature averages expected to be reached somewhere between 45 and 90 days per year seven decades from now (US EPA 2016), it is likely that *H. mabouia* will still be able to survive despite this drastic increase. This is further evidenced by the fact that current heat waves in Florida average between 26.9 °C and 31.9 °C and are expected to increase only by about 4–6 °C over the course of the next decade (Raghavendra et al. 2019), meaning that these geckos should be safe from population decline for the near fu-

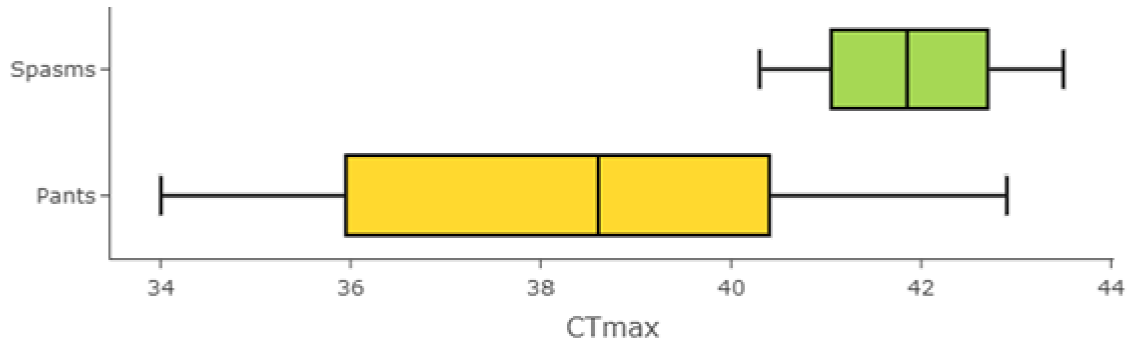

Figure 1. A box and whisker plot showing the distribution of CT_{max} (spasm) (green) compared to CT_{max} (pant) (yellow) of the 28 lizards that were tested for both endpoints. The inner two quartiles of data for each method of testing are within the boxes, while the ends of each bar show the extremes of the data. The values recorded for CT_{max} (spasm) have a much smaller distribution than those recorded at the panting endpoint.

ture, at least as far as temperature changes. However, *H. mabouia* may still be at risk from the increase of extreme weather events in Florida such as drought, excess precipitation, or hurricanes due to global warming (Binita et al. 2020). Future studies testing CT_{max} against other thermal measurements such as righting response may further support this conclusion.

Our results clearly indicate that measuring CT_{max} using spasms does not produce similar results to using panting as an endpoint. The two averages for CT_{max} produced from each method (38.5 °C and 41.9 °C respectively) are dissimilar to each other and the variances for each method were markedly different, indicating that the distribution of values was far broader for the panting and much narrower for spasms, as evidenced by Figure 1. This suggests that CT_{max} (spasm) is more precise and reliable. While righting response remains a common endpoint for many lizard species who may not exhibit spams near or at their CT_{max} (Taylor et al. 2021), we found it to be unreliable for our species and testing environment, thus we did not include this method in this study. The righting response endpoint has been effective for some species (Brusch et al. 2016; Taylor et al. 2021) but has been shown to be unreliable for others (e.g., Doan et al. 2022; this study) and does not represent the true critical maximum because lizards tend to lose their righting response prior to onset of spasms (Camacho and Rusch 2017). Lutterschmidt and Hutchinson (1997) found that determining CT_{max} by the onset of spasms in species of fish, amphibians, and reptiles produced less varied results than using the righting response method. Additionally, studies using righting response are best performed in a controlled testing environment with a dedicated laboratory set up. Special, expensive equipment is needed to accurately test righting response, such as transparent tubes in which to place lizards that can be easily placed into a gradually heated tub and repetitively turned over (Lapwong et al. 2021).

Lapwong et al. (2021) used righting response to measure CT_{max} in a relative of our species, *Hemidactylus frenatus*, and produced results that were similarly distributed to the spasm endpoint in this study. Although our study produced highly significant results to support the fact that using spasms as an endpoint for CT_{max} is less varied than panting, no study has been performed to compare all three endpoint methods on the same species, which would be an excellent avenue of additional research.

Although there is limited information available on the comparison between the different known methods of measuring CT_{max} (but see Camacho and Rusch, 2017), the data produced in this study were highly significant, and we therefore confidently conclude that using spasms as an endpoint for measuring CT_{max} is a more precise method than using panting. Our methodology of testing both endpoints on the same lizards simultaneously removed much potential variation, rather than if the individuals had been split into two treatment groups and/or tested at different times. Considering that *H. mabouia* is an exotic species in Florida (Meshaka 2000), its abundance makes these geckos good test subjects for developing more precise methods for determining the thermal tolerance of lizards.

Although we did not find a significant relationship between CT_{max} and lizard age class or CT_{max} and body size (SVL) for either method of testing, we did find that sex and CT_{max}, as measured by spasms, showed a significant difference. Although there is no previous research on these differences in *H. mabouia* specifically, a study conducted by Liwanag et al. (2018) reported that female Italian Wall Lizards, *Podarcis siculus*, had both a lower CT_{min} and broader range of CT_{min} and CT_{max} values than the male specimens, citing behavioral and hormonal differences as possible explanations for this result. Winne and Keck (2005) observed that newborn female *Nerodia rhombifer,* Diamond-backed Water Snakes, had a higher thermal tolerance than newborn males, suggesting that a difference in heat shock protein expression between sexes might be the cause of this phenomenon. However, other studies, such as that conducted by Yang et al. (2008), reported that there was no difference in thermal tolerance between male and female China Grass Lizards, *Takydromus septentrionalis*, arguing that thermal acclimation and environmental factors are more responsible for the thermal tolerance of a lizard than physiological features. Doan et al. (2022) produced similar results, reporting no difference in thermal tolerance between male and female *Proctoporus unsaacae* and *P. sucullucu* from Peru. Unfortunately, given that there is still very little information about the relationship between sex and thermal tolerance for reptiles, more research is needed in this area before an explanation can be provided for why female *H. mabouia* specimens had a significantly higher CT_{max} (spasm) than males.

Although climate change will continue to be one of the leading causes of reptile extinctions around the globe (Taylor et al. 2021), hope is not entirely lost for squamates (Doan et al., 2022). Some lizard species, including *H. mabouia*, will not be immediately impacted by the rising temperatures in Florida. This is because their thermal tolerance for high temperatures exceeds the expected temperature increases for this region over the course of the next seven decades (US EPA 2016), averaging CT_{max} values higher than both the predicted heatwave temperatures in Florida over the next ten years as well as the 35 °C temperature average expected to become more frequent by 2070 (US EPA 2016; Raghavendra et al. 2019). Continuing research on thermal tolerance is essential because of the variation of expected impacts among species due to climate change.

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