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Thermal and Behavioral Ecology of the Mexican Beaded Lizard (*Heloderma horridum*)

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THERMAL AND BEHAVIORAL ECOLOGY OF THE
MEXICAN BEADED LIZARD (*HELODERMA HORRIDUM*)

A Thesis

Presented to

The Graduate Faculty

Central Washington University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

Kerry Lee Holcomb

May 2017

CENTRAL WASHINGTON UNIVERSITY

Graduate Studies

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ABSTRACT

THERMAL AND BEHAVIORAL ECOLOGY OF THE MEXICAN BEADED LIZARD (*HELODERMA HORRIDUM*)

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Previous investigations in the field of biological thermoregulation have primarily focused on small organisms that inhabit ecosystems that are not as strongly seasonal as the tropical dry forests found along the Pacific Coast of Jalisco, Mexico. Small organisms have little or no appreciable thermal inertia, and thus, reach thermal equilibrium with their immediate surroundings relatively rapidly. In this investigation, we describe the behavioral and thermal ecology of the Mexican beaded lizard (*Heloderma horridum*), which commonly weighs more than 1kg. This large body size means that this species has significant thermal inertia, which, depending on the characteristics of the immediate thermal gradient, can cause its core-body temperature (T_b) to lag behind surrounding operative temperatures (T_e) by as much as 20 minutes. A lag of this length negates shuttling as a thermoregulatory strategy because it would be too time intensive to be ecologically feasible. Beaded lizards are also resource limited by the strongly seasonal dry forests that they inhabit, and must carefully budget energy and water reserves to survive. T_b and T_e were recorded every 15 minutes from a group of six beaded lizards and two copper T_e models, respectively, using iButton dataloggers. T_b and T_e records were used to explore body temperature time series and to estimate the timing

of refuge emergence and refuge emergence-immersion intervals. These data support the hypothesis that beaded lizards have a relatively cool active T_b range, which is maintained by precisely timing refuge emergence and by modulating the length of refuge emergence-immersion intervals. Strategic maintenance of a cool active T_b range when T_e models demonstrate that warmer ranges are available directly contradicts the “hotter is better” hypothesis, which posits that warmer adapted phenotypes will exhibit increased Darwinian Fitness relative to cooler adapted phenotypes.

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Chapter I

JOURNAL ARTICLE

THERMAL AND BEHAVIORAL ECOLOGY OF THE
MEXICAN BEADED LIZARD (*HELODERMA HORRIDUM*)

1. Introduction

Based on the latest conservation phylogenetic prospective presented by Reiserer et al (2013), the Mexican beaded lizard (*Heloderma horridum*, Wiegmann, 1829) is one of four species that carries the beaded lizard moniker, along with the Río Fuerte beaded lizard (*Heloderma exasperatum*, Bogert and Martín del Campo, 1956), Chiapan beaded lizard (*Heloderma alvarez*, Bogert and Martín del Campo, 1956), Guatemalan beaded lizard (*Heloderma charlesbogerti*, Campbell and Vannini, 1988). Beaded lizards are the nominate species within the *Heloderma* genus (Beck, 2005). Bead lizards are longer snout to vent, have longer tails, and weigh more than Gila monsters (*Heloderma suspectum*). Beaded lizard coloration is also less aposematic than that of the Gila monster. Its coloration ranges from uniformly black or brown to patterns of intricate black, brown, and yellow speckles (Beck, 2005).

All extant members of the family Helodermatidae possess venom glands on each side of their mandible (Beck, 2005). Most venomous snakes use venom to subdue or immobilize prey and begin digestion (Green, 1997). Helodermatid lizards, however, feed on the defenseless young or eggs of other vertebrates and do not appear to envenomate their prey (Beck, 1990; Beck, 2005). They instead use venom primarily for defense, which alleviates their need to escape predators with rapid sprint speed alone (Beck, 2005). Therefore, Helodermatid lizards are not tied to the maintenance of an optimal core-body temperature (T_b) for the purposes of capturing prey or evading predators. This

freedom from a physiologically optimal temperature could possibly explain this species' evolution of a relatively low mean active temperature, which also serves to slow metabolic and reduce evaporative water loss rates. Additionally, this relatively low mean active temperature enables Helodermatid lizards to be active nocturnally, thus expanding their range of activity time options.

Beaded lizards inhabit the lowland tropical dry forests of western Mexico and southeastern Guatemala's Motagua Valley (Beck, 2005). Dry forest can be divided into two distinct habitat types, the most expansive of these is the upland forest found on hillsides, ridgelines, and plateaus. The second type, however, is constricted to the deepest arroyos and is thus referred to as the arroyo forest. Dry forests, and the species that inhabit them, are characterized and shaped by a strongly seasonal precipitation pattern. Mean annual precipitation at the *Estacion de Biologia Chamela* (EBCh) is approximately 790 mm (García-Oliva et al., 2002). On average, 85% of mean annual precipitation is received during the wet season months between July and early November. This precipitation causes the vegetation to flush with leaves, covering the landscape in a short, dense canopy (Murphy and Lugo, 1986). Shade from this dense canopy profoundly affects the distribution of operative temperatures (T_e), where T_e refers to the temperature of an organism when it is in thermal equilibrium with its immediate surrounds, following the zeroth law of thermodynamics. But the lack of water during the dry season triggers the vegetation throughout the upland and in many of the shallower arroyos to shed leaves and become dormant. This strategy enables plants to conserve water and survive this extreme dry period (Murphy and Lugo, 1986). In the deepest arroyos, where subsurface water is available longer into the dry season, many of the tallest trees maintain leaves year round

(see Lott, 1985; Lott et al., 1987; Perez, 1982). Many animals also become less active or alter their activity pattern in the dry season, choosing to shelter for long periods in tree cavities, rock crevices, and earthen refuges (Butterfield et al., 2017; Garcia et al., 2010; Valenzuela and Ceballos, 2000). Since beaded lizards are only rarely encountered outside tropical dry forest biomes, this species is often referred to as a dry forest endemic or denizen of the dry forest (Reiserer et al., 2013).

The competitive advantage that Helodermatid lizards exhibit in seasonal biomes is the result of anatomical, physiological, and behavioral adaptations that specifically address the challenges of seasonal resource scarcity. These lizards have large fat bodies in the tail and peritoneal cavity that allow them to store energy resources (Beck, 2005). Additionally, Gila monsters, and possibly bead lizards, have the ability to store water in their bladders and reabsorb that water across the bladder epithelium, which help them maintain plasma osmolality within an acceptable range even during long period without access to liquid water (Davis and DeNardo, 2010). These two adaptations enable Helodermatid lizards to survive on spatially and temporally patchy supplies of liquid water and prey.

Physiological and behavioral adaptations enable Helodermatid lizards to budget energy and water reserves, thus enabling them to survive for long periods without access to liquid water or prey (Beck, 2005). Helodermatid lizards have a standard metabolic rate that is half that predicted for other reclusive squamates of this size (Beck and Lowe, 1994). In fact, Helodermatid lizards have a standard metabolic rate that is slower than even fossorial lizards, which Andrews and Pough (1985) described as having the lowest standard metabolic rate of any group they analyzed. Energy consumption is lowered

further still by a preference for a relatively cool mean activity temperature that ranges between 27.2 and 30.2°C (Beck, 2005). This cool mean activity temperature also helps Helodermatid lizards conserve water, as water loss through evaporation is temperature dependent (DeNardo et al., 2004). Finally, these lizards spend extended periods of time inactive and at T_b of less than 20°C for Gila monsters and less than 25°C for beaded lizards while in refuges. Some populations of Helodermatid lizards allocate only 70 to 130 hours per year to activity, though some populations are much more active (Beck, 2005). These adaptations enable Helodermatid lizards to conserve energy and water reserves in strongly seasonal biomes.

T_b management is quintessential to the careful management of energy and water reserves for most species that inhabit seasonally harsh biomes. For this reason, thermoregulation is of great interest. Previous investigations of thermal regulation have focused on small (<50g) lizards, which have little or no appreciable thermal inertia (Angilletta, 2009; Christian et al., 2006; Seebacher and Shine, 2004). Lack of thermal inertia enables small lizards to more easily maintain relatively stable T_b 's that matches their preferred T_b and physiological optimal temperature. Control of T_b in these smaller lizards is achieved by shuttling between hot and cool microhabitats, a pattern that has led to productive investigations of thermoregulation effectiveness (Angilletta, 2009; Hertz et al., 1993). The *Heloderma horridum* investigated in this study, however, had weights that averaged over 1kg (1068g during dry season; 1299g during wet season). These larger lizards have substantial thermal inertia, which causes their T_b to lag behind T_e by more than 20 minutes for every 10°C increase in T_e (Seebacher et al., 2003). For this reason, the classic model for evaluating thermoregulation effectiveness may not be

appropriate for *Heloderma horridum*. Therefore, we applied a time series approach in this study that seeks to test the hypothesis that *Heloderma horridum* thermoregulates. If this species thermoregulates we predict 1) that daily mean T_b will be cooler than daily mean T_e , 2) that long term trends in daily mean T_b will be less steep than trends in daily mean T_e , 3) that the variance of detrended T_b series will be less than the variance of detrended T_e series, and 4) that emergence timing and amount of time spent outside of refuges results in repeated patterns (long-term series memory) within and among T_b series.

We also use T_b and T_e records to explore the timing of emergence and length of emergence-immersion intervals. To accomplish this we modified a Temperature Based Activity Estimator presented by Davis et al. (2008) to instead of focus on refuge use. This enabled us to ask if timing of emergence and length of emergence-immersion intervals varied as a function of season. This also enabled us to test whether seasonal modification in behavior could result in similar T_b between seasons, thus further supporting our hypothesis that this species thermoregulates.

2. Methods

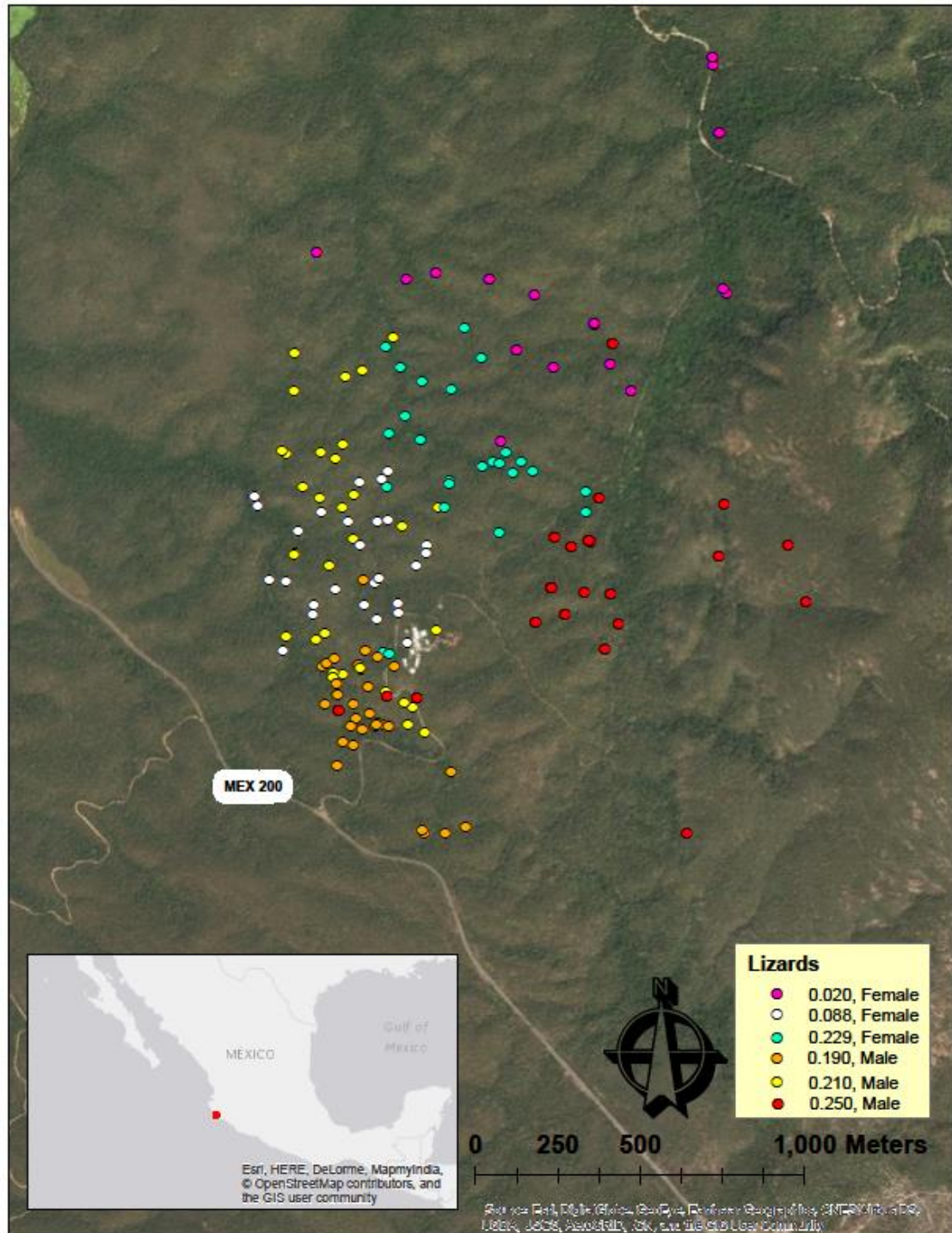


Fig. 1. Overview Map: *Estacion de Biologia Chamela* and the locations of the beaded lizards (*Heloderma horridum*) tracked during this study.

2.1. Study Area

We conducted our field work at *Estacion de Biologia Chamela* (EBCh), a model system to study the evolutionary consequences of seasonality on thermal biology and behavior of Mexican beaded lizards, as well as other species of ectotherms (Reiserer et al., 2013; Garcia et al., 2010). The EBCh is a 3,319 ha reserve of the *Universidad Nacional Autonoma de Mexico* (UNAM), located less than 5 km east of the Pacific Ocean, at approximately 19°30'N, 105°03' W in the state of Jalisco, Mexico. Elevation ranges from 10 to 584 m above standard mean sea level (Map 1). In our study, lizards were tracked across ~ 400ha of the reserve directly adjacent to the EBCh housing and research facilities.

The EBCh is situated in a strongly seasonal lowland tropical dry forest, where approximately 80% of mean annual precipitation occurs during the wet season (July through early November), while the remaining ~7.5 months see minimal precipitation on average (Bullock, 1986). Leaves sprout at the beginning of the wet season and drop from most trees during the mid to late dry-season, and as foliage cover changes so does the distribution of operative temperature in the forest understory. Nevertheless, mean monthly standard air temperature is relatively stable, with an annual mean temperature of 24.4°C, a monthly mean maximum temperature range of 29.1-32.0°C and monthly mean minimum temperature range of 17.8 to 22.9°C.

The EBCh harbors two forest habitat types: a deciduous upland forest (upland forest) and a semi-deciduous arroyo forest (arroyo forest, as termed by Lott et al., 1987). The upland forest is the most expansive of the two habitat types, and occurs on crests, shoulder slopes, and in upper reaches of some arroyos. Its short, sparse 'canopy' is

typically 4-15 m tall, which facilitates the formation of a dense and well-developed understory, composed of shrubs, small vines, and, during the wet season, herbaceous vegetation. Conversely, the arroyo forest is restricted to the floodplain, toe, and lower toe slopes of deep arroyos. It has a tall, dense continuous canopy that is largely evergreen (see Lott, 1985; Lott et al., 1987; Perez, 1982).

2.2. Study Periods

To isolate the effects of seasonality on the thermal biology and behavior of Mexican beaded lizards, observations discussed herein were made with respect to a late dry season study period (May 17 - June 20, 2011) and an early wet season study period (June 29 - August 2, 2011). These two 35 day observation periods were then compared with respect to refuge/shelter use, core-body temperatures, and operative temperatures. Data collected outside of these periods were excluded from this analysis because the transitional period between the dry and wet season was too short to be satisfactorily comparably to the other two study periods (June 21 to June 28).

2.3. Initial Lizard Capture and Morphometrics

Initially, beaded lizards were located by searching trails and arroyos, and by searching areas where lizards had been seen recently by other researchers and staff working at EBCh. Later, additional lizards were located while tracking radio tagged individuals. Once captured, lizards were immediately transported to the laboratory where morphometric data were recorded. Weight was measured from each lizard to the nearest gram using an Ohaus Scout Pro scale; total length was measured with a standard tape

measure mounted to a laboratory work bench. Tail volume was measured with displacement. Each lizard's tail up to the vent was submerged in a 1000 ml graduated cylinder prefilled with enough water to overflow the cylinder. The amount of water displaced was then measured by refilling the 1000ml cylinder with water from a second 200 ml cylinder (modified from Davis et al., 2008). Weigh, tail volume, and total length measurements recorded during the late dry season (May 1-6) and mid wet season (August 3-14) were tested for predicted increases, with one-tailed paired T-tests.

2.4. Radiotransmitter and Datalogger Implantation

Lizard location, movements, and body temperatures were monitored with implanted, calibrated radiotransmitters (IMP-200L, Telonics, Mesa, Arizona). Body temperature was also recorded with two implanted iButton Thermometers (DS1922L, Thermochron, Baulkham Hills, Australia). Two iButtons were implanted in each lizard to increase data storage capacity, and thus loggers were programmed to record core-body temperature every 30 minutes, but were staggered so that the logger combination would collect core-body temperature every 15 minutes. iButtons were dipped in blue Plasti Dip (Plasti Dip International, Blaine, Minnesota) before implantation following Pittman and Dorcas (2009). Surgeries were performed under Isoflurane anesthesia. Both transmitters and iButtons were inserted through a 3cm transverse incision 20-25 scale rows anterior to the vent through the ventral dermis and peritoneum into the peritoneal cavity. The transmitter (23g) plus two iButtons (3.3g each) together weighed 29.6g, which comprised 4.2% of our smallest lizard's weight during the dry season and 3.2% of our smallest lizard's weight during the wet season. On average the implanted payload was 2.8% and

2.3% of the weight of this group of lizards during the dry and wet seasons, respectively. These percentages are similar to those reported in Beck and Lowe (1991). Incisions were then sutured using chromic gut, starting with the peritoneum and then moving to the muscular tissue and finally the dermis.

Six lizards were implanted with a radiotransmitter and two iButtons and data collection began greater than or equal to 10 days post implantation. Five of these lizards were monitored between May 17 and August 2, 2011. A sixth lizard was monitoring between June 29 and August 2, 2011. After the effect of Isoflurane had subsided, lizards were released at the exact location that they were captured. For two weeks after the implantation procedures lizards were handled once per week to assess the condition of the incision. After this, lizards were infrequently captured to measure weight and body temperature (Schultheis thermometer). Transmitters and iButton dataloggers were surgically removed from lizards at the end of the study using similar procedures as described above.

2.5. Refuge Use and Distance between Relocations

To determine dry versus wet season patterns of refuge depth preference, lizards were located every day when possible, but equipment malfunction and environmental conditions precluded daily observations at times, especially during the wet season. Lizards were tracked with a TR2 receiver and directional H-configured antenna (Telonics). At each location, the lizard's refuge use status was qualitatively assigned to one of three categories: 1) surface active, 2) in a tree refuge, or 3) in a ground refuge. If the lizard was found in a refuge, it was further classified 'shallow', 'arboreal', or 'deep'.

Shallow refuges were those refuges where lizards could be seen at the back of the burrow and have a depth of less than 60cm. Arboreal refuges were those refuges that occurred in trees. And Deep refuges were those refuges where lizards could not be seen because they were not visible and the refuge was greater than 60 cm deep.

Patterns of the timing of emergence from refuges, emergence-immersion intervals (time spent outside of shelters), and proportion of time spent within shelters were estimated by calculating a set of five dry season and 6 wet season Core-body Temperature Refuge Use Estimator (CTRUE) series. These series are binary (0 or 1) vectors of the same length as the T_b vector (derived from 3,360 i-button temperature samples taken at 15min intervals per season per lizard), where a value of “0” indicates that the lizard was in a refuge and a value of “1” indicates that the lizard is not in a refuge. CTRUE was adapted from the Temperature Based Activity Estimation (TBAE) technique developed in Davis et al. (2008), who applied the technique to estimate the activity of *Heloderma suspectum s.* in Arizona. Our CTRUE method, however, emphasizes refuge use rather than activity because refuge use is characterized by a more unambiguous T_b signal, relative to activity.

CTRUE series were estimated for each lizard by viewing a plot of synchronized operative temperatures recorded from a shaded copper model (see T_{e-min} in the *Thermal Biology* section below of a more thorough explanation) and T_b series in program-R (3.3.3) using a time series graphics tool (function “ts.plot”, package “stats”). With this figure, a single observer (KLH) “estimated” whether the lizard was inside (“0”) or outside (“1”) of a refuge for every iButton temperature record by applying the criteria used in Davis et al. (2008). The accuracy of CTRUE was analyzed by calculating a two-way agreement type

Intra-class Correlation Coefficient, or ICC (in contrast to a kappa test used by Davis et al., 2008). ICC was deemed superior to the kappa test because ICC takes into account that each set of observer “estimations” is an ordered set, while the kappa test is not designed to test agreement of ordered sets. But like a kappa test, an ICC quantifies the degree of similarity between “estimations” generated by two observers or two observation tools. The ICC was then classified as poor, fair, good, or excellent following Cicchetti (1994).

The hypothesis that emergence times differed significantly between the dry and wet seasons was analyzed with a Kolmogorov-Smirnov Test (function “ks.test”, package “stat”). Dry versus wet season percent refuge occupancy generated using CTRUE was analyzed for significant differences with a one-tailed paired T-test.

The straight-line distances between each successive observation were measured as a proxy for distance traveled between observations. These distances were not corrected for non-linear movements because these measurements are only meant to be compared between dry and wet season study periods. For this reason, our analysis assumes that non-linear movements do not differ significantly between the dry and wet season.

2.6. Thermal Biology

To address the ecological and evolutionary consequences of dry forest seasonality on the thermal biology of *Heloderma horridum*, we concomitantly recorded discrete core-body temperature (T_b) and operative temperature (T_e) time series (series). T_b series were recorded for five lizards during the dry season and six lizards during the wet season with iButton temperature dataloggers implanted into the peritoneal cavity of each lizard as

described above (see *Radiotransmitter and Datalogger Implantation* section above). T_e series were recorded from two T_e models, which were strategically placed to measure the minimum and maximum equilibrium temperatures available at the EBCh (Bakken, 1992; Dzialowski 2005). Equilibrium temperature here refers to the T_b of an organism in thermal equilibrium with its immediate environment. Thermal equilibrium means that the net flow of heat energy between an organism and its immediate environment equals zero, thus satisfying the Zeroth Law of Thermodynamics. These series were recorded with iButton temperature dataloggers placed inside two separate T_e models. T_e models consisted of capped hollow copper pipes, 47.0cm long X 5.1cm in diameter, and weighed 335g. T_e models were painted with flat brown Krylon Rust Protector to approximate the reflectance of a beaded lizard (Bakken and Angilletta, 2014).

T_b and T_e series were synchronously sampled every 15 min starting at 00:00 hrs, for a total of 96 samples per series per day and 3360 samples per series per study period. Not surprisingly, all observed series were dominated by the daily temperature cycle. For this reason, each series was assigned a frequency of 96—i.e., 96 samples per cycle (i.e., series season, which in this case is one day), where one day equals one cycle—while being converted into time series objects (function “ts”, package “stat”) in program R (version 3.3.3). Ideally, T_b would have been recorded at twice the rate of the fastest oscillation, which in this case equals 3.5 minutes, to capture the full extent of this fastest oscillations present in the continuous T_b series being estimated, which would have provided a more unambiguous estimation of the continuous time series being estimated and analyzed (Nyquist, 1928). Nevertheless, the thermal stability of the 0.8 to 1.5 kg

lizards under observation here is assumed to mitigate the importance of these faster oscillations (Seebacher and Shine, 2004).

Upon removal, the clocks of iButtons implanted into lizards were found to be slow by an average of approximately 1hour 51minutes (range ~ 1:50 to 1:53 hours) by comparing the iButton clock to the lock from a laptop. Plotting T_b against operative temperature demonstrated that time was not lost evenly between May and August. Dry season records were less affected by this malfunction, since this time error was additive over the course of the entire study. Therefore, simply realigning the datasets by the respective time error would not correct this issue. Instead, T_b and time records from each telemetry location, measured with temperature calibrated radiotransmitters, were used to estimate the actual alignment of the datasets. Each radiotransmitter was calibrated by recoding the time in seconds necessary for the transmitter to produce 15 beeps at temperatures between 12 and 39°. Temperature dependent changes in the amount of time necessary for 15 beeps were found to be strongly correlated ($y = -1.4807x + 68.194$, $r^2 = 0.9993$).

To measure the minimum and maximum T_e available to beaded lizards, one T_e model was placed on the ground on top of leaf litter in full shade (arroyo forest) and a second T_e model was pressed 1 cm into a sandy substrate in full sun on a hill top. The full shade model was used to estimate the minimum T_e available to beaded lizards at the EBCh during both the dry and wet seasons, and is thus referred to as T_{e-min} . The full sun model was used to estimate the maximum T_e available to beaded lizards at the EBCh and is thus referred to as T_{e-max} .

To determine whether beaded lizards controlled average T_b and T_b variance, daily averages (trend) and detrended series (observed series minus daily averages) were compared within and among study periods. Trend was calculated using a 96 point moving average (function “ma”, package “forecast”) using program R. Mean functions (time dependent estimation of the mean) were then calculated from trend series using least-squares regression, where temperature was the dependent variable of time.

A mean function is analogous to an arithmetic mean, but is not restricted to a single value; rather it is a time dependent linear function that can vary from 1 to an infinite number of values. If the value of a mean function is the same for all points in time (i.e., independent of time), then the series is classified as “stationary” and the mean function has only one value. If the value of a mean function changes with time (is time dependent), then the series is classified as “non-stationary” and the mean function has a range of values.

To determine if beaded lizards exhibited thermoregulation within season, T_b trend was compared to T_{e-min} and T_{e-max} trend in terms of mean function slope and mean function maximum values with one sample t-tests, which enabled us to test whether 1) T_b and T_e share the same slope and 2) T_b was cooler than T_e . To determine if beaded lizards exhibited thermoregulation between seasons, dry season T_b trend series were compared to wet season T_b trend series in terms of mean function slope and mean function maximum values. To determine whether T_b mean functions differed significantly between seasons, paired two-tailed T-test were used to compare mean function slopes and mean function maximum values . Among season comparisons enable us to test whether T_b differed

seasonally in terms of mean function slope and mean function maximum value. If T_b did not differ seasonally, this would be further evidence of thermoregulation.

To compare T_b variance with T_e variance, we calculated detrended series by subtracting the daily average series (trend) from the observed series, which resulted in locally stationary series with a time independent mean function equal to zero. Within seasons, detrended T_b was compared to detrended T_{e-min} and detrended T_{e-max} in terms of within day maximum and minimum deviations with one sample t-tests. Between seasons, dry season detrended T_b series were compared to wet season detrended T_b in terms of the maximum and minimum deviations with paired t-tests. These tests enable us to evaluate whether emergence timing and emergence-immersion interval modulation strategies restrict T_b variation relative to T_e variation. In total, 20 t-tests were calculated. The original critical p-value (α) is equal to 0.05. Therefore, a Bonferroni Correction indicated that the critical p-value for 20 t-tests should equal 0.0025 (i.e., corrected $\alpha = 0.05/20$; Dunn, 1961).

To determine if activity timing caused T_b to exhibit repeated patterns over the course of the respective study period and among animals, auto- and cross- correlation functions were calculated. Autocorrelation functions were calculated by comparing the degree of similarity between the observed T_b series and that of a time shifted (lagged) version of that same series. Comparing a series to a lagged version of the same series enables us to test whether the series repeats or whether it is unique throughout. In this way, within animal and season comparisons of the entire T_b series were made. Cross-correlation functions were calculated by comparing the degree of similarity between the two observed series, where one series is not shifted in time and the other is shifted

(lagged). Comparing a series to a lagged version of a distinct series enables us to test whether the two series share a similar set of repeating patterns or whether they are unique. When applied to T_b series, significant correlation demonstrated by auto- and cross- correlation functions indicate a repeating of emergence time and emergence-immersion intervals lengths, which indicates a behavioral mode of thermoregulation (Angilletta, 2009).

3. Results

Table 1 Seasonal Morphometrics: Mean body mass (g), tail volume (cc), and total length (cm) of adult *Heloderma horridum* at *Estacion de Biologia Chamela* during a dry and a wet season. Significant dry to wet season increases are signified with an asterisk (*).

Season	N	Weight*	Tail Volume*	Total Length
Dry (SD)	5	1068 (303.27)	156 (58.13)	69 (3.53)
Wet (SD)	5	1299 (295.14)	192 (56.52)	70 (6.11)
Mean Difference	5	231	36	1.2
Mean Percent Increase	5	21.6	23.1	1.4
Paired T-test of dry<wet (df)	5	p = 0.00168 (4)	p = 0.00002 (4)	p = 0.19890 (4)

3.1. Seasonal Morphometrics

Of the six adult *Heloderma horridum* monitored during the study, 5 showed a significant increase in mass (21.6%) and tail volume (23.1%) between the late dry season and early wet season (table 1). The sixth lizard was not included because it was not initially captured over a month after the initial 5 lizards were captured and measured.

3.2. Refuge Use Patterns and Distance between Relocations

Heloderma horridum occupied shallow earthen and rock crevice refuges, deep earthen refuges, and arboreal refuges. Lizards selected deeper refuges, and occupied them for longer periods during the dry season than during the wet season. Of 88 observations

during the dry season, beaded lizards were observed in deep burrows 91% and shallow burrows 9%, but were never found sheltering in tree cavities. Of 25 refuge observations during the wet season, beaded lizards were found in deep burrows 44%, shallow burrows 44%, and tree cavities 12%. These data indicate a significant seasonal shift in refuge choice by beaded lizards (paired t-test, $t = 2.96$ p-value = 0.03).

As described above, a Core-body Temperature Refuge Use Estimator (CTRUE) was developed to explore seasonal patterns of refuge use and timing of emergence. We evaluated the accuracy of this estimator by testing the agreement between CTRUE predictions and field observations with an Intra-class Correlation Coefficient (ICC) for each season (*see methods*, ICC is derived from a Kappa test, used by Davis et al., 2008). During the dry season, the CTRUE correctly identified the refuge occupancy status of beaded lizards on 23 of 25 (92%) refuge occupancy status trials (5 lizards with 5 replicates per lizard). During the wet season, CTRUE correctly identified the refuge occupancy status on 22 of 25 (88%) refuge occupancy status trials (5 lizards; 5 replicates per lizard). The Intra-class Correlation Coefficients test indicated that CTRUE predictions were “good” for the dry season (ICC = 0.714 ± 0.148 [95% CI], p-value <0.001) and “excellent” for the wet season (ICC = $0.766, \pm 0.124$ [95% CI], p-value <0.001). CTRUE predictions during the wet season were calculated to have a larger ICC because during this season errors occurred more evenly across the two observations classes (i.e. in refuge and outside refuge), thus the predictor did not exhibit a bias for a particular classification as it did during the dry season. These results suggest that emergence times, emergence-immersion intervals (time spent outside of refuges or shelters), and the proportion of time *Heloderma horridum* spend within shelters can be

accurately estimated from core body temperature data (CTRUE) generated from iButton dataloggers (Davis et al., 2008).

In both the dry and wet season study periods, beaded lizards emerged from refuges during the daylight and dawn twilight hours (88.3%, $n = 163$), and occasionally at night (19 occasions, or 11.7%, $n = 163$; Fig. 1). During the dry season, beaded lizards showed a bimodal pattern of refuge emergence with a strong peak between 16:00 and 18:59 hrs that includes 46.5% of all dry season emergences, and a smaller peak between 06:00 and 08:59 h that included 20.6% of all dry season emergences (Fig. 1). During the wet season, beaded lizards showed a pattern of emergence that fit a more normal distribution, with a peak between 13:00 and 16:59 h that included 48.5% of observations (Fig. 1). The distribution of dry and wet season emergence times were found to differ significantly (Kolmogorov-Smirnov Tests, $D = 0.288$, $p = 0.0006$)

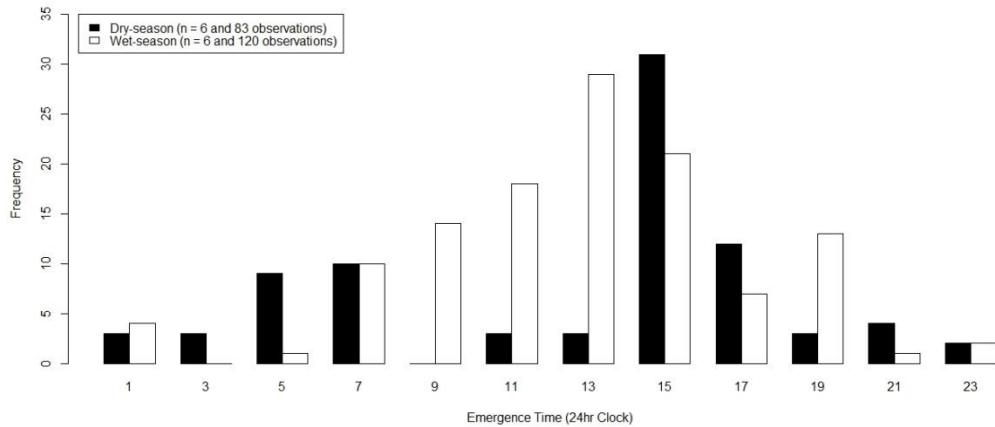


Fig. 2. Refuge Emergence Time By Season: Timing of emergence (2 hour bins) by *H. horridum* from refuges, based on a Core-body Temperature Refuge Use Estimator (CTRUE). Beaded lizards showed significantly different patterns of emergence between the Dry and Wet-seasons (Kolmogorov-Smirnov Tests, $D = 0.288$, $p = 0.0006$).

During the dry season, beaded lizards remained on the surface for relatively brief periods as compared to the wet season (dry season median = 3.5 hrs and wet season median = 9.6 hrs); emergence-immersion interval frequency peaked between 0 and 3 hours (47.0%, n = 83). During the wet season, lizards spent more time on the surface; emergence-immersion interval frequency peaked between 5 and 10 hours (34.2%, n = 120). Both dry and wet season emergence-immersion interval frequencies were positively skewed, as a result of occasions when beaded lizards spend extended periods outside of shelters on the surface. These extended periods of surface emergence were more common during the wet season, when beaded lizards spent much less time in burrows (Fig. 2). On average, beaded lizards remained in shelters 90.8% of the time (range = 87.8 to 92.6, n = 5) during the dry season and only 58.5% of the time (range = 43.4 to 79.2, n = 6) during the wet season (one-tailed paired t test, $t = -4.629$, $p = 0.005$, Table 2). Although lizards spent much more time in refuges during the dry season, they did not necessarily travel proportionately shorter distances between relocations. Distances between relocations during the dry season averaged 291 m, while wet season distance traveled averaged 369 m (n = 6, paired t-test, $t = -0.606$, $p = 0.6$) (Fig. 3).

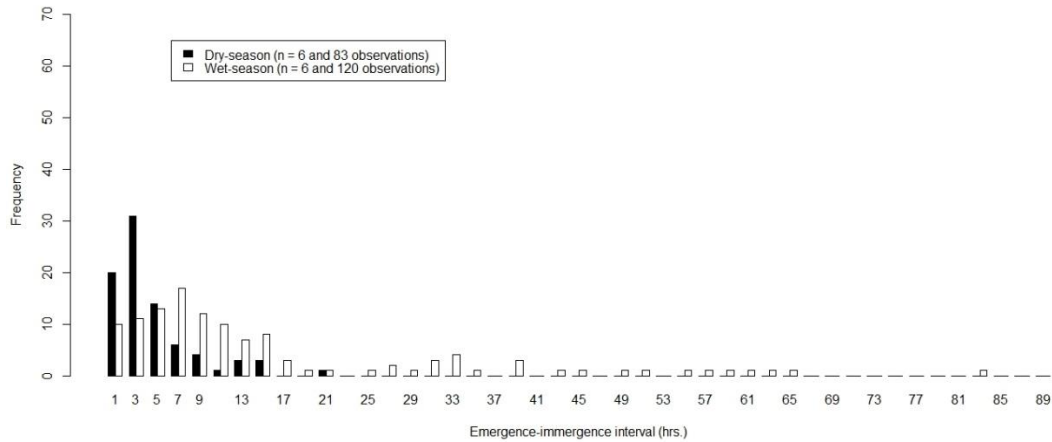


Fig. 3. Emergence-immersion Intervals by Season: Hours spent outside of refuges (emergence-immersion intervals) dry vs wet season (n = 57 and n = 105, respectively). On average, beaded lizards spent 32% more time outside of shelters during the wet season than during the dry season (see table 2)

Table 2 Percent Refuge Use by Seasons: Percent refuge use during the dry season (May 17- June 20) was significantly greater than during the wet season sampling period (June 29 - August 02; p = 0.005)

Lizard No.	Dry-season	Wet-season
0.229	90.7	57.7
0.088	90.7	43.7
0.210	92.2	59.8
0.250	91.2	64.5
0.190	88.2	80.4
0.020	N/A	51.7
mean	90.6	59.6

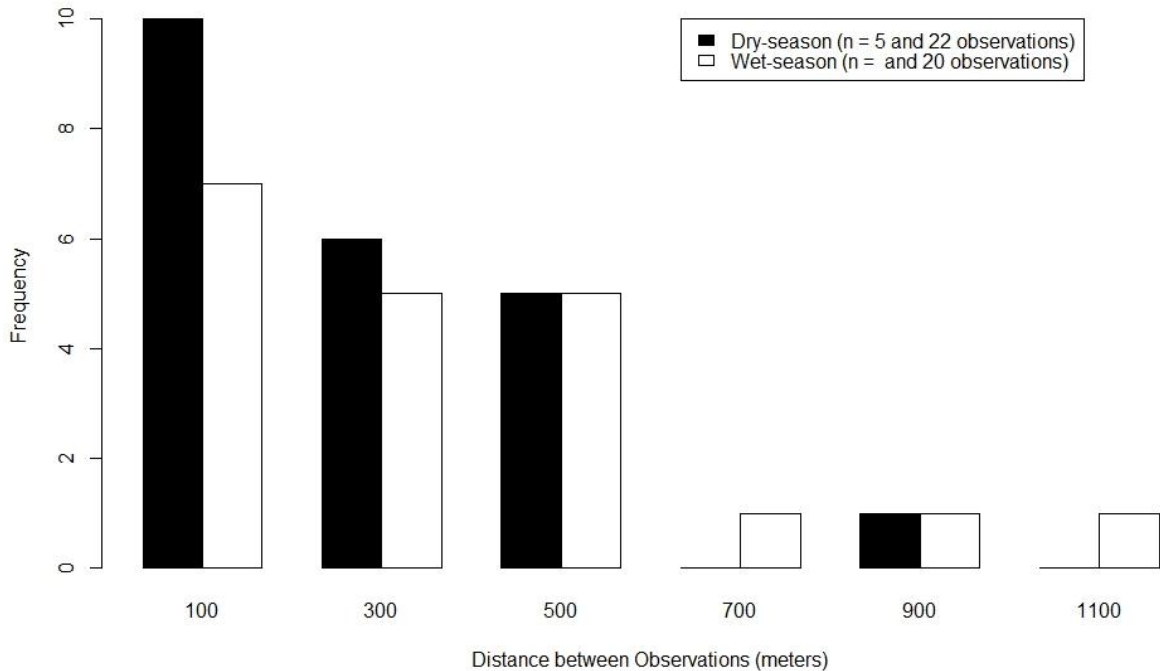


Fig. 4. Straight-line Distance between Relocations by Season: Comparison of straight-line distances between relocations of 6 beaded lizards between dry and wet seasons. The average dry-season movement was estimated to be 291m, while the average wet-season movement was estimated to be 369m (paired t-test, $p \sim 0.58$).

3.3. Thermal Biology

Despite marked seasonal differences in T_e series, T_b series from this group of *Heloderma horridum* showed little variation between seasons and exhibited daily means that ranged from 26.1 to 30.1°C in both seasons ($n = 6$ lizards). In addition to being independent of season, daily mean T_b series were cooler than measured T_e , with the notable exception of wet season T_{e-min} which was strongly correlated with wet season T_b . During the dry season, the temperature of the full shade copper model (T_{e-min}) ranged between 19.5 and 46.0 °C (difference = 26.5 °C) while the temperature of the full sun

copper model (T_{e-max}) ranged between 19.5 and 60.5 °C (difference = 41 °C; Figure 4 & Table 3). During the wet season, T_{e-min} and T_{e-max} ranged between 22.5 and 33.0 °C (difference = 10.5 °C) and 22.0 and 57.5 °C (difference = 35.5°C), respectively (Fig. 4).

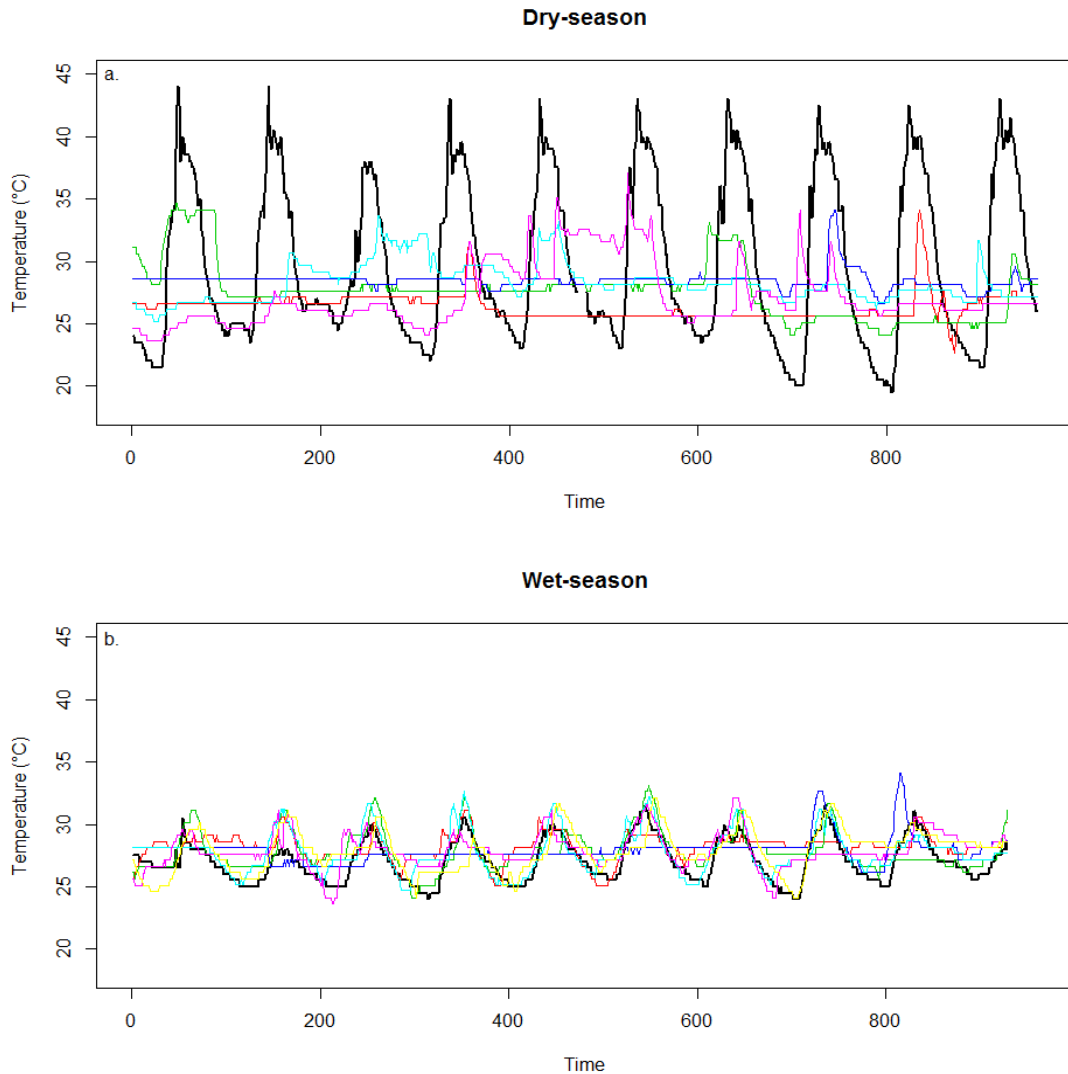


Fig. 5. Dry and Wet Season T_b and T_e Time Series Plots: Ten day comparison of core-body temperature (T_b , green, blue, red, pink, purple, and yellow) and minimum operative temperature (T_{e-min} , black). (a.) T_b during the dry season exhibited long periods of homeothermy that were punctuated by spikes in T_b that correspond to refuge emergence. (b.) T_b during the wet season was strongly correlated with T_{e-min} . X-axis is time, measured here in 15 minute steps, that is, 96 steps equals 24 hours. Zero on the x-axis of plot ‘a.’ is equal to May 17, 2011 at 0:00 hours. Zero on the x-axis of plot ‘b.’ is equal to June 29, 2011 at 0:00 hours

As demonstrated in the preceding sections, *Heloderma horridum* exhibit seasonal differences in refuge use and emergence timing, and these seasonal adjustments lead to daily mean T_b time series that in terms of mean function slope and mean function maximum value do not differ seasonally (Welch two sample t-test: slope $t = -0.178$, slope $p = 0.864$ and maximum value $t = -0.605$, maximum value $p = 0.571$; Bonferroni Correction $\alpha = 0.0025$; Table 3). Refuge use and emergence timing were also evident in T_b series in terms of repeated patterns of T_b . During the dry season, late afternoon spikes in T_b were repeated multiple times by all lizards over the course of this study period and the timing of these T_b spikes during a twenty-four hour day were consistent as is demonstrated by significant auto- and cross- correlation functions ($p < 0.001$) at lags equal to ± 96 (1 day), ± 192 , (2 days) ± 288 (3 days), etc). During the wet season, T_b was strongly correlated to $T_{e-\min}$ when animals were not in refuges. As a result, these series also showed significant auto- and cross- correlation structure, which also referred to as short- and long- term series memory (auto- and cross- correlation functions $p < 0.001$, lags ± 96 , ± 192 , ± 288 , etc). These results demonstrate that *Heloderma horridum* maintained consistent T_b series throughout each study period despite variable T_e , which would only occur if these lizards were thermoregulating.

Table 3 Time Series Measures of Thermoregulation Effectiveness: *Heloderma horridum* demonstrated control over core-body temperature (T_b) relative to within and among season operative temperature (T_{e-min} and T_{e-max}) variation.

	Mean Function Slope ($^{\circ}\text{C}$)	Maximum Mean Function Value ($^{\circ}\text{C}$)	Maximum Positive Detrended Deviation ($^{\circ}\text{C}$)	Maximum negative Detrended Deviation ($^{\circ}\text{C}$)
Mean dry season T_b	0.00032	28.6	7.8	4.5
Mean wet season T_b	0.00033	28.3	5.4	3.8
Dry season T_e maximum	0.00090	34.4	27.0	13.5
Dry season T_e minimum	0.00100	31.7	17.2	10.5
Wet season T_e maximum	0.00200	34.9	27.6	11.4
Wet season T_e minimum	0.00030	27.0	7.0	3.6

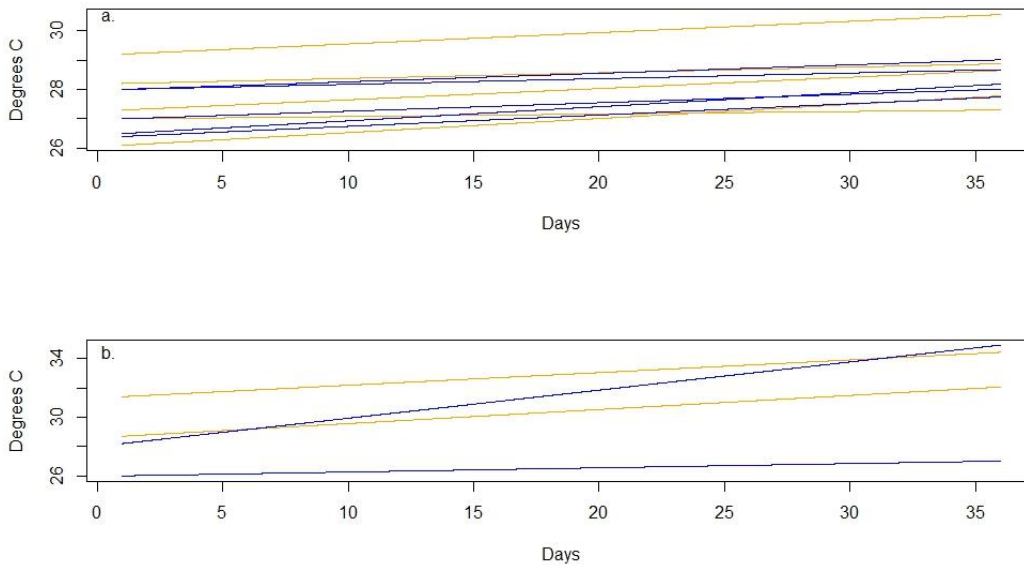


Fig. 6. T_b and T_e Mean Functions by Season: T_b series recorded from *Heloderma horridum* exhibited mean functions that were both cooler and flatter than series recorded from T_e models. Approximation of the mean function (μ_{xt}) calculated from core-body temperature (T_b) and operative temperature models (T_{e-min} & T_{e-max}). (a.) approximate mean function of T_b measured during the dry (orange) and wet (blue) seasons. (b.) approximate mean function of T_{e-min} & T_{e-max} measured during the dry (orange) and wet (blue) season.

Heloderma horridum also excreted control over their daily mean T_b by avoiding relatively hot T_e , as is evidenced by dry and wet season T_b mean functions that had significantly smaller slopes relative to dry season T_{e-min} & T_{e-max} and wet season T_{e-max} mean functions (one sample one tailed (less than) t-tests: dry season T_{e-min} $t = -9.094$, $p = 0.0004$, $H_o = 0.001$; dry season T_{e-max} $t = -7.761$, $p = 0.0015$ $H_o = 0.0007$; and wet season T_{e-max} $t = -39.528$, $p = 0.0000001$, $H_o = 0.002$; Bonferroni Correction $\alpha = 0.0025$; Fig. 5). The maximum values of T_b mean functions were also significantly cooler than the maximum value of dry season T_{e-min} , dry season T_{e-max} , and wet season T_{e-max} mean functions (one sample t-test: dry season T_{e-min} $t = -5.6102$, $p\text{-value} = 0.0025$, $H_o = 31.7^\circ\text{C}$; dry season T_{e-max} $t = -10.528$, $p\text{-value} = 0.0002$, $H_o = 34.4^\circ\text{C}$; and wet season T_{e-max} $t = -33.259$, $p\text{-value} = 0.0000002$, $H_o = 34.9^\circ\text{C}$; Bonferroni Correction $\alpha = 0.0025$; Fig. 6). Conversely, wet season T_b series did not differ from wet season T_{e-min} in terms of slope (one sample less than t-test: $t = 0.791$, $p\text{-value} = 0.7675$, $H_o = 0.0003$; Bonferroni Correction $\alpha = 0.0025$), but wet season T_b mean function maximum value of 28.3°C was warmer than wet season T_{e-min} mean function maximum value of 27.0°C (one sample less than t-test: $t = 6.351$, $p\text{-value} = 0.001$, $H_o = 27.0^\circ\text{C}$; Bonferroni Correction $\alpha = 0.0025$). Finally, all daily mean values for T_b series were cooler than all mean values for dry season T_{e-min} and T_{e-max} and wet season T_{e-max} . By sheltering in refuges when preferred T_e was not available during the dry season and utilizing wet season T_{e-min} enabled *Heloderma horridum* to insulate themselves from extreme T_e , thus producing T_b series that are independent of long term increases in Dry and wet season T_e . This strategy also resulted in cooler T_b 's relative to the available T_e in both seasons.

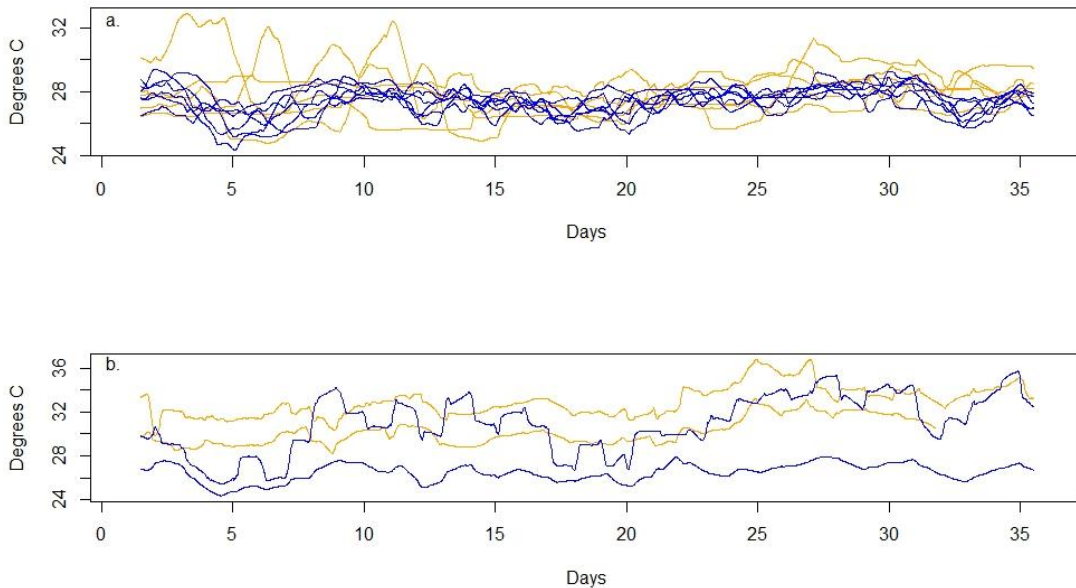


Fig. 7. Daily average T_b series showed remarkable similarity within and between seasons, while Daily average T_e varied greatly by location and season. Daily averages calculated from core-body temperature (T_b) and operative temperature models (T_{e-min} & T_{e-max}). (a.) Daily average T_b measured during the dry (orange) and wet (blue) seasons. (b.) Daily average T_{e-min} & T_{e-max} measured during the dry (orange) and wet (blue) season.

Seasonal adjustments to refuge use and emergence patterns also enabled *Heloderma horridum* to limit within day T_b variations. Within day variations are measured herein in terms of maximum positive and negative deviations from a mean zero detrended T_b series. Within day maximum positive and negative deviations of T_b were similar between seasons (paired t-test, maximum positive deviations p-value = 0.0547 and maximum negative deviations p-value = 0.0549; Bonferroni Correction $\alpha = 0.0025$). This variance similarity between seasons points to a threshold limit for maximum positive and negative T_b deviations, which could only be achieved through thermoregulation. Within day maximum positive and negative deviations of dry season

T_b were significantly less than within day maximum positive and negative deviations of dry season T_{e-min} (one sample less than t-test: maximum positive deviations $t = -12.055$, $p\text{-value} = 0.0001$, $H_o=17.2^\circ\text{C}$ and maximum negative deviations $t = -34.298$, $p\text{-value} = 0.000002$, $H_o=10.5^\circ\text{C}$; Bonferroni Correction $\alpha = 0.0025$) and dry season T_{e-max} (one sample t-test, maximum positive deviations $t = -24.651$, $p\text{-value} = 0.000008$, $H_o=27.0^\circ\text{C}$ and maximum negative deviations $t = -51.504$, $p\text{-value} = 0.0000004$, $H_o=13.5^\circ\text{C}$; Bonferroni Correction $\alpha = 0.0025$). Within day maximum positive and negative deviations of wet season T_b were significantly less than within day maximum positive and negative deviations of wet season T_{e-max} (one sample less than t-test, maximum positive deviations $t = -68.017$, $p\text{-value} = 0.0000001$, $H_o=26.7^\circ\text{C}$ and maximum negative deviations $t = -39.387$, $p\text{-value} = 0.000001$, $H_o=13.5^\circ\text{C}$). Finally, wet season T_b did not vary significantly less than T_e in terms of maximum positive deviations (one sample less than t-test, $t = -4.633$, $p\text{-value} = 0.005$, $H_o = 7.0^\circ\text{C}$; Bonferroni Correction $\alpha = 0.0025$) and maximum negative deviations (one sample less than t-test, $t = 0.895$, $p\text{-value} = 0.79$, $H_o = 3.6^\circ\text{C}$; Bonferroni Correction $\alpha = 0.0025$). These results indicated that *Heloderma horridum* behaviorally lowered the variance of all measured T_b series relative to the variance present in dry season T_{e-min} and T_{e-max} and wet season T_{e-max} . Nevertheless, conformity to wet season T_{e-min} caused wet season T_b to match wet season T_{e-min} in terms of directions and degree of variance.

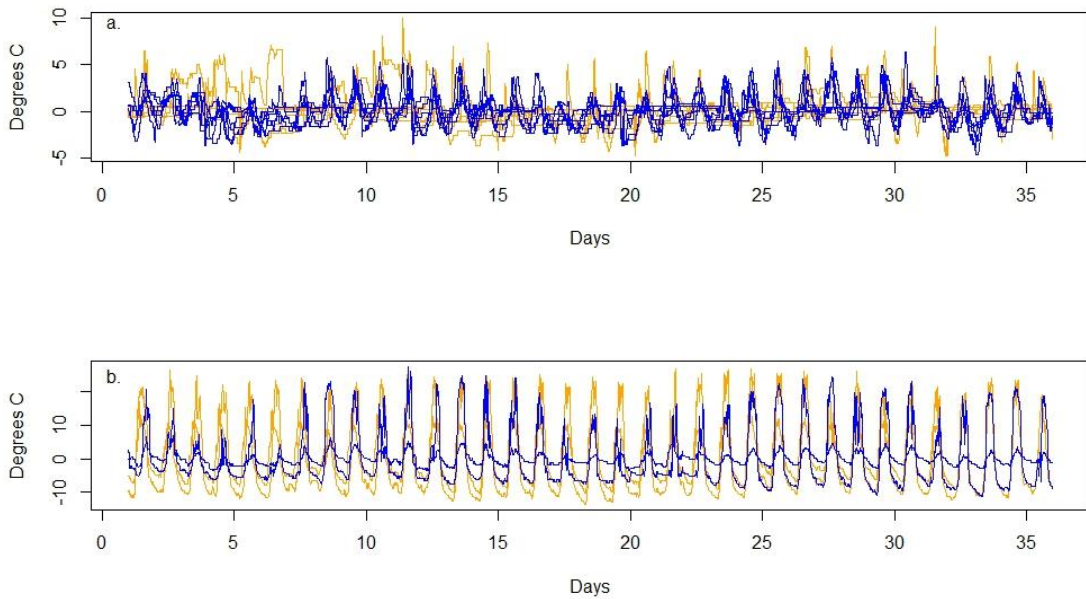


Fig. 8. Detrended T_b series show similar maximum positive and negative deviations among and within seasons, while Detrended T_e series exhibit seasonal and location dependent variations in maximum positive and negative deviations. Detrended time series recorded from core-body temperature (T_b) and operative temperature models (T_{e-min} & T_{e-max}). (a.) detrended T_b measured during the dry (orange) and wet (blue) seasons. (b.) detrended T_{e-min} & T_{e-max} measured during the dry (orange) and wet (blue) season.

4. Discussion

4.1. Seasonal Morphometrics

During the wet season, *Heloderma horridum* body weight and tail volume increased, as predicted. Seasonal weight gains have previously been observed in *Heloderma suspectum* s. and *Heloderma horridum* (Beck and Lowe, 1991; Davis and DeNardo, 2010). However, weight gain is limited in its utility to predict the energetic status of a lizard, as weight can change with a single meal, defecation, or drink of water (Beck and Lowe, 1991; Davis and DeNardo, 2007). Since Helodermatid lizards store lipids in their tail, tail volume provides a better prediction of the lizard's energetic status (Beck, 2005; Bogert and Martin del Campo, 1956; Davis and DeNardo, 2009). Seasonal increases in tail volume have been observed in *Heloderma suspectum* (Davis and DeNardo, 2009) and we present evidence that tail volume is also seasonally dependent in *Heloderma horridum*. The increase in tail volume we observed in the wet season is likely a result of increased foraging success and to a lesser extent to the increased availability of liquid water (Davis and DeNardo, 2007, 2009, 2010).

Energy and water reserves, therefore, are replenished each wet season. These reserves are then budgeted to sustain the lizard through periods of resource scarcity encountered during the dry season. As a result, *Heloderma horridum* during the dry season are less active and primarily emerge from refuges in the late afternoon (~15:00 hrs) when operative temperatures are dropping but are also still within the activity range of this species. In combination, these strategies minimize dry season expenditure from energy and water reserves (Gienger et al., 2014).

4.2. Refuge Use Patterns and Distance between Relocations

As predicted, *Heloderma horridum* at the Chamela field station avoided hot operative temperatures during the dry season by selecting deeper refuges, by primarily emerging from refuges in the late afternoon when operative temperatures are dropping, and by spending a greater proportion of the dry season in refuges. Conversely, during the wet season lizards selected shallower refuges, spent less time in refuges, and emerged from refuges at more diverse times of day. Seasonal timing of emergence and the proportion of time spent in shelters in this study agrees with those reported from other studies of *Heloderma horridum* (Beck and Lowe, 1991) and *H. charlesbogerti* (Ariano-Sánchez and Salazar, 2015). Seasonal differences in resource availability influence the type of refuges selected, the amount of time spent in refuges, and the distance traveled by many different reptiles in many different seasonal biomes (Ariano-Sánchez and Salazar, 2015; Beck, 1990; Beck and Lowe, 1991; Beck and Jennings, 2003; Bulova, 1994; Davis and DeNardo, 2010; Hyslop et al., 2009; McCaster and Downs, 2006). In seasonally dry tropical forest, seasonality drives the availability of water, food, and suitable operative temperatures. Dry forest species, therefore, have evolved behavioral adaptations to cope with this seasonality (Ariano-Sánchez and Salazar 2015; Beck and Lowe, 1991; Beck, 2005). Accordingly, we interpret dry season preferences shown by *Heloderma* for deep refuges, more strictly defined emergence times, and increased refuge occupancy as responses to avoid the high operative temperature extremes characteristic of the dry season. Furthermore, wet season behaviors indicate a willingness to conform to the relatively cool operative temperatures that prevail during the wet season and to exploit more favorable surface conditions that enable beaded lizards to forage and build water as

well as lipid reserves after the summer rains arrive. The avoidance of dry season extremes has also been observed in *Rhinoclemmys rubida perixantha*, which is only rarely observed on the surface during peak dry season conditions (Butterfield et al., 2017).

4.3. Thermal Biology

Despite marked differences in dry and wet season operative temperatures *Heloderma horridum* maintain daily mean T_b that were statistically similar in both seasons. Daily mean T_b varied around a set of mean functions that ranged from 26.1 and 30.1 in both seasons, which brackets the mean activity T_b (29.5°C) of *Heloderma horridum* reported by Beck and Lowe (1991) and encompasses the range of active *Heloderma suspectum* s. core-body temperatures reported by Beck (1990). Daily means during the dry season are strongly influenced by long periods of homoeothermy achieved within deep shelters. Daily means during the wet season, however, are most strongly influenced by T_{e-min} because lizards conformed to this temperature while outside of refuges.

Heloderma horridum maintained consistently cooler and less variable T_b as compared to dry season T_{e-min} and T_{e-max} and wet season T_{e-max} models by limiting activity to daily and seasonally optimal times and selection of deep refuges during the dry season. During the wet season, lizard T_b conformed to T_{e-min} , which was relatively cool and stable. Wet season T_{e-min} was also similar to dry season T_b , which lead to consistent T_b mean functions (μ_{xt}) over the dry and wet season. Seasonal activity shifts and microhabitat selection has been observed in other large reptiles as a means to regulate T_b

(Christian & Weavers, 1996; Seebacher et al., 1999; Seebacher et al., 2003).

Accordingly, we interpret our observations of cooler and less variable T_b as evidence of behavioral thermoregulation and as an adaptation for avoiding seasonally and spatially T_e extremes.

The behavioral selection of a relatively cool T_b when a warmer T_b is available runs counter to the prevailing hypothesis that the maintenance of a hotter T_b leads to an increase in Darwinian fitness, and is thus favored over the long-term (Angilletta et al., 2009; Huey and Kingsolver, 1989). The ‘hotter is better’ hypothesis hinges on the fact that foraging behaviors, fight or flight responses, digestion, etc. are optimized at a high T_b (Hertz et al., 1982; Seebacher, 2005). But the constraint of seasonal resource scarcity present in dry forest biomes forces the inhabiting species to carefully manage their energetic and water reserves (Beck and Lowe, 1991; Murphy and Lugo, 1986). As such, *Heloderma horridum* have evolved a preference for a relatively cool mean T_b , which allows them to slow both their metabolism and evaporative water loss, leading to both energy and water reserve savings (Beck et al., 1995; DeNardo, 2004; Gillooly, 2001; Gienger et al., 2014). Furthermore, the Helodermatid and their Monstersaurian ancestors have evolved to prey on the slow and largely helpless eggs and young of other species and use venom as their primary defense against predators, both of which alleviates the need to maintain a high T_b to be able to capture prey or evade predators (Beck 2005; Gienger et al. 2014). For ‘lizards in the slow lane’ a cool internal body temperature suits the purpose of carefully managing energy and water stores, allowing this and other dry forest species to survive where most others would perish.

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