

THERMAL ECOLOGY OF TEXAS HORNED LIZARDS (*PHRYNOSOMA CORNUTUM*) IN
SMALL TEXAS TOWNS

by

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INTRODUCTION

Organisms occupy different habitats based on trade-offs between maintaining proper physiological processes within certain limits and avoiding predators, foraging, and reproductive opportunities (Huey 1991). Lizards are ectothermic and entirely dependent on their surroundings to maintain proper body temperatures which are potentially strong determinates of habitat choice (Cowles and Bogert 1944, Vitt et al. 2008). Lizards employ a variety of physiological adaptations, behaviors, and microhabitats to maintain ideal body temperatures throughout the day even as daytime temperatures fluctuate by as much 17 °C in some areas like the American southwest (Angilletta 2009). The importance of a lizard's thermal environment cannot be understated, and they are largely dependent on this environment to forage for food, reproduce, and avoid predation (Angilletta 2009). When lizards are exposed to operative environmental temperatures (T_e ; Table 1) that are greater than their preferred body temperatures (T_{sel} ; Table 1) their activity is restricted. Because of this, lizards are particularly vulnerable to extinction from climate change because at higher temperatures females must spend more time thermoregulating in the shade and less time foraging out in the open. This lower foraging efficiency decreases the number and quality of offspring they can produce leading to declining populations and eventual extinction (Sinervo 2010). At least 20% of all lizard species are predicted to be extinct by 2080 under current climate models (Sinervo et al. 2010).

In squamates, most physiological mechanisms are driven by temperature, therefore body temperature (T_b ; Table 1) is carefully regulated within a narrow range via behavioral adjustments (Cowles and Bogert 1944). The majority of thermal studies use T_b data collected from the field in contrast to preferred body temperature (T_{sel}) which is measured in laboratory conditions.

Preferred body temperature (T_{sel}) is the range of body temperatures an ectotherm chooses to maintain by behavioral adjustments so it can continue normal activities (Brattstrom 1965).

Suitable thermal habitat is fundamental for lizards and other squamates (Heatwole 1977, Dunham et al. 1989, Huey 1991). The availability of microhabitats that offer temperatures suitable for lizards determine how far lizards must move and how much energy they expend in finding an ideal thermal environment (Grbac and Bauwens 2001; Sears et al. 2016). While optimal body temperature may be achieved by behavior, physiology, and morphology, reptile ranges and activity patterns are constrained by the distribution of microhabitats across space and time (Grbac and Bauwens 2001). An understanding of the thermal regimes in different microhabitats is important to understanding thermoregulatory behavior, habitat quality, and cost of living in different types of environments.

Lizards living in urban environments face additional challenges when it comes to thermal environments. Urban areas are often warmer and warm faster than natural areas because roads, buildings, and other concrete surfaces lower albedo rates (Ackley et al. 2015, Kolbe et al. 2016, Taha 1997). Research has shown that different types of landscaping in urban areas can have a large effect on whether temperatures are within optimal ranges for lizards (Ackley et al. 2015). It has been shown that mesic landscaping with spray irrigation and increased heterogeneity of plants can keep areas significantly more cooler and within lizards' preferred temperature range 100% of their active period compared to xeric and native landscaping in some areas (Ackley et al. 2015). The importance of thermal microhabitats in urban areas for determining the densities of lizards living in urban areas is currently unknown.

Table 1: Metrics and indices of thermal ecology used in this study (Hertz et al. 1993)

Index	Definition
T_{sel}	Selected body temperature; central 50% of body temperatures measured in thermal gradient
T_e	Operative environmental temperature, measured by models in microhabitats
d_e	Thermal quality of habitat, measured as mean absolute deviation of T_e from T_{sel}
T_b	Field active cloacal temperature
d_b	Accuracy of thermoregulation, measured as mean absolute deviation of T_b from T_{sel}
$d_e - d_b$	Effectiveness of thermoregulation of Blouin-Demers and Weatherhead (2001)
E	Effectiveness of thermoregulation; $E = 1 - d_b/d_e$

Texas horned lizards inhabit arid and semi-arid open habitat with some vegetation. Horned lizards are often active over longer periods of time than sympatric species and display variable body temperatures which is attributed to relaxed thermoregulation (Pianka and Parker 1975). Texas horned lizards have a high preferred body temperature (T_{sel}) of 34.2—38.5 °C (Prieto and Whitford 1971, Lara-Reséndiz et al. 2015, Table 2). Their upper critical temperature (CT_{max}), the temperature at which they lose the ability to move, is also very high (45.9 - 48.1 °C) (Ballinger and Shrank 1970, Kour and Hutchison 1970, Prieto and Whitford 1971). These temperature tolerances are higher and significantly more variable than other sympatric species of desert lizards (Pianka and Parker 1975). Due to their ecology of being an ant specialist, it is likely that this relaxed thermoregulation allows horned lizards to withstand direct sunlight for longer periods of time while foraging for ants in the open. Their cryptic camouflage and ability to withstand higher temperatures for longer also aids in reducing predation risk since they do not have to make themselves visible when shuttling back and forth from shade (Pianka and Parker 1975, Guyer and Linder 1985).

Table 2: Selected body temperatures (T_{sel}) of Texas horned lizards and T_{sel} range (25 and 75 quartiles) in °C.

N	T_{sel}	T_{sel25}	T_{sel75}	References
10	38.5 ± ND	37.5	39	Prieto and Whitford 1971
97	34.2 ± 0.1	32.5	36	Lemos-Espinal and Smith 2009; Lara-Resendiz et al. 2015
19	35.7 ± 0.3	33.5	38.5	Present study

The Texas horned lizard (*Phrynosoma cornutum*) is a threatened species in the state of Texas (Texas Conservation Action Plan - TCAP 2012) due to widespread population declines. These declines are attributed to a variety of factors including habitat loss, introduction of the Red Imported Fire Ant (*Solenopsis invicta*) (RIFA), loss of their preferred prey Harvester ants (*Pogonomyrmex spp.*), and over-collecting for the pet trade (Donaldson et al. 1994, Dixon 2000, Henke 2003). They are, however, found in two small towns in south Texas, (Kenedy and Karnes City) at higher-than-normal densities (52 lizards/ha) than are observed in the wild (3-10 lizards/ha) (Whitford and Bryant 1979, Whiting et al. 1993, Ackel 2015). Research has shown that the high density of lizards observed in these towns may be due to a variety of factors including: isolation due to roads and buildings (Wall 2014), a dietary shift to consuming smaller more abundant prey items (Alenius 2018), and reduced predation pressure as compared to natural areas by some types of predators (Mirkin et al. 2021). Despite high densities, Texas horned lizard populations in these towns have been declining since the 1990s (Wade Phelps pers. comm.). Reasons for these declines are unknown but it has been observed that when residents remove vegetation from around trees and along fence rows from the areas that lizards inhabit the lizards disappear from those areas or become less common (unpub. data). With reduced predation pressure in town, it is unlikely the lizards disappear from cleared areas due to predation. Another factor that may be responsible for these local extirpations is that when vegetation is removed the

thermal environment is altered and no longer capable of offering ideal temperatures for Texas horned lizards.

We hypothesize that vegetation is important for thermal regulation in Texas horned lizards and their decline in these towns could in part be due to degradation of the thermal landscape caused by the removal of important microhabitats. The goal of this project is to assess the quality and variability of the thermal environment for Texas horned lizards in our study sites and to determine if thermal quality are correlated to lizard presence and/or density. We also determined the selected body temperature (T_{sel}) in a laboratory gradient to better understand temperature preferences at our field sites. We determined body temperatures (T_b) of horned lizards in the field and also placed models with temperature loggers in different microhabitats to better understand the range of operative temperatures (T_e) available to horned lizards.

METHODS

Fieldwork

We have been monitoring Texas horned lizards in two small towns (Kenedy and Karnes City, TX) since 2013 and have established 15 plots (3 in Kenedy and 12 in Karnes City) where we monitor horned lizards during the summer months. The plots are in school yards, alleyways, and abandoned lots and vary in size from 0.07-1.11 hectares. The habitat is dominated by Honey Mesquite (*Prosopis glandulosa*), Anacua (*Ehretia anacua*), and Sugarberry (*Celtis laevigata*) along with native grasses and ornamental plants. The 15 plots are censused (by walking transects with 2-4 people) between 8:00-12:00 and 16:00-20:00 which corresponds to active periods for Texas horned lizards (Moeller et al. 2005). Transects are conducted at each site 8 times each summer, divided up into three sampling periods: 2 weeks in late May/early June, 1 week in early

July and 1 week in late July and early August. Red Harvester Ant (*Pogonomyrmex barbatus*) and RIFA mounds are mapped in these plots and horned lizards are captured and belly spots pictured (for identification), sexed, measured (snout to vent length in mm and weight in grams), and a DNA sample is obtained by swabbing the cloaca with a small Q-tip (Williams et al. 2012).

To determine the thermal quality of our sites, we used 3D printed models of adult Texas horned lizards (Watson and Francis 2015, Mirkin et al. 2021). Models were printed with acrylonitrile butadiene styrene (ABS) and painted with 33% reflective paint (Rustoleum™ gray primer) that corresponds to the reflectivity of horned lizards (Adolph 1990, Lara-Resendiz et al. 2015). The underside of the model had a recessed opening that held a DS1922L Thermochron™ temperature logger that records the temperature at a resolution of $\pm 0.2^\circ\text{C}$ (Fig.1). Self-fusing repair tape was used to seal the temperature logger in the model.



Figure 1: Horned lizard model equip with a DS1922L Thermochron™ temperature logger embedded in the belly area to approximate T_e available to lizards.

In 2019, a total of 15 models were placed at five sites from June 2 – 8 and 30 models (after we were able to purchase more ibuttons) at 10 sites from June 30 – July 6 and Aug. 1 – 8. In 2020 and 2021, a total of 45 models were placed at 15 sites from June 1– June 14, July 1– 6, and August 1– 6. At each site one model was placed in the open, one under vegetation, and one buried ~2 cm under the soil surface to mimic the microhabitats horned lizards utilize (Dzialowski

2005). Models were placed in areas horned lizards had been previously observed for most sites. Temperature was recorded every 10 minutes from 7:00 – 20:00 to estimate T_e throughout the horned lizard's activity period (Lara-Resendiz et al 2015). The models were calibrated against live lizards by first capturing a lizard and measuring the cloacal temperature of the lizard (using a small temperature probe connected to a digital thermometer; GDEALER Model DT8, accuracy ± 1 °C, resolution ± 0.1 °C) within 30 seconds of capture and then placing a model in the same spot as the captured lizard and recording the temperature on the data logger after 10 minutes (Dzialowski 2005, Kolbe et al. 2016).

Laboratory work and thermoregulation indices

In 2021, T_{sel} was recorded using a laboratory thermal gradient that consisted of a plastic box 88.6 cm x 42.2 cm x 15.6 cm (length, width, and height) that was filled with 2-3 cm of sand (Hertz et al. 1993, Angilletta 2009, Sinervo et al. 2010) (Fig. 2). At one end of the box, a Phillips™ 250 W heat light bulb was placed 33.7 cm above the substrate to create a thermal gradient from 25-60 °C (Fig. 3). The gradient was housed in a climate-controlled room at a constant temperature of 20 °C. We captured adult lizards (> 69 mm) in the field and allowed them to acclimate in the thermal gradient overnight (between 12-23 hours).

Artificial lighting mimicked the natural daylight cycles at our field location (lizards were exposed to natural lighting through windows and artificial lighting) and lizards remained in the gradient from 8:00 – 20:00. T_{sel} was measured every two hours starting at 8:00 with the same temperature probe utilized in the field for cloacal temperatures and with a Etekcity Lasergrip 774 infrared thermometer (resolution ± 0.1 °C) for body surface temperature. Body surface temperature approximates core body temperatures in smaller lizards because of rapid heat transfer between the core and the body surface (Bakken 1992, Luna et al. 2013, Thompson et al.

2018). We validated this finding for Texas horned lizards by comparing the cloacal and body surface temperatures. The 25 percent and 75 percent quartiles of the lizard's thermal gradient interquartile range (T_{sel25} and T_{sel75}) were used as the upper and lower T_{sel} (Hertz et al. 1993, Lara-Resendiz et al. 2015).



Figure 2: Thermal gradient set up with heat lamp on one end of the box to create a gradient of temperatures that the lizard can choose from. Hotter temperatures are closer to the light while getting progressively cooler towards the other end of the box.

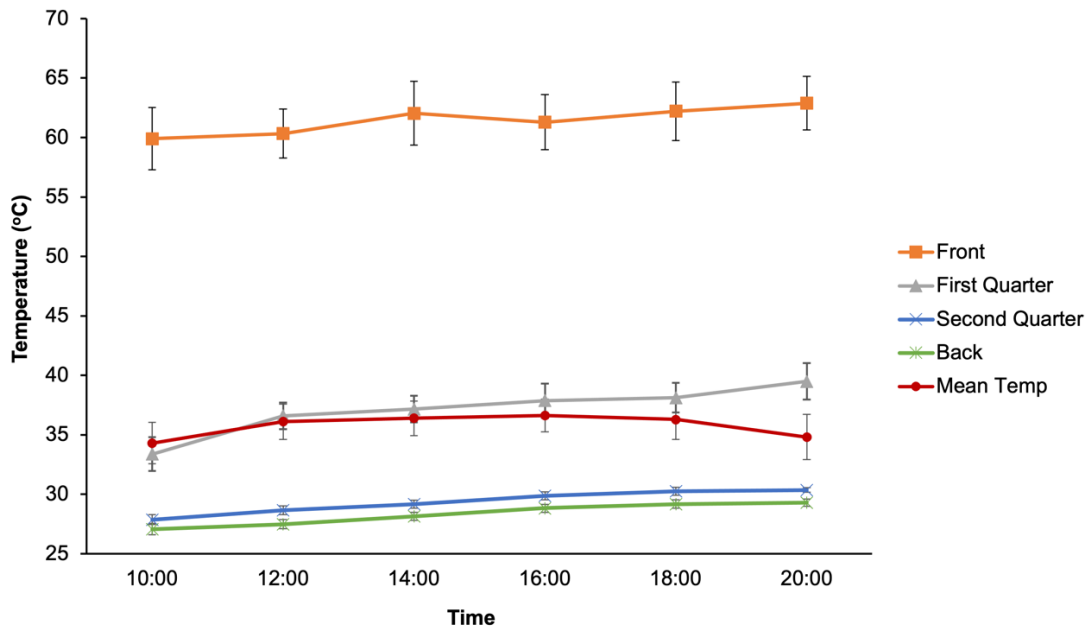


Figure 3: Mean temperatures over time in the four quarters of the thermal gradient. Error bars represent ± 2 SE. Orange represents the front of the box that is directly underneath the heat lamp, grey is the first quarter, blue is the second quarter, and green is the back of the box and is the furthest away from the heat lamp. The red line represents the mean cloacal temperatures from all lizards in the thermal gradient (n=19).

The data on T_b , T_{sel} , and T_e were used to calculate the accuracy index of thermoregulation (d_b) and habitat thermal quality (d_e) as follows: if T_b or $T_e < T_{sel}$, then $d_b = T_b - T_{sel25}$ and $d_e = T_e - T_{sel75}$, and if T_b or $T_e > T_{sel}$ then $d_b = T_b - T_{sel75}$ and $d_e = T_e - T_{sel25}$, respectively. When T_b or T_e values were within T_{sel} range, d_b and d_e were considered equal to zero. High values of d_b and d_e indicate a low accuracy index and low thermal quality, while values equal to or near zero indicate high accuracy of thermoregulation and represent thermally ideal environments. Subsequently, thermoregulation efficiency (E) was calculated using averages of d_b and d_e using the following equation: $E = 1 - (d_b / d_e)$. An E index near to one is indicative of an organism that actively thermoregulates, because environmental temperature is far from its physiological requirements. These organisms are subject to thermal stress and must increase or decrease their T_b with respect to T_e . In contrast, an E value equal or near to zero is indicative of a thermoconformer that is not regulating temperatures actively because environmental temperature is within its physiological requirements (Hertz et al 1993). However, as recognized by Hertz, Huey and Stevenson (1993), a given value of E can result from a variety of d_b and d_e combinations. For example, two species can therefore face different thermal environments and exhibit different thermoregulatory strategies and still have the same value of E if their ratios between d_b and d_e are the same (Blouin-Demers and Weatherhead 2001). Thus, it is also important to consider the magnitude of d_b and d_e in interpreting E (Blouin- Demers and Nadeau 2005). Following Blouin-Demers and Nadeau (2001) we measured the index of effectiveness of thermoregulation ($d_e - d_b$) to quantify the extent of departure from perfect thermoconformity. We also calculated the percent time each thermal microhabitat (open, buried, or under vegetation) fell within their preferred temperature (T_{sel}) and exceeded the critical thermal maximum (CT_{max}).

Statistical analysis

Body temperature in the field (T_b)—We performed a generalized linear model (Minitab® Version 19) to explore the variability in T_b temperature among lizards. T_b temperature was added as the response variable and time of capture (grouped into two hour blocks), month, year, and microhabitat classification were added as factors. Tukey post hoc tests were then performed on significant factors to see what groups were significantly different from one another.

Mean preferred body temperature (T_{sel}) —We performed a mixed effects model (Minitab® Version 19) with lizard ID as a random effect and month and time of day as fixed effects. We used a mixed effects model to account for repeated measurements of the same lizard. We then found the model predicted means and compared them to the observed means to find our mean preferred body temperature (T_{sel}). We performed a student's t-test to see if there was a significant difference between model predicted means and actual mean preferred body temperature.

Assumptions of normality were analyzed visually and by using Kolmogorov-Smirnov test. Homogeneity of variances were analyzed using Levene's test. Regression analysis were conducted using Microsoft Excel® and Minitab® Version 19. We used the formula $T = (\text{slope} - 1) / SE$ ($df = n - 2$) to test if the slope was significantly different than one. To explore differences in d_e between years and microhabitats we used Kruskal-Wallis and Dunn's post hoc test and to explore differences in alley vs fields we used student's t-test. We used spearman rank correlation to see if horned lizard presence correlated to average d_e score.

RESULTS

Body temperature in the field (T_b)

One hundred and fifty-three *P. cornutum* were captured (66 in 2019, 47 in 2020, and 40 in 2021) while they were active from 8:00—20:00. We found 37 in the open, 17 in open overcast, and 48 in shade/vegetation. The highest observation frequency was between 9:00—11:00, with 10:00 having the most observations falling within their optimal temperature range (Fig. 5). The overall T_b was 33.6 ± 0.3 °C ($n=153$, range= 23.6 — 41.2 °C, Fig. 4). There was a significant difference in T_b found between years ($F= 3.78$, $P= 0.025$), specifically between 2020 ($n=47$, 34.3 ± 0.52 °C) and 2021 ($n=40$, 32.3 ± 0.60 °C). T_b fluctuated through time of day ($F=13.44$, $df=3$, $P < 0.001$, Appendix 1) with “8:00 & 9:00” categories being significantly cooler in temperature from “10:00 & 11:00” (difference in means = -3.19 ± 0.89 °C, $P < 0.001$), “17:00 & 18:00” (difference in means = -5.10 ± 0.88 °C, $P < 0.001$), and “19:00 & 20:00” categories (difference in means = -3.87 ± 1.06 °C, $P < 0.001$). T_b also differed by microhabitat ($F=9.27$, $df=2$, $P < 0.001$, Appendix 1) with lizards found in shade/vegetation being on average 3 ± 0.70 °C cooler than ones found in the open ($P < 0.001$). There was no significant difference in T_b between months ($F=0.18$, $df=2$, $P= 0.84$, Appendix 1).

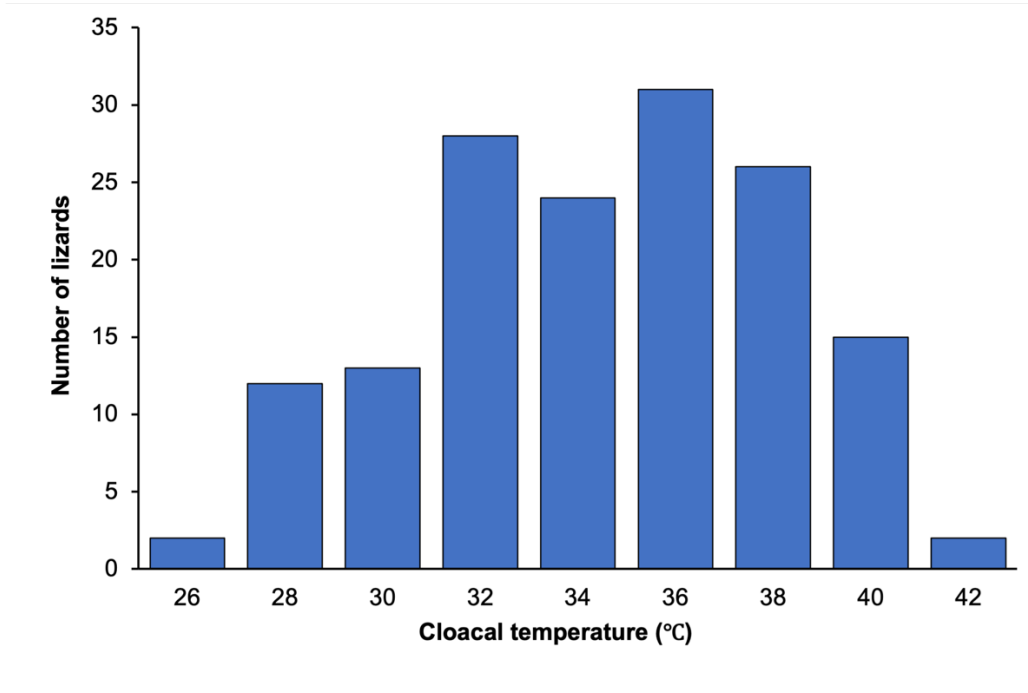


Figure 4: Frequency distribution of horned lizard T_b cloacal temperatures from Karnes City, TX over 2019-2021. Average T_b was 33.6 ± 0.3 °C.

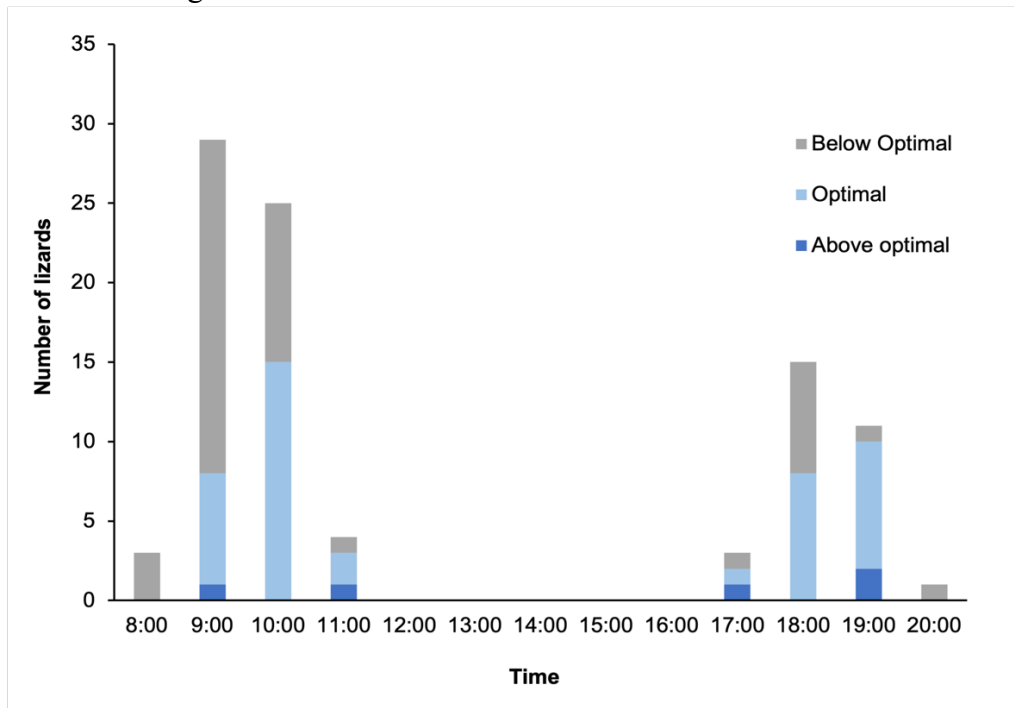


Figure 5: Capture times of *P. cornutum* (n=91) with T_b falling in optimal temperature range (33.5—38.5 °C) shown in light blue, above optimal in dark blue, and below optimal in grey. The time gap is due to sampling being restricted to 8:00-12:00 and 16:00 and 20:00 which corresponds to active periods for Texas horned lizards (Moeller et al. 2005).

Preferred body temperature in the laboratory (T_{sel})

Individual lizard temperatures did not explain variability in T_{sel} temperatures ($P=0.061$). Time of day ($F=1.75$, $df=5$, $P=0.13$) and month ($F=1.99$, $df=2$, $P=0.17$) also had no significant effect on T_{sel} (Appendix 2). Model predicted means averaged to 36 ± 0.47 °C. We decided to use the observed mean of 35.7 ± 0.33 °C since it was not statistically different than the model predicted mean ($t=0.45$, $df=26$, $P=0.65$). Therefore, preferred body temperature in the thermal gradient was 35.7 ± 0.33 °C ($n=19$, range= 27.2 — 41.5 °C). The interquartile range (T_{sel25} and T_{sel75}) of T_{sel} was 33.5 — 38.5 °C. Cloacal and body surface temperature showed a highly significant relationship ($y = 1.07x - 1.32$, $R^2=0.95$, $P=0.002$ Fig. 6) and an average difference between body surface temperature and internal temperature of 1.4 ± 0.1 °C. The slope was not significantly different from 1.0 ($n=19$, $t_{0.05(2),66} = 0.074$, $P=0.94$, Fig. 6).

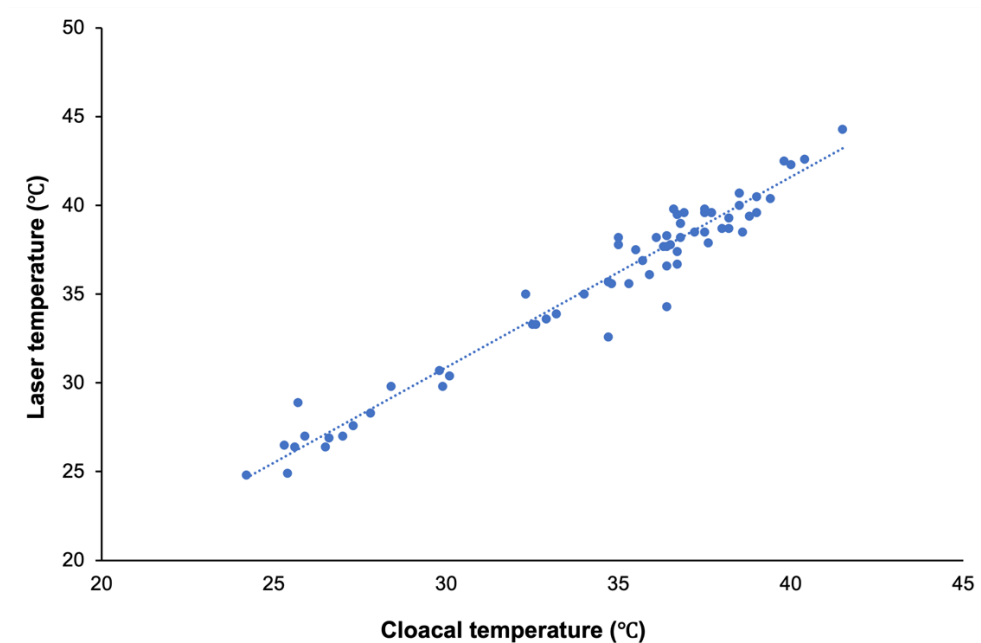


Figure 6: Relationship between cloacal temperature and laser temperature from lizards in the thermal gradient. Justifies using a laser as a good approximation of internal temperature and a less invasive method.

Operative temperatures (T_e)

There was a highly significant linear relationship between field T_b and T_e ($y = 0.80x + 6.57$, $R^2=0.89$, $P=0.02$, Fig. 7) and the slope was not significantly different than 1.0 ($n=71$, $t_{0.05(2),69} = -0.159$, $P=0.87$), suggesting that models accurately measured T_e available to horned lizards during their active hours. Dirt microhabitat was above their critical temperature for 12.4 percent of the day and within their optimal temperature range 21.6 percent of the day. Open microhabitat was above their critical temperature for 31 percent of the day and within their optimal temperature range 16.3 percent of the day. Vegetation microhabitat was above their critical temperature for 0.2 percent of the day and within their optimal temperature range 17.9 percent of the day (Fig. 8 and Fig.9). All microhabitats were significantly different from each other for percent time at critical temperature (Fig. 8; Dunn, $P < 0.001$). Percent time at optimal temperature was only significantly different between dirt and open and dirt and vegetation (Fig. 9; Dunn, $P < 0.001$).

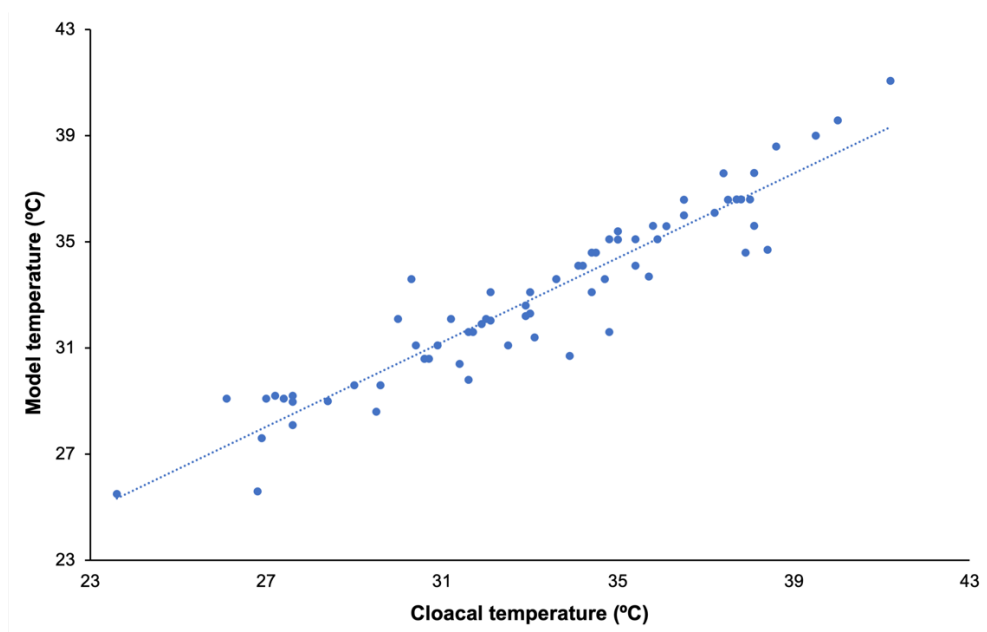


Figure 7: Relationship between cloacal temperature from lizards in the field and model temperature.

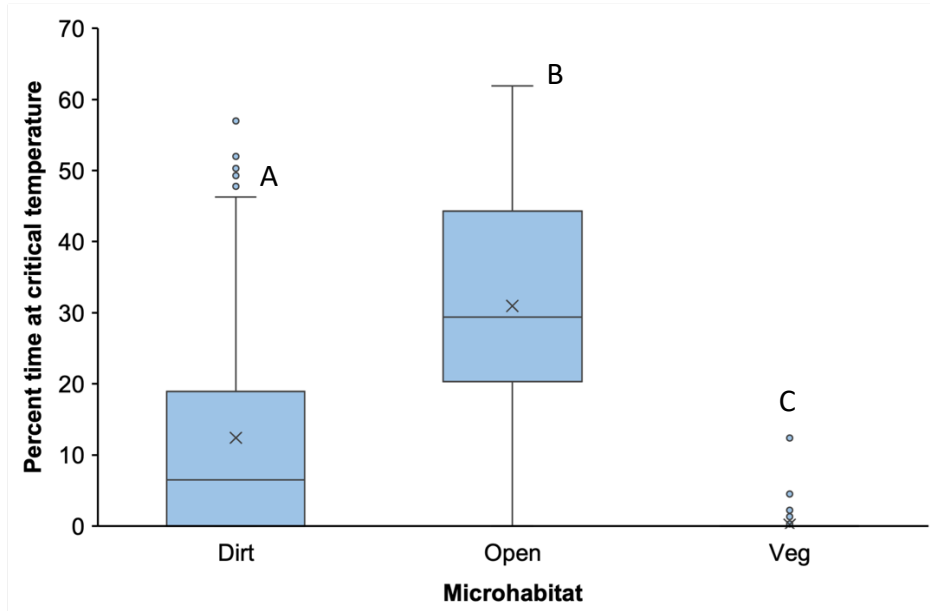


Figure 8: Boxplot of percent time T_e was above critical temperature (CT_{max} ; 45.9 °C) in three different microhabitats from 2019-2021. The dark bar represents the median and the “x” represents the mean. The boxes are the interquartile range and whiskers represent highest and lowest values that are not outliers. Circles are outliers and extreme values. Groups with different letters are significantly different from each other.

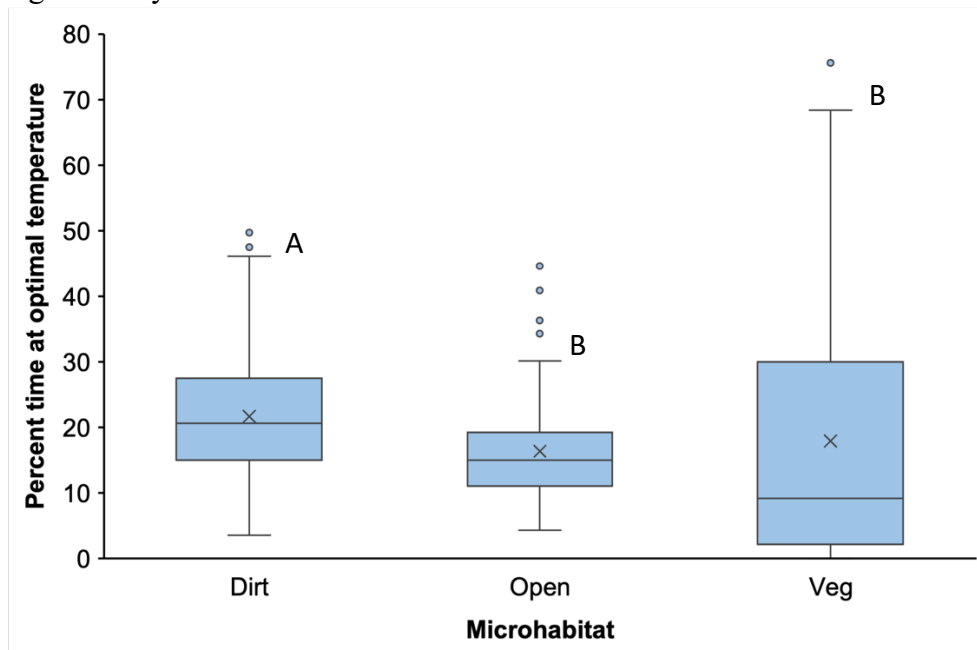


Figure 9: Boxplot of percent time T_e was within optimal temperature range (T_{sel} ; 33.5—38.5 °C) in three different microhabitats from 2019-2021. The dark bar represents the median and the “x” represents the mean. The boxes are the interquartile range and whiskers represent highest and lowest values that are not outliers. Circles are outliers and extreme values. Groups sharing a letter are not significantly different from each other whereas different letters are significantly different from each other.

Operative temperatures for open microhabitat in 2019 averaged 40.8 ± 0.83 °C (n=88, range=26.7—51.8 °C); in 2020 it was 41.3 ± 0.91 °C (n=79, range=28.7—51.2 °C); and in 2021 it was 36.1 ± 0.64 °C (n=78, range=26.4—42.9 °C). Average open microhabitat temperatures exceeded the critical thermal maximum (CT_{max}) 6 hours in the middle of the day in 2019 and 2020 but never reached the threshold in 2021 (Fig. 10). Open microhabitats fall in optimal temperature range in the morning (9:00-10:00) and are probably important for increasing body temperature during the beginning of their activity period (Fig. 10).

Operative temperatures for dirt microhabitat in 2019 averaged 36.1 ± 0.5 °C (n=88, range=27.2—42.5 °C); in 2020 it was 36.3 ± 0.58 °C (n=79, range=27.8—42.8 °C); and in 2021 it was 33.4 ± 0.47 °C (n=78, range=26.5—38.8 °C). Average dirt microhabitat temperatures never reached CT_{max} in all three years but temperatures exceeded T_{sel} range in the middle of the day in 2019 and 2020 (Fig. 10A-B). Dirt microhabitat temperatures stayed within T_{sel} range for the majority of the day in 2021 (Fig. 10C).

Operative temperatures for vegetation microhabitat in 2019 averaged 32.1 ± 0.28 °C (n=88, range=26—34.9 °C); in 2020 it was 31.6 ± 0.32 °C (n=79, range=26.7—35.1 °C); and in 2021 it was 28.6 ± 0.29 °C (n=78, range=25.6—30.7 °C). Vegetation microhabitat provided temperatures within T_{sel} during the hottest parts of the day in 2019 and 2020 when open and dirt microhabitats were above optimal temperatures and sometimes at CT_{max} temperatures (Fig. 10A-B). Average vegetation microhabitat temperatures never reached the T_{sel} range in 2021 and stayed in the below optimum range the whole day (Fig. 10C).

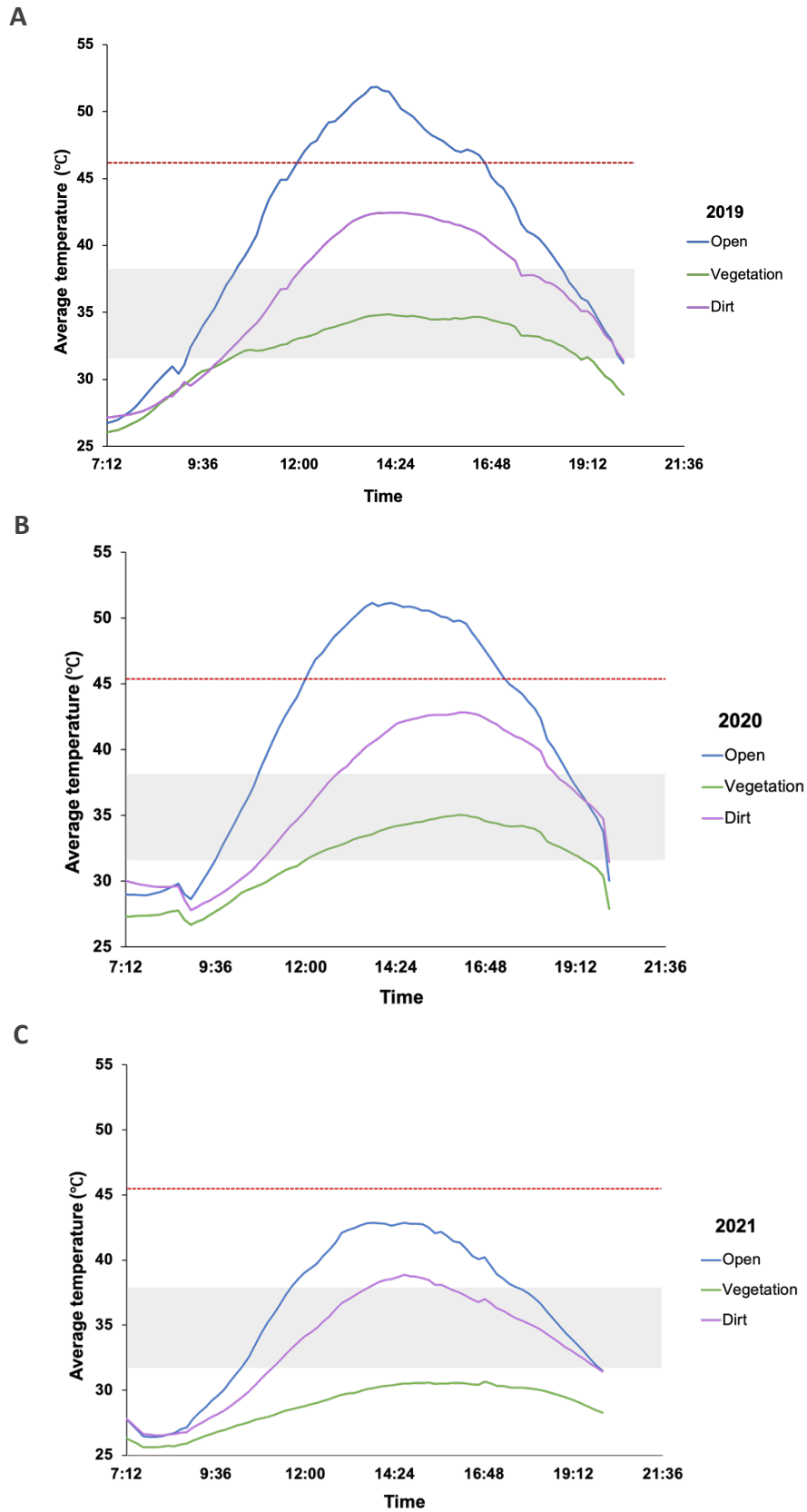


Figure 10: Average operative temperatures (T_e) over Texas horned lizard's active period measured by models in open, dirt, and vegetation microhabitats for 2019-2021(A-C). The blue line represents open, purple line represents dirt, and green line represents vegetation. The grey box represents their preferred temperature (T_{sel}) interquartile range (33.5–38.5 °C). The red dashed line represents their critical thermal maximum (CT_{max} ; 45.9 °C)

Thermoregulation indices

Thermal quality of habitat (d_e) did not differ between years (2019-2021; Kruskal-Wallis, $P=0.92$). There was a negative correlation between the average number of horned lizards and average quality score (d_e) across sites ($r_s = -0.54$, $P_{0.05(2)} = 0.039$, Fig. 11). Quality scores (d_e) were lower (i.e. better) for sites that had horned lizards (4.5 ± 0.27) than sites where they were absent (5.5 ± 0.33 ; $t=2.38$, $df=12$, $P=0.035$). The average quality score (d_e) was lower for vegetation than dirt or open microhabitats (Dunn, $P < 0.001$ in both cases) (Fig. 12). The dirt microhabitat quality score was also lower than the open quality score (Dunn, $P < 0.001$) (Fig. 12). The quality score (d_e) was lower for alleyways (4.4 ± 0.7) than fields (5.5 ± 0.9 ; $t = -2.78$, $df=12$, $P=0.017$).

Thermoregulatory indices suggests that *P. cornutum* exhibits accurate thermoregulation ($d_b = 1.6$, Table 4). Thermal efficiency indices ($d_e - d_b$ and E) indicate *P. cornutum* was efficient at thermoregulation in general (Table 4) but differed in efficiency in different microhabitats (Table 3). As thermal quality values (d_e) increased (indicating poor thermal habitat) thermal efficiency (E) increased (indicating more efficient thermoregulation; Table 3).

Table 3: Operative temperatures (T_e) in Celsius, available thermal quality (d_e), and thermal efficiency ($d_e - d_b$ and E) from Kenedy and Karnes City, TX from 2019—2021. Showing mean \pm SE.

Microhabitat	T_e average	d_e	$d_e - d_b$	E
Open	39.5 ± 1.0	7.8 ± 0.4	6.2	0.80
Dirt	35.4 ± 0.8	4.2 ± 0.3	2.6	0.62
Vegetation	30.7 ± 0.7	2.9 ± 0.2	1.3	0.45

Table 4: Field body temperature (T_b), operative temperature (T_e), preferred temperature in laboratory (T_{sel}) and T_p range (25 and 75% quartiles) in Celsius, and accuracy of thermoregulation (d_b), habitat thermal quality (d_e), and thermoregulatory efficiency (d_b-d_e and E). Showing mean \pm SE.

Species	T_b	T_e	T_{sel}	T_{sel} range (25-75%)	d_b	d_e	d_b-d_e	E
<i>Phrynosoma cornutum</i>	33.6 ± 0.3	35.2 ± 1.1	35.7 ± 0.33	33.5–38.5	1.59 ± 0.2	4.97 ± 0.2	3.38	0.68

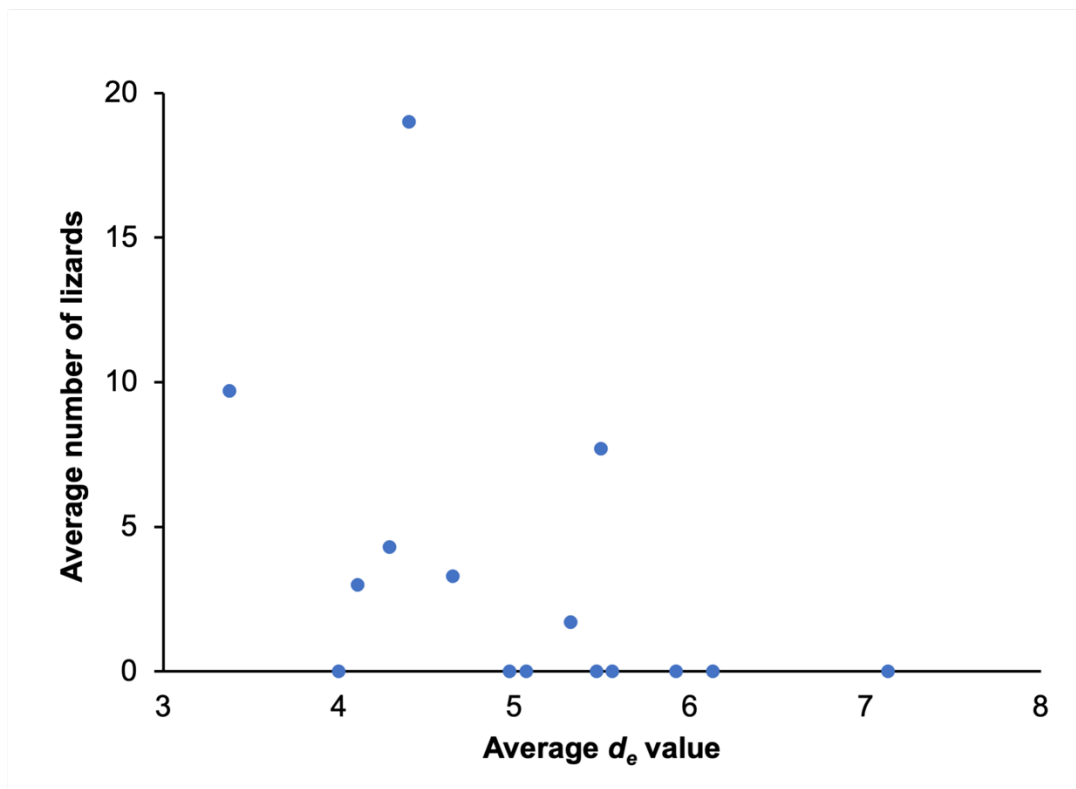


Figure 11: Scatterplot showing the relationship between average index value and average number of horned lizards for 2019-2021. Total number of sites: n=15.

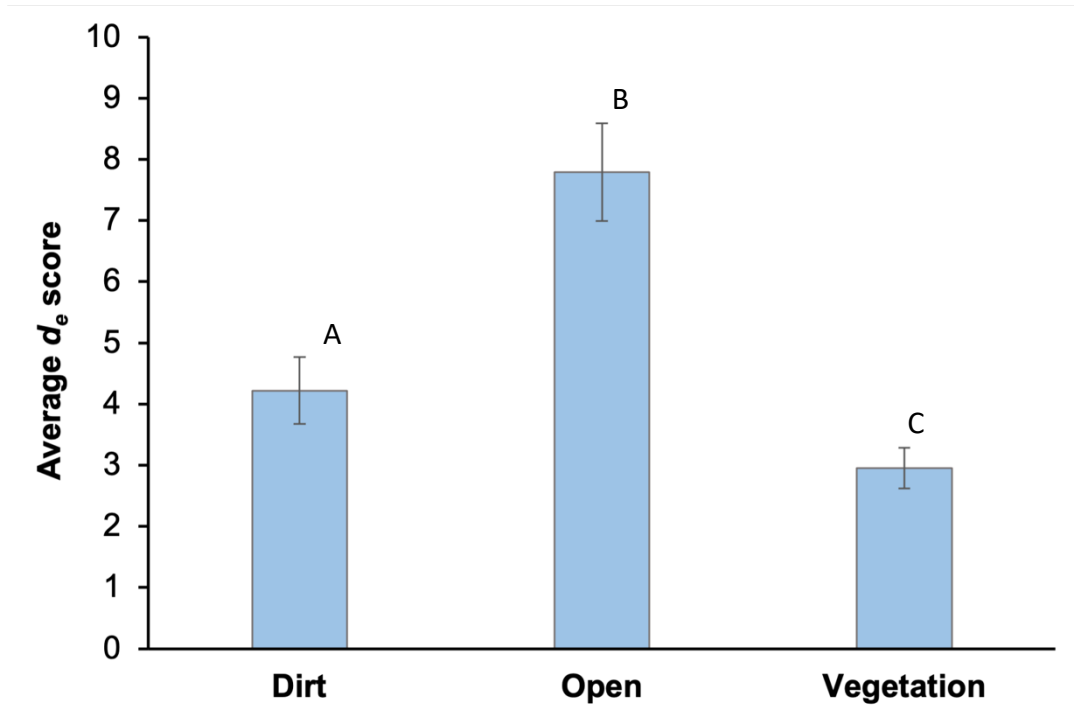


Figure 12: Bar graph showing the average quality score (d_e) for three different microhabitats. Error bars represent ± 2 SE. Groups sharing a letter are not significantly different from each other whereas different letters are significantly different from each other.

DISCUSSION

We found that vegetation plays a vital role in thermoregulation for horned lizards and we have noticed when vegetation is removed from fence rows and the bases of trees that the lizards there eventually disappear or occur at smaller densities. Other studies have found that vegetation cover relative to horned lizard spatial distribution is governed by habitat rather than prey availability with lizards clumped at microhabitats with numerous patches of heterogeneous disturbed habitat (Whiting et al. 1993). Vegetation helps to create heterogeneity and a dispersed thermal landscape with favorable microhabitats close together, which is preferred compared to clumped thermal resources (Sears et al. 2016). Clumped thermal resources (e.g. like singular trees in a field) are less favorable because of the energetic costs of shuffling between different clusters of microhabitats (Huey and Slatkin 1976, Sears et al. 2016). Additional removal of

vegetation from around trees or removal of brush piles make the thermal environment more homogeneous and decrease favorable microhabitats and thermal refugia from mid-day heat. In habitats with clumped thermal resources this would be detrimental. We think that vegetation removal from our sites that had clumped thermal resources resulted in the decline and eventual disappearance of horned lizards there. Alleyway sites also exhibited a steep decline in horned lizards following vegetation removal but we still find them in lower densities there. Their persistence could be due to the way alleyways are configured with dispersed thermal resources (e.g. landscaping, trees, vegetation along fence rows, and bare ground) that have heterogeneous microhabitats in close proximity to each other. Previous studies have shown that ectotherms thermoregulate more accurately when thermal resources are dispersed through space rather than clumped (Sears et al. 2016). Landscaping and irrigation next to the alleyways could allow for extended activity due to shade and humidity levels (Ackley et al. 2015) which could also explain lower d_e values in alleyways compared to fields ($P=0.035$). Previous studies at our field location also found higher concentrations of horned lizards in alleyways due to dense vegetation with a bare road in the middle which would allow lizards to sun and forage then retreat from the heat in the vegetation (Ackel 2015).

Thermal quality (d_e) of habitat is regarded as high quality when $5 > d_e > 3$ and low quality when outside this range (Hertz et al. 1993, Vickers et al. 2011). Overall thermal quality (d_e) for our sites was 4.97 ± 0.2 which is indicative of poor thermal quality. However, thermal quality by microhabitat differed, with vegetation (2.9 ± 0.2) having the highest thermal quality followed by dirt (4.2 ± 0.3) and open (7.8 ± 0.4) microhabitats (Table 3). Low thermal quality (high d_e values) was associated with higher levels of thermoregulatory efficiency (d_b-d_e and E; Table 3) which is consistent with the extended cost-benefits model for thermoregulation (Vickers et al.

2011). This model proposes that lizards will thermoregulate more accurately and efficiently when T_e is higher and thermal quality is lower like open microhabitat in our study (see Table 3). Lizards can exhibit more accurate and efficient thermoregulation in habitats that have high T_e to avoid extreme T_b levels and an increased risk of mortality (Vickers et al. 2011).

T_{sel} (35.7 ± 0.3 °C) was in between reported T_{sel} from other studies of Texas horned lizards (Table 2) but close to the average T_{sel} of 20 species of *Phrynosomatids* (35.1 ± 2.2 °C, Clusella-Trullas and Chown 2014). Our T_{sel} interquartile range ($T_{sel25} - T_{sel75}$) was larger than other studies by 1.5—3.5 °C (Table 2). T_b (33.6 ± 0.3 °C) was lower than other reported T_b (Appendix 3) for Texas horned lizards but falls within the lower T_{sel} range for lizards at our location (Table 2). However, T_b is lower than environmental operative temperatures available to them (T_e ; Table 4) which happens to be very close to their preferred body temperature (T_{sel} ; Table 3). Horned lizards at our site could be keeping their T_b lower because precise thermoregulation is less important than other activities like foraging which could be prolonged in shaded areas with lower temperatures (vegetation $T_e = 30.7 \pm 0.7$; Table 3). Horned lizards thermoregulated with intermediate effectiveness ($E=0.68$) which also points to less precision and relaxed thermoregulation found in *Phrynosoma sp.* (Pianka and Parker 1975).

Lizards at our field site eat mainly smaller ants and termites (Alenius 2018). The termites found in their diet, *Tenuirostritermes cinereus*, live in the soil and break down plant material for food; they do not damage man-made structures like other termites species. *T. cinereus* exhibits diurnal open-air foraging but these termites are constrained by temperature and humidity and are usually found foraging in overcast and humid conditions that lack direct sunlight (Nutting et al. 1974, Scheffrahn and Rust 1983) Vegetation could provide shade and a humid microenvironment for termites and increase foraging time for horned lizards. *T. cinereus* has

been reported to forage underneath tree canopies during the day which would correspond with horned lizard foraging (Scheffrahn and Rust 1983).

Previous studies have shown that horned lizards need a mosaic of bare ground, herbaceous plants, and woody vegetation to create microhabitats for foraging and thermal refugia to avoid midday temperatures (Burrow et al. 2001, Henry 2009, Anderson 2012, Anderson et al. 2017). This seems to hold true for our study site in a small town as well. In our study system, T_e underneath vegetation never exceeded their upper T_{sel} range (38.5 °C) or CT_{max} (45.9 °C; Fig. 10) where as temperatures in the open often exceeded CT_{max} by 6 °C during the middle of the day (Fig. 10). Open microhabitats (e.g. bare ground) are still important for thermal regulation during the morning and evening hours to reach adequate T_b (Fig. 10) and to forage for ants that also have a bimodal pattern of activity (Whitford and Bryant 1979). Dirt T_e often was above their upper T_{sel} range during midday and would not be an adequate thermal refugia but is necessary for burrowing when temperatures are appropriate (Fig. 10). These findings support other studies that demonstrated that horned lizards need a mosaic of these different microhabitats in close proximity to each other since temperatures and food availability fluctuate throughout the day (Burrow et al. 2001, Anderson et al. 2017). These studies also emphasized the importance of shrubs and woody vegetation for thermal refugia and suggested maximizing the availability of these microhabitats to increase lizard densities (Burrow et al. 2001). Thermal preferences of the species and timing of activity will determine whether a species can persist in a specific habitat (Kearney et al. 2009). While we cannot change species adaptive mechanisms, we should preserve vegetation for thermal refugia for small ectotherms to increase the probability of persistence as our climate gets warmer and select heterogeneous landscaping styles that will maximize available microhabitats.

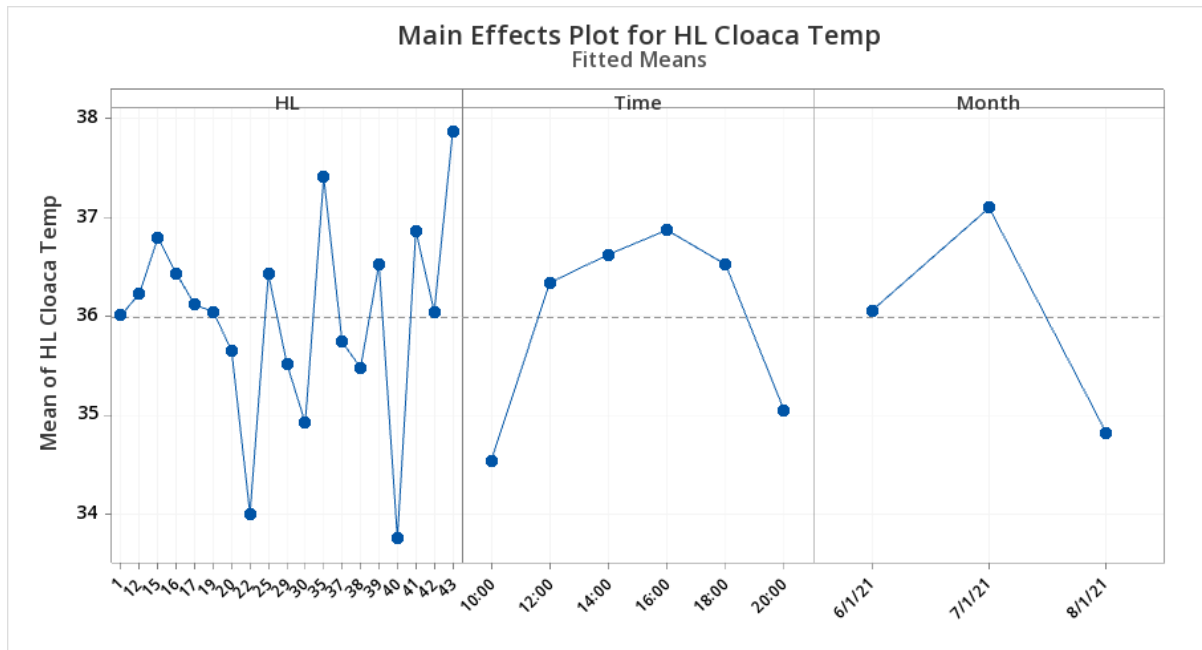
APPENDIX

Appendix 1: GLM results for field temperatures (T_b) for lizards from 2019-2021.

Analysis of Variance

Source	DF	Adj SS	Adj MS	F-Value	P-Value
Year	2	109.64	54.820	6.04	0.003
Month	2	3.26	1.628	0.18	0.836
Time of Capture	3	366.07	122.022	13.44	0.000
Microhabitat Classification	2	168.46	84.230	9.27	0.000
Error	92	835.53	9.082		
Lack-of-Fit	40	286.26	7.156	0.68	0.899
Pure Error	52	549.27	10.563		
Total	101	1443.89			

Appendix 2: Main effects plot for individual horned lizards (HL), time, and month.



Appendix 3: Body temperatures (T_b) of Texas horned lizards in °C.

N	T_b	References
4	35.7 ± ND	Brattstrom 1965
42	35.8 ± 0.7	Ferguson et al. 2015
83	33.4 ± 0.45	Lara-Reséndiz et al. 2015
153	33.6 ± 0.3	Present study

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ABSTRACT

THERMAL ECOLOGY OF TEXAS HORNED LIZARDS (*PHRYNOSOMA CORNUTUM*) IN SMALL TEXAS TOWNS

by Mary Rachel Tucker, M.S., 2021
Department of Biology
Texas Christian University

Thesis Advisor: Dean A. Williams, Professor of Biology

Texas horned lizards (*Phrynosoma cornutum*) have disappeared from many areas in Texas probably in large part due to loss of suitable habitat; however, some populations of this lizard still persist in the towns of Kenedy and Karnes City in southern Texas. Our previous studies revealed that horned lizards occur at unusually high densities at some of our study sites in these towns. These high densities may be the result of decreased movement, a switch to smaller prey items, and reduced predation. Nevertheless, this species has continued to decline and disappear from these towns. We hypothesize this may in part be due to the degradation of the thermal landscape for these lizards caused by the removal of important microhabitats. We propose in this study to determine how the quality of the thermal environment for horned lizards varies across our study sites and whether this is related to horned lizard presence or density.