

STUDIES OF THERMOREGULATION IN SMALL IGUANINE LIZARDS:
FEASIBILITY OF THE USE OF REMOTE LASER SENSING EQUIPMENT TO
DETERMINE DEEP BODY TEMPERATURES OF SMALL LIZARDS AND
THERMOREGULATORY PRECISION IN THE FIELD

by

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INTRODUCTION

It is widely recognized that lizards maintain their body temperature within fairly narrow limits by adjusting to variations in their thermal environment (Adolph 1990, Angilletta 2001). Thermoregulation is not an end in itself, but rather a process that facilitates survival in a variety of environmental conditions (Huey 1982). Critical body functions and behaviors including active digestion, reproduction, and predator avoidance are closely coupled with the maintenance of suitable body temperature (Cowles and Bogert 1944). In *Sceloporus undulatus*, Angilletta (2001) determined that passage time of food items decreased significantly with increasing temperature. As body temperature increases, performance initially improves, but levels off at some “optimal” temperature range, and then deteriorates rapidly as temperatures rise above this range (Huey 1982). It has been proposed that many reptiles may have multiple physiological optimal temperatures, depending on the physiological function or activity in question. At the boundaries of these optimal temperature ranges are limits at which the lizard can no longer function normally. These points are referred to as the upper and lower critical temperatures. Even so-called “optimal” temperatures can become unfavorable if experienced for prolonged periods of time (Huey 1982). To avoid these unsafe temperatures, many lizard species actively thermoregulate to maintain their optimal body temperature.

Since body temperature is so important, the ability to measure the deep body temperatures of lizards is central to studying their physiology. Non-intrusive methods are preferred because they cause the least disruption to the animal’s natural behavioral patterns. In this study, we tested the feasibility of using the remotely sensed dorsal

surface temperature of a lizard and air temperature to predict the deep body temperature of a lizard without the requirement of inserting a cloacal thermometer. We empirically constructed a regression model relating these three temperature variables. In addition, we used a modified version of the Alberts and Grant (1997) model of non-contact temperature prediction (developed for Cuban rock iguanas, mass range 120-850 g) and adjusted it for use on smaller lizard species (mass range 2-7 g). We also conducted heating and cooling studies in the lab to estimate the lability of temperatures when lizards are exposed to changes in heat sources and sinks. This allowed us to evaluate the potential accuracy of our readings as we pursued lizards among these sources and sinks and to more accurately assess the stability of readings that we obtained. Finally, we conducted chase studies to evaluate the effects of pursuit on lizard body temperature and to assess the impact that our collection methods may have had on our data.

MATERIALS AND METHODS

Field Studies. – Data were collected during May and June, 2005. The four lizard species studied were *Uta stansburiana stejnegeri* (Monahans Sandhills State Park, Ward Co., TX), *Holbrookia maculata* (Rita Blanca National Grassland, Dallam Co., TX), *Anolis carolinensis* and *Sceloporus undulatus* (Kisatchie National Forest, Natchitoches Parish, LA). Lizards were located and then watched for five minutes prior to capture to ensure that they had spent at least this much time in a given thermal context. Temperatures of the dorsal surface of the lizard were measured on the ground before capture using a

Raytek (PM-30, Santa Cruz, CA) non-contact temperature recorder. Capture was achieved using a noose or, rarely, by hand. Lizards were handled as little as possible while data were collected in order to minimize heat transfer from the researcher to the lizard. Air temperature (obtained 5 cm from the ground at the capture site) and cloacal temperature were measured with a Miller and Webber (T-6000, NY) cloacal thermometer. After capture, the substrate temperature and both the dorsal and ventral surface temperature of the lizard (using the sky as background) were measured using the Raytek. Mass was measured to the nearest tenth of a gram using a Pesola scale. Snout-vent length, sex, time to capture, and a subjective assessment of exposure to the sun (full sun, partial sun, shade) of the lizard prior to capture were also noted for each individual. Five to seven individuals of each species except for *A. carolinensis* were collected and brought back to the TCU lab for the additional studies described below. Due to space and time limitations, *A. carolinensis* was not studied in the lab.

Lab Studies. – Lab studies were conducted from June to October of 2005 to assess ecologically relevant heating and cooling rates. The purpose of these studies was to assess the likelihood and rate at which a moving lizard might change its dorsal and deep-body temperature when moving among heat sources and sinks (either voluntarily or when chased by the investigator). Lizards were maintained in individual 11.4-liter plastic terrariums measuring approximately 28 x 18 x 18 cm. A heat gradient of about 26 to 40°C was established by placing a Flexwatt heat strip under part of the enclosure. The terrariums were fitted with quarter-inch mesh tops to allow air circulation and access to UV light provided by Reptisun 5.0 fluorescent tubes (Zoo Med, San Luis Obispo CA)

illuminated 8-12 h per day. Lizards were fed appropriate-sized crickets 2-3 times per week and the cages were misted daily.

The rates of heating and cooling via radiation, conduction, and convection were examined for each species in the lab. For most studies each lizard's limbs were taped onto a 7.5- by 12.5-cm index card which had a 2.5 by 5 cm section cut from its center. The opening in the card allowed the lizard's ventral surface to come into contact with the substrate. In all experiments, lizard cloacal temperature was recorded continuously by inserting a constantan thermocouple held in place by taping the thermocouple wire to the substrate or card. Another thermocouple was used in some experiments to continuously record the temperature of the sand substrate where it contacted the ventral skin of the lizard. The thermocouples were attached to a Wescor 2-channel thermocouple thermometer (TH-65, Logan, UT).

Once the heat source was applied readings were recorded at 30-second intervals. Readings continued at 30-second intervals for five minutes after the heat source was removed.

Radiative Heating

Radiative heating studies were performed to assess the potential effect of sun exposure and its cessation on the heating and cooling rates of the study species (Trial 1). The lizard was placed on a stand with each leg taped to the end of a 25-cm wooden stilt below a 120-Watt flood lamp hung 20-cm above the lizard. The ecological relevance of this distance was determined by allowing a dead lizard to heat for ten minutes outdoors on a

sunny day in direct sun at 1100 hours. The lamp distance in the lab was adjusted to achieve the same heating rate. Lizards were allowed to heat until their cloacal temperature reached 35°C or ten minutes had elapsed, whichever occurred first. At the stop point, the lamp was unplugged and the lizard was allowed to cool for five minutes. In a repeat of this experiment (Trial 3) the lizard was taped to a 7.5- x 12.5-cm card with the center removed. The card was taped on to a 10-cm diameter plastic lid onto which a few mm of play sand substrate was added. The lid was taped onto the ends of the wooden stilts. Thus, rather than being suspended in the air during the heating and cooling process, the lizard was in contact with a sand substrate during the process.

Conductive Heating

Conductive heating studies were used to isolate the potential effect of warm substrate and its removal on the heating and cooling rates of the study specimens (Trial 4). The lizard was placed on a double layer of Flexwatt heat tape that had been covered with a thin layer of sand. The sand was allowed to heat to 39°C before the lizard, taped to a card with the center removed, was placed on the sand. Two trials were conducted on each lizard. The lizard was first heated with full substrate contact until the cloacal temperature reached 35°C or until ten minutes had elapsed, whichever occurred first. At the stop point, the lizard was removed from the heat strip and placed onto an unheated metal tabletop. The temperature of the table was recorded with the Raytek prior to placing the lizard on top. The lizard was then allowed to cool for five minutes. The lizard was then heated again with the front of the card propped up on a pencil to allow only the posterior half of the lizard's ventral surface to come into contact with the substrate. This was done

to simulate behavior we observed in the field where the front of the lizard was raised off of the substrate using the forelegs. In a repeat of this experiment (Trial 5) the lizard was left on the heated sand substrate to cool after the heat source was turned off.

Convective Heating

Convective studies were performed to test the potential effect of warm or cool air on the heating and cooling rates of the study specimens (Trial 2). The lizard was placed on the same stand used for the radiative studies. The ends of the stilts were taped to a small circular lid onto which a few mm of sand was placed. As in the repeat of the radiative study, the lizard was taped to the card with the center removed and the card in turn taped to the lid. The stand was placed into a Revco BOD10A14 constant temperature chamber (GS laboratory equipment, Ashville NC) set to 40°C. The lizard was allowed to heat until the cloacal temperature reached 35°C or until ten minutes had elapsed, whichever occurred first. At the stop point, the lizard setup was removed from the heat chamber and the lizard and substrate were allowed to cool at room temperature with the lizard in continuous contact with the sand substrate for five minutes.

Preferred Temperature

Preferred temperatures of *U. stansburiana stejnegeri*, *S. undulatus*, and *H. maculata* were determined in the lab in order to assess how these might change during pursuit by an investigator (see chase studies below). Three 85L polyethylene storage bins measuring 86 by 37 cm were used as terrariums. Sand substrate was provided. A heat gradient of 26 to 45°C was established using a 150-W flood lamp. Lizards were offered a choice of

brick, wood plank, or cardboard egg carton as hiding/basking spots. Leashes 15 cm in length made out of dental floss were tied securely but comfortably around each lizard's waist to allow for quick capture later on. Each lizard was allowed to acclimate to the new enclosure for seven days prior to data collection. After the acclimation period, each lizard was caught and its internal temperature recorded. This was repeated over the course of several days until five readings of the lizard when exposed were accumulated. Ambient and substrate temperatures were recorded where each lizard was located prior to capture. Exposure to sun/shade and substrate choice was also noted.

Chase Studies

Chase studies were performed to assess the influence of stress and movement among heat sources and sinks on a lizard's cloacal temperatures. Each lizard that had been actively thermoregulating for at least an hour was chased by hand once a minute for 10 minutes and its internal temperature recorded after the last chase was performed. Lizards were only chased long enough to stimulate them to move from one end of the enclosure to the other. A point was made to chase the lizard from a cool spot in the enclosure to a warm spot and vice versa to simulate what happens in the field during data collection. (Researchers spot lizards in the open, chase them under cover, roust them out, etc.) The temperature of a lizard after the chase period was compared to the previously determined preferred temperature of that individual.

RESULTS AND DISCUSSION

Predicting Cloacal Temperatures in the Field. – The relationship between dorsal skin surface temperature (T_s) and internal body temperature (T_b) was determined by regression for all lizards studied. At any ambient temperature (T_a), an animal's estimated internal body temperature can be predicted from its skin surface temperature using the following equation:

$$\text{Estimated } T_b = 0.892(T_s) + 0.187(T_a)$$

This model produces highly accurate results, with an r^2 value of 0.9. Deviation of predicted from actual internal body temperature using this model averaged 0.20°C and had a standard deviation of $\pm 1.43^\circ\text{C}$. How accurately the model, based on studied populations, could predict the cloacal temperature of a new population, i.e., the robustness of our model, was tested by generating the model based on each possible combination of three species and using this to predict the internal body temperature of the fourth. Deviations among predicted and actual internal body temperatures were small (less than $\pm 1.3^\circ\text{C}$) for all models generated and tested. Our model is more accurate for small lizards than the model of Alberts and Grant (1997):

$$\text{Slope of } (T_s, T_b) \text{ relationship} = -0.0003(\text{mass}) + 0.926$$

$$\text{Estimated } T_b = (\text{slope of } [T_s, T_b] \text{ relationship})(T_s - T_a) + T_a$$

The model of Alberts and Grant (1997) is based on larger lizards (mass range 120-450 grams) and tends to underestimate cloacal temperature of the smaller lizards used in this study by about 2°C (Table 1, Fig. 1a). However, with a constant incorporated into the Alberts model, the two models have virtually equivalent predictability (Fig. 1b).

$$\text{Estimated } T_b = (\text{slope of } [T_s, T_b] \text{ relationship})(T_s - T_a) + T_a + 2.1$$

Accuracy of Raytek readings

In the field, dorsal temperatures of free-living lizards measured with the Raytek and substrate temperatures were nearly identical (Fig 2). There are at least two possible explanations for this. Usually, the measured field of the temperature gun (22-mm circle) was larger than the width of the lizard. As a result, the reflected heat of the substrate contributed more to the reading than heat from the lizard. Another explanation is that the smaller species used in this study are able to acclimate to their microclimate quickly, so the lizard surface and ground were the same temperature. Because dorsal temperatures measured with the Raytek after capture of the lizard and with the sky as the background (no non-lizard reflectance) were more dissimilar to the substrate temperature, the first explanation is more likely (Fig. 2). To test the accuracy of the Raytek reading with the sky as background, we simultaneously took temperature readings from the dorsal surface of a lizard suspended in the air using the Raytek, cloacal thermometer pressed onto the lizard, and thermister pressed onto the lizard. These readings were very similar (Table 2, average deviation 0.4°C).

Heating and Cooling Rates – Heating and cooling coefficients ranged between 1.62 and -1.22 (Table 3). This means that regardless of the heat source or sink, small lizard body temperature can rise or fall one to two degrees C per minute. As expected, potential heating and cooling rates in the laboratory varied with body size (mass being the best predictor) and context. Regardless of heating/cooling setup, larger lizards heated and cooled slower than smaller lizards (Figs 3a, 3b).

Within the one to two degree per minute range of heating and cooling, the speed at which a lizard can adjust its body temperature to match the thermal environment is determined by degree of contact with the heat source. Lab studies concluded that lizards heated the fastest (Fig 4 and Table 3, trial 3) and cooled the slowest (Fig 4 and Table 3, trial 5) when in contact with a warm substrate. The heating rate in trial 3 was significantly faster than those in the other trials (RMANOVA $P = 0.001$ overall effect, $F = 16.9$, Holm-Sidak pairwise comparison below critical level for all comparisons with trial 3). The cooling rates also differed significantly (RMANOVA, $P < 0.001$, overall effect, $F = 17.5$). Cooling occurred significantly more quickly when a lizard was suspended in the air without any contact with a substrate (Fig 4 and Table 3, trial 1,) and significantly more slowly when allowed to cool in contact with substrate previously warmed along with the lizard (Trial 5, Holms-Sidak pairwise comparison below critical levels for all comparisons with trials 1 and 5).

The results of our lab studies showed that selection of heat source and sink context can offer ecologically relevant advantages to lizards. The heating rate of the species was slowest when the lizard was forced to avoid radiant heat and rely on ambient air temperature as the only heat source (such as in a shady area on a hot day) and was

fastest when the lizard was exposed to radiant heat while sitting on a heating substrate (such as on sun-warmed sand early and late in the day) (Fig. 4, trial 3). Cooling rates were slowest when the lizard remained in contact with a warm substrate and fastest when the lizard was exposed to cooler ambient air conditions with no substrate (such as when perched on a branch) (Fig. 4, trial 1). Accordingly, lizards can seek out particular microhabitats in order to manipulate their cooling or heating rate.

Preferred Temperature. – Preferred temperature of each species was determined in the laboratory by measuring cloacal temperature only when each lizard appeared to be actively thermoregulating in a thermal gradient (Table 4). Using this method, it was determined that the preferred temperature of *U. stansburiana stejnegeri* was $35.9^{\circ}\text{C} \pm \text{s.d. } 0.66$. The preferred temperature of *S. undulatus* and *H. maculata* were $35.6^{\circ}\text{C} \pm \text{s.d. } 1.12$ and $37.6^{\circ}\text{C} \pm \text{s.d. } 0.62$, respectively.

Chase Studies. – After ten minutes of being pursued alternately between brightly lighted and shady microhabitats, lizards in the lab showed no significant change in body temperature (Table 5). This finding adds credence to our field results, as we often had to chase lizards for several minutes before catching them for data collection. This was especially true for *U. stansburiana* as this was the warriest of the species we studied.

Importance of Temperature Measurement. – For any model to be predictive there must be a stable relationship between the independent and the dependent variables. The ability of air and dorsal surface to predict a higher deep body temperature with some precision

suggests that during most days of this study a stable gradient between air, surface, and core was established and maintained. Whether this relationship remains relatively stable or varies seasonally or daily with changing weather conditions needs to be explored in more detail.

Studies focusing on comparisons between surface and body temperatures in lizards are rare. Burrage (1973) performed extensive temperature studies on two *Chamaleo* species in Africa. His study revealed distinct gradients between the surface and internal temperatures of his study specimens which varied as a function of ambient temperature and species. These same types of patterns almost certainly exist in other lizard species.

To fully explore the applicability of our model, more species should be tested for goodness of fit. Additional populations of small lizards (mass range 2-7 grams) need to be studied to assess the universality of our model for lizards of this size. In addition, species of both smaller and larger size should be studied to establish any correction factors that might be needed to make our model appropriate for those species. Testing species in different climates and at different times of year would also be beneficial in order to determine possible seasonal and geographical variations in the lizard's thermal gradient. It would also be valuable to test our model on lizards that have been implanted with thermal recording devices. This would allow serial comparison between the model-generated predicted temperature and the actual core body temperature of the individual with minimal invasion to the animal.

The fact that small lizards can rapidly change deep-body temperature (one to two degrees C per minute) when constantly exposed to heat sources or sinks suggests that

time between spotting, capturing and measuring deep-body temperature should be minimized. Alternatively, if a lizard shuttles rapidly among heat sources and sinks yet is captured relatively quickly (within one or two minutes), body temperature probably changes little as shown by our laboratory “chase studies.”

Thermoregulation in U. stansburiana, S. undulatus, and H. maculata

It appears that none of the species was able to effectively maintain preferred temperatures in the field within $< 1^{\circ}\text{C}$ (Table 3, Fig 5). This is likely due to the weather conditions at each location during the study period. In Monahans Sandhills, the weather was hot with little cloud cover. These conditions apparently pushed *U. stansburiana* beyond its preferred body temperature. At the Kisatchie field site, afternoon showers lowered the substrate temperature and reduced basking opportunities, preventing *S. undulatus* from achieving its preferred temperature. *Holbrookia maculata* was the closest to achieving its preferred body temperature in the field. Intermittent cloud cover produced shade at various times throughout the day while the lizards were exposed and probably prevented this species from matching preferred temperature precisely. Unfortunately, we did not assess available operative temperatures in the field using copper models (Bakken 1992). Thus we could not be certain that deviant field temperatures reflect unavailability of appropriate heat sources and sinks.

Each of these species displayed unique behavioral patterns in the field, allowing them to approach, if not precisely maintain, their preferred body temperatures within their habitats. *Uta stansburiana* was often found on the edges of clusters of vegetation, where it had easy access to shady conditions and retreat sites. It was frequently observed on

sandy substrate and only retreated into thick vegetation or burrows when startled and during the hot afternoon hours. *Sceloporus undulatus* was spotted primarily on stone fences or on the trunks of mature trees. During midday, these lizards, especially the females, retreated to the shade. *Anolis carolinensis* was seen almost exclusively perched on the branches of shrubs or young trees. They appeared to remain there throughout the day. *Holbrookia maculata* was found basking on small rocks or on the roadside throughout the day, seldom retreating into shady conditions. This observation reflects those by Hager (2001).

Mechanisms of Thermoregulation. – In order to maintain suitable body temperatures, lizards must change their microhabitat use in accordance with daily, seasonal, or geographic variation in the thermal environment (Adolph 1990). Previous studies of three of the taxa examined in this study suggest that they are active behavioral thermoregulators. Angert et al. (2002) determined that early in the year, *S. undulatus* spends considerable time in rocky areas that retain heat well (a condition simulated by laboratory trials 2 & 5, Fig.4) . Later in the season, the lizards retreat to trees and other cooler habitats, allowing them to maintain the same body temperature even as ambient temperatures are rising (Angert et al. 2002). Sartorius et al. (2002) studied *U. stansburiana* in New Mexico and found that the species utilized warm, sunny microsites during the morning and afternoon hours and retreated to the shade at midday. Tinkle (1967) noted that this species rarely retreats underground during the heat of the day, instead remaining on the surface beneath the shade of yucca or mesquite. Sena (1978) examined the thermal characteristics of *H. maculata* and found that the lizards found on

arboreal perches had the highest cloacal temperatures recorded during the study. This suggests that these individuals were seeking arboreal microhabitats to induce cooling, as simulated in my laboratory trial 1. All of these lizards have an advantage in their small size. Smaller species are capable of more rapid heating and cooling than larger lizards (Cowles and Bogert 1944).

Thermoregulation as a Function of Body Size. – The surface-to-mass ratio of lizards has a profound impact on their ability to efficiently thermoregulate. Small lizards, such as those in this study, are able to quickly adjust to changes in their thermal environment. Larger lizards take longer to adjust their body temperatures. This is due to a decrease in the effectiveness of convective heat exchange with the environment (Stevenson 1985). Alberts and Grant (1997) captured 8 juvenile *Cyclura* exposed to sun at midday and each individual had a higher body surface than internal temperature, indicating that they were heating. Of 61 much smaller lizards captured in the field in this study between 1000 and 1800 h, 55 had higher internal body temperatures, indicating that they were cooling. Only 6 had the same temperature for both surface and internally, indicating equilibrium. It would be interesting to determine the body-size threshold below which lizards spend most of their time cooling and above which lizards spend most of their time heating.

Influences on Thermoregulation. – My study suggests that thermoregulation in strongly thermoregulating species may not always be precise. Studies have shown that thermoregulatory precision is often affected by competitors, predators, food supply, time of day, season, weather, and environmental heterogeneity (Huey 1982). Competing

species often exclude each other from certain microhabitats. These pressures force both species to utilize other areas and may eventually lead to the evolution of new thermal preferences in one or both species (Adolph 1990, Angert et al. 2002). Predators have a similar impact in that they limit thermoregulatory precision by restricting access to certain microhabitats and forcing movement to less favorable spots. The availability of food items is another factor that determines the degree to which a lizard can precisely thermoregulate. A lizard that has an abundant food supply can spend less time hunting and more time thermoregulating. Thermoregulatory precision is also confined by the time of day. For example, many lizard species are not active during the hottest midday hours. In addition, studies have shown that the thermal quality of habitats varies depending on the season. In the northern hemisphere, thermal quality tends to be lowest in the spring and fall. Row and Blouin-Demers (2006) found that milk snakes thermoregulated more precisely during these sub-optimal conditions. Weather is yet another constraint. Irwin (1965) found that male *U. stansburiana* moved an average of 127 feet per hour on cloudy days compared with only 48 feet per hour under sunny skies at the same time of day. Finally, the amount of environmental heterogeneity (that is, how many different microclimates are in a given area) influences thermoregulatory precision. A reptile living in a homogeneous thermal environment, such as might be found in a lab enclosure without a suitable gradient, will not be able to thermoregulate as precisely as it would in its natural environment. Other environmental variables should also be taken into account. When given a choice between open habitats and forested areas, milk snakes showed a strong preference toward the open habitat. They thermoregulated less precisely under these conditions, suggesting that habitat selection and thermoregulation are tightly

linked (Row and Blouin-Demers 2006). In order to fully understand the mechanism and purpose of thermoregulation, it is important to consider all possible factors influencing its precision.

APPENDIX

Fig 1a. Comparison of measured vs. predicted cloacal temperatures using the present study model and the Alberts and Grant model. The Alberts and Grant model tends to underestimate the cloacal temperature of the small lizards in this study by about 2°C. See text for models.

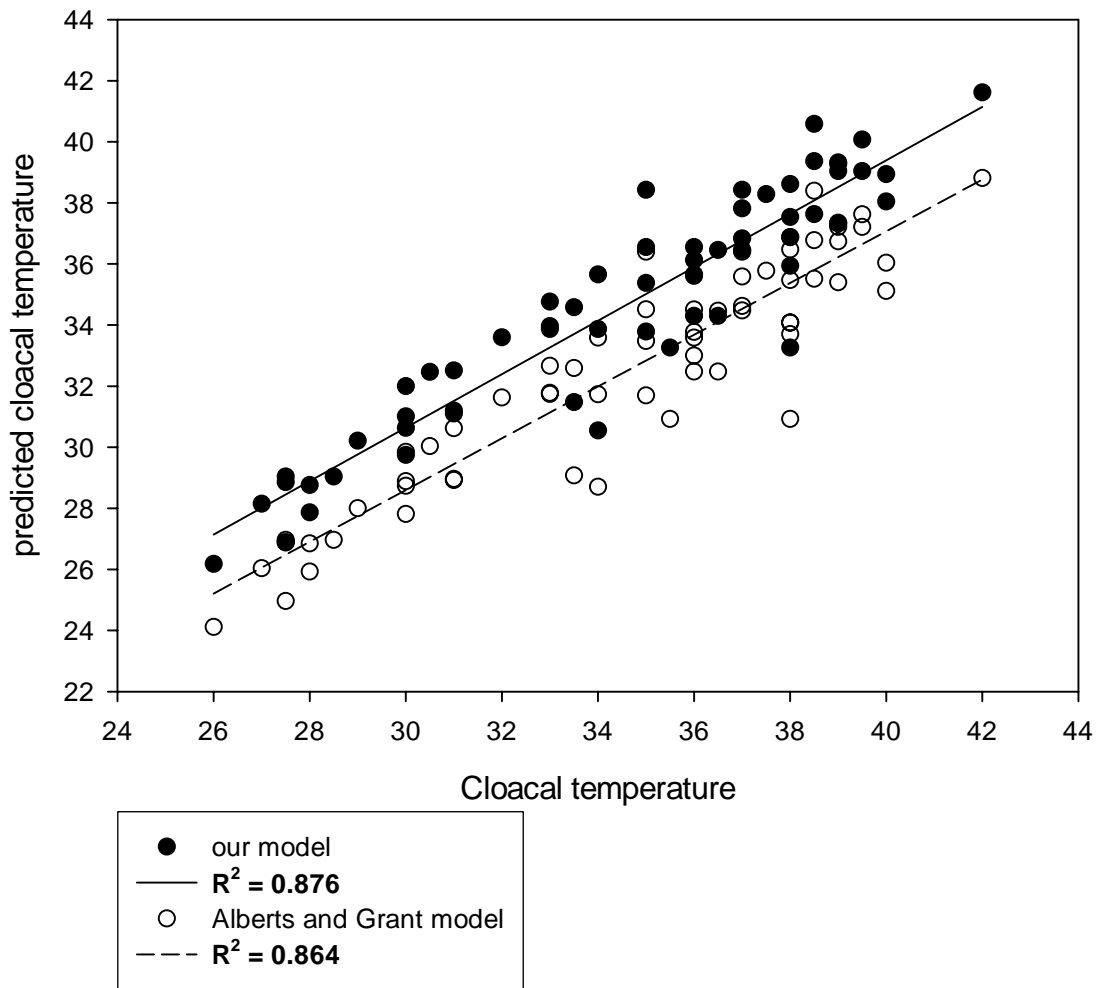


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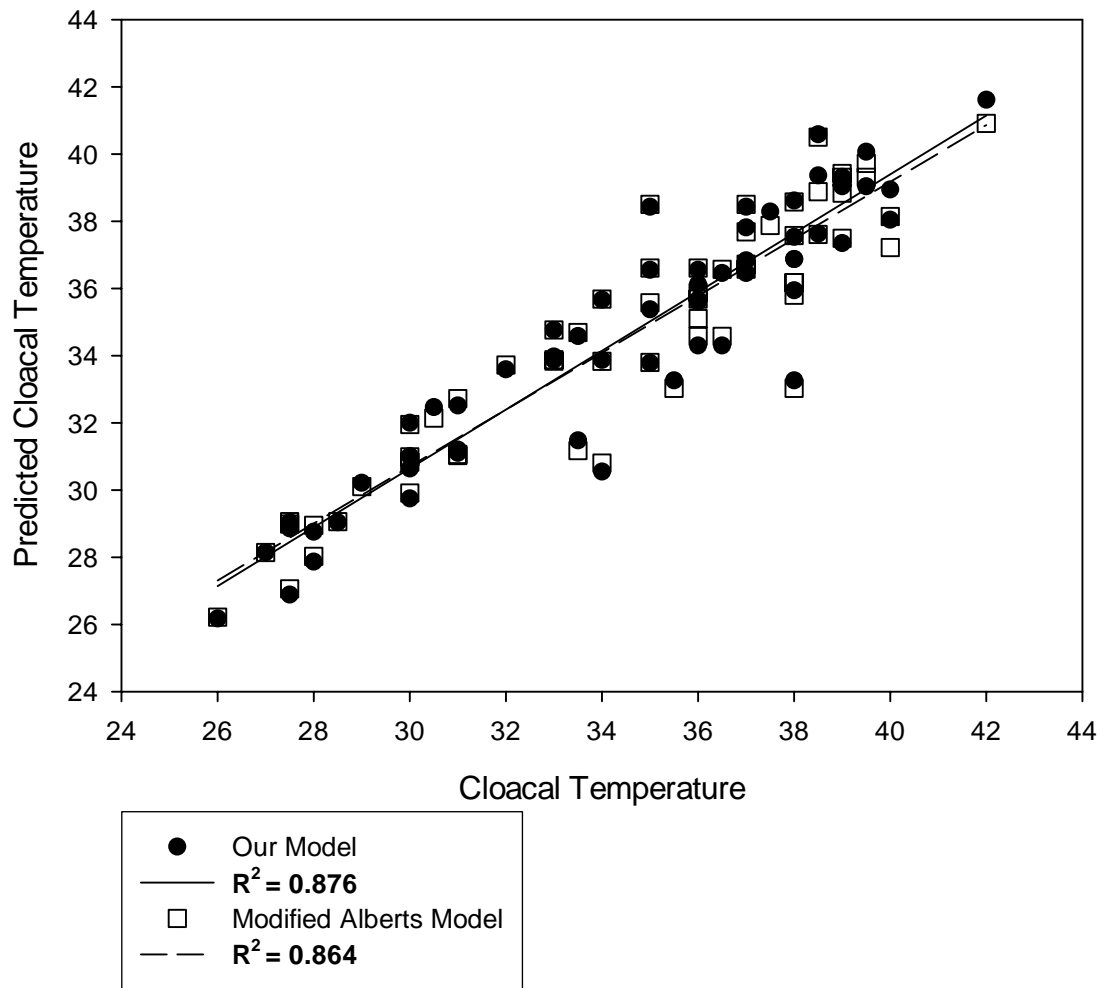


Fig 2. Comparison of measured dorsal temperature for each species (N) when lizard was on substrate, dorsal temperature with the sky as a background, and substrate temperature. Dots represent mean temperature for each scenario. N = number of observations. Dorsal temperature against substrate is very similar to substrate temperature, so using the sky as a background is a truer method of dorsal temperature measurement

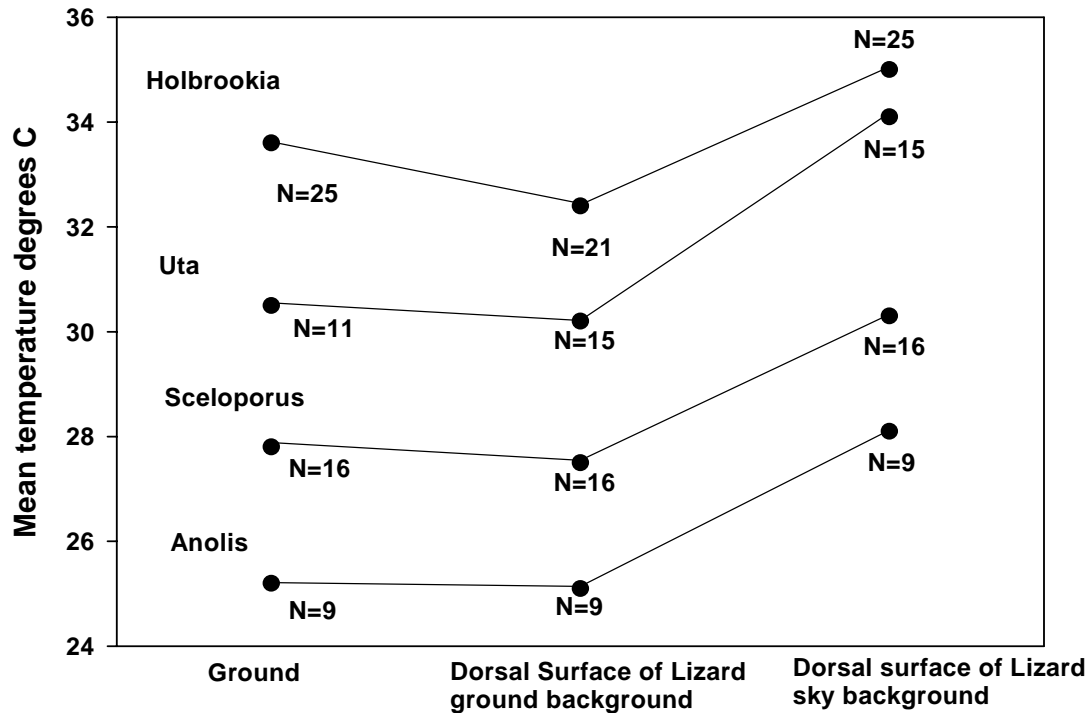


Fig 3a. Cooling coefficients (linear slope of temperature vs. time regression) for all three heating experiments (air, substrate, and radiant) as a function of lizard mass. Thirteen lizards were included for the radiant heating experiments; 12 for the other experiments.

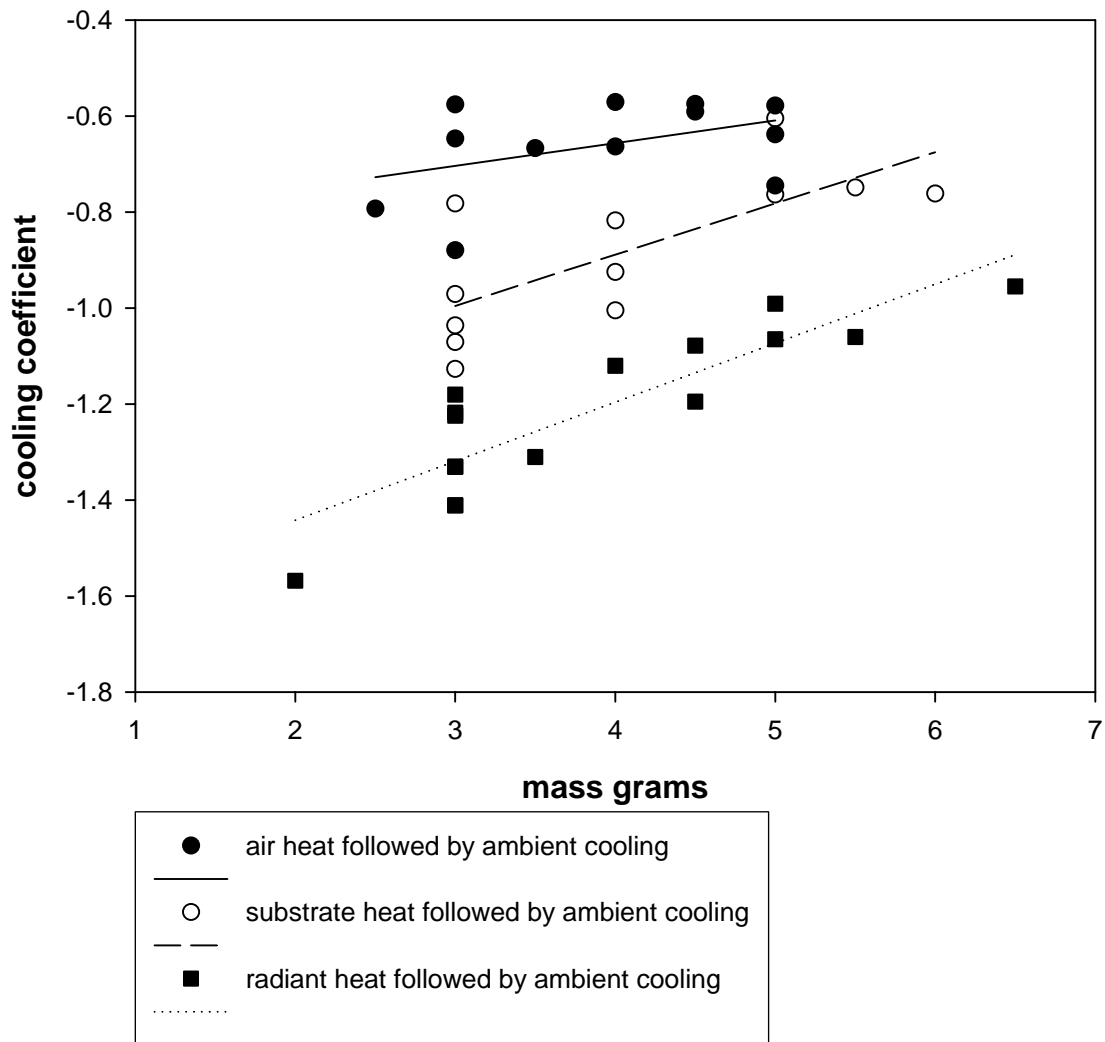


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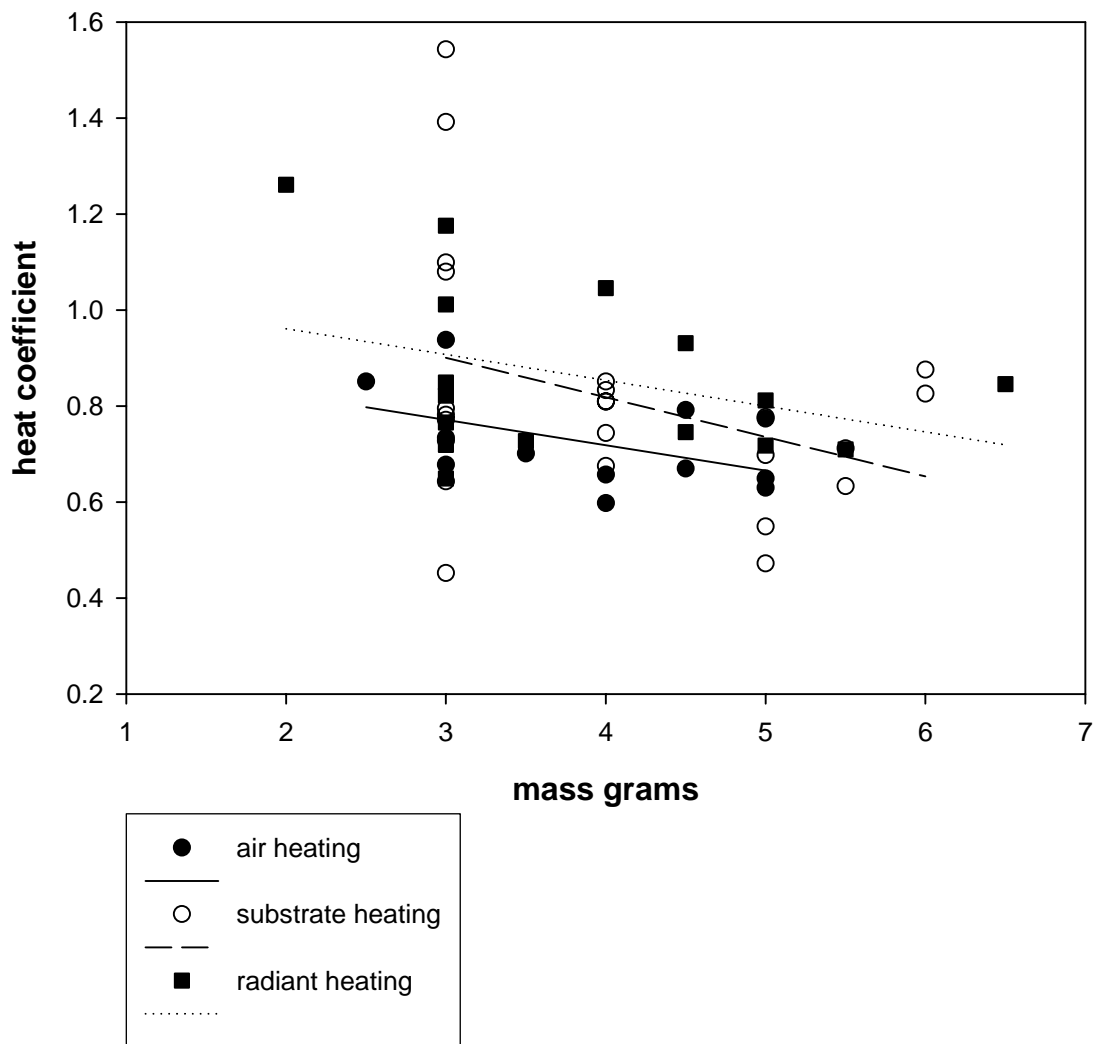


Fig 4. Heating and cooling rates for each of the 5 laboratory trials (lamp with no substrate, heat chamber, lamp with substrate, heat strip with table cool, and heat strip with strip cool). Longer bars indicate faster heating or cooling. Vertical capped lines are one standard error. Heating rate for trial 3 was significantly faster than that for the other trials. Cooling rates for trials 1 and 5 were significantly different from each other and that of the other trials.

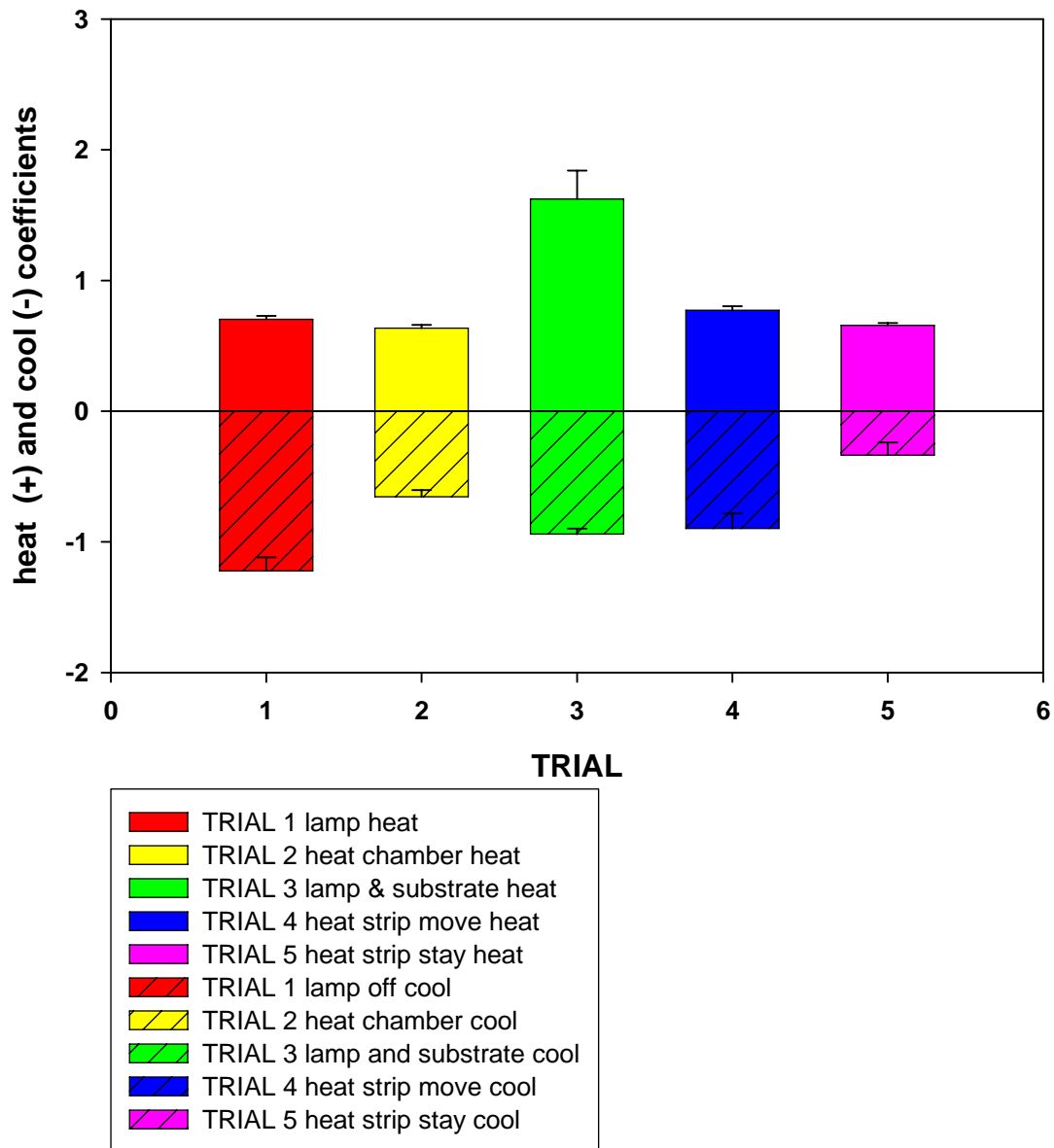


Fig 5. Comparison of cloacal temperatures measured in the field vs. cloacal temperatures measured in the lab for three species. Overlapping values are not shown.

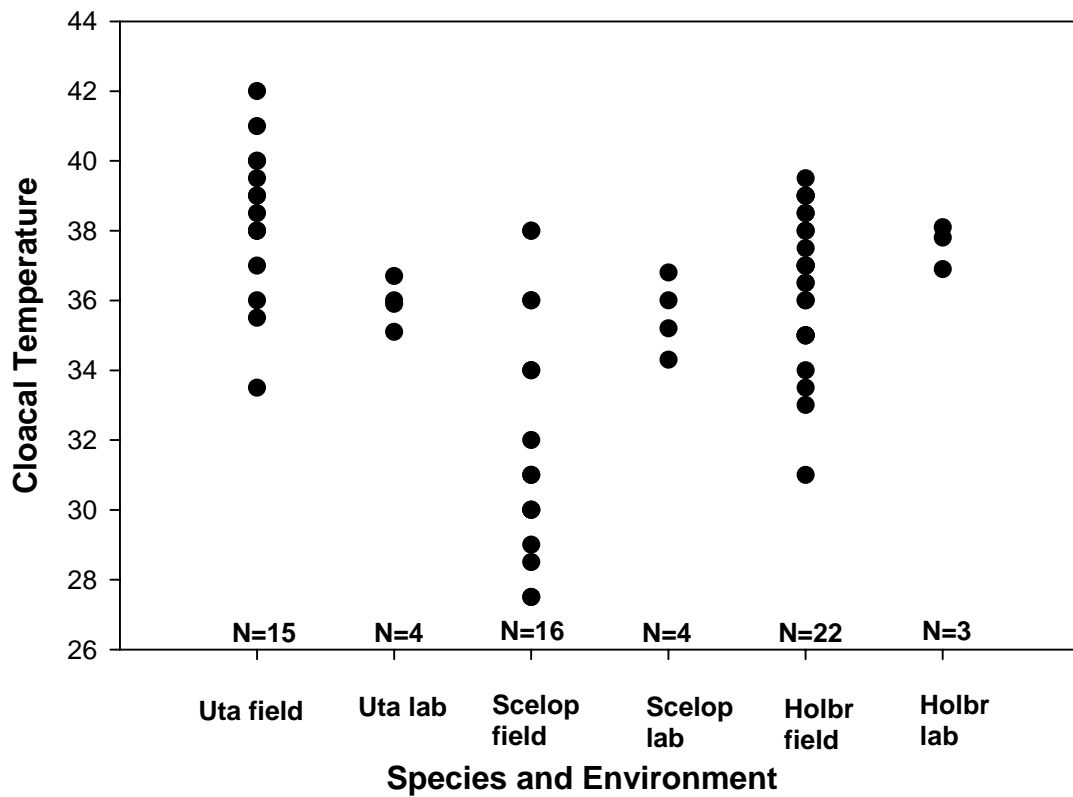


Table 1. A comparison between measured and predicted internal body temperatures using present study model and Alberts and Grant (1997) model for each size-class of lizard studied. Predicted temperatures were calculated using a median of the range for the size category. Actual average deviation using data collected from each specimen was $0.20^{\circ}\text{C} \pm \text{s.d. } 1.43$. Our model is a much more accurate predictor of internal body temperature than is the original Alberts and Grant model for lizards of this size.

Mass (g)	# of Specimens	Mean Ts °C	Mean Ta °C	Mean Measured Tb °C	Predicted Tb °C Bucklin & Ferguson	Predicted Minus Measured	Predicted Tb °C Alberts & Grant	Predicted Minus Measured
2.0 – 2.9	6	29	28	30.8	31.1	0.3	28.9	-1.9
3.0 – 3.9	18	32	28	33.5	33.8	0.3	31.7	-1.8
4.0 – 4.9	14	33	29	35.7	34.9	-0.8	32.7	-3.0
5.0 – 5.9	18	34	30	36.7	35.9	-0.8	33.7	-3.0
6.0 – 6.9	7	31	31	36.4	33.4	-3.0	31.0	-5.4
7.0 – 7.9	2	29	26	30.0	30.7	0.7	28.8	-1.2
AVERAGE DEVIATION:						-0.5		-2.7
AVERAGE ABSOLUTE DEVIATION:						1.0		2.7

Table 2. A comparison of dorsal temperatures as measured by three different instruments in the field. The primary measurement tool (Raytek) is highly accurate.

Species	Specimen Number	Dorsal Temperature as Measured By:			Average of Thermistor and Cloacal Thermometer	Deviation of Raytek from Average
		Raytek	Thermistor	Cloacal Thermometer		
<i>H. maculata</i>	1	28.0	30.8	-	30.8	-2.8
<i>H. maculata</i>	2	31.0	31.0	31.0	31.0	0.0
<i>H. maculata</i>	3	33.0	31.0	31.0	31.0	2.0
<i>H. maculata</i>	4	34.0	34.0	34.0	34.0	0.0
<i>H. maculata</i>	5	38.5	37.0	36.0	36.5	2.0
<i>S. undulatus garmani</i>	1	34.0	31.7	32.0	31.9	2.2
<i>S. undulatus garmani</i>	2	32.0	33.3	31.5	32.4	-0.4
	AVERAGE:	32.9	32.7	32.6		0.4

Table 3. Heating and cooling coefficients (linear slope of cloacal temperature versus time) of 3 lizards (one each of *Uta stansburiana*, *Sceloporus undulatus*, *Holbrookia maculata*) subjected to various heat sources and sinks in the laboratory. Different superscript letters indicate statistically significant differences (see text).

Trial	Context	Heating Rate (mean \pm S.E.)	Cooling Rate (mean \pm S.E.)
1	HEATING: half- body and air radiant COOLING: full- body cool air	0.70 \pm 0.03 ^b	- 1.22 \pm 0.10 ^a
2	HEATING: half- body and substrate convective air COOLING: half- body cool air, half- body cooling substrate	0.64 \pm 0.02 ^b	- 0.65 \pm 0.05 ^b
3	HEATING: half- body and substrate radiant COOLING: half- body cool air, half- body warmed substrate	1.62 \pm 0.22 ^a	- 0.94 \pm 0.04 ^b
4	HEATING: half- body conductive COOLING: half- body cool air, half- body cool substrate	0.77 \pm 0.03 ^b	- 0.90 \pm 0.12 ^b
5	HEATING: half- body conductive heating COOLING: half- body cool air, half- body warmed substrate	0.66 \pm 0.02 ^b	- 0.34 \pm 0.10 ^c

Table 4. Average cloacal temperatures (N) of 3 species in the field and in the lab. Air temperatures (N) are provided for comparison. All field N's are based on one reading per lizard. All lab N's are based on multiple readings of a few lizards as indicated.

	Average Temperature °C		Higher	Mean Air Temp Field	Mean Air Temp Lab
	Field	Lab			
<i>U. stansburiana</i>	38.3 (15)	35.9 (21 readings of 4 lizards)	Field	33.9 (11)	26.6 (32 readings near 4 lizards)
<i>S. undulatus</i>	32.0 (16)	35.6 (17 readings of 4 lizards)	Lab	27.7 (16)	26.3 (33 readings near 4 lizards)
<i>H. maculata</i>	36.5 (25)	37.6 (17 readings of 3 lizards)	Lab	28.5 (25)	27.4 (28 readings near 3 lizards)

Table 5. Cloacal temperatures of five lizards before and after ten minutes of chase. Predicted temperature was mean cloacal temperature of that lizard (Number of readings) measured during several days prior to the chase when the lizard had been active for at least an hour prior to each reading and presumably thermoregulating. See text for details.

Species	Specimen i.d.#	Predicted Temp Before Chase °C	Average Cloacal Temperature After Chase °C	Deviation	Absolute Deviation
<i>U. stansburiana</i>	U 3	36.7 (3)	36 (3)	0.7	0.7
<i>U. stansburiana</i>	U 5	35.9 (3)	36.3 (3)	-0.4	0.4
<i>S. undulatus</i>	S 1	35.2 (3)	36 (3)	-0.8	0.8
<i>H. maculata</i>	H 3	38.1 (4)	36.8 (4)	1.4	1.4
<i>H. maculata</i>	H 5	36.9 (3)	35.7 (3)	1.2	1.2
AVERAGE:				0.4	0.9

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ABSTRACT

STUDIES OF THERMOREGULATION IN SMALL IGUANINE LIZARDS: FEASIBILITY OF THE USE OF REMOTE LASER SENSING EQUIPMENT TO DETERMINE DEEP BODY TEMPERATURES OF SMALL LIZARDS AND THERMOREGULATORY PRECISION IN THE FIELD

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Many lizards maintain their body temperature within a fairly narrow range, despite spatial and temporal variation in microclimates. The ability to measure these temperatures is central to studying lizard physiology. Non-intrusive methods are preferred because they cause the least disruption to the animal's natural behavioral patterns. I modified the Alberts and Grant (1997) model of non-contact temperature prediction of Cuban rock iguanas (mass range 120-850 g) for use on four species of smaller lizards (mass range 2-7 g). I also developed an empirical model expressing the relationship between skin surface temperature (T_s) and internal body temperature (T_b) as a regression. Using this model, and given an ambient temperature (T_a), a lizard's internal body temperature can be estimated within $0.2 \pm 1.43 \text{ SD}^\circ\text{C}$ from its remotely determined dorsal skin surface temperature. The modified Alberts and Grant model and my model had similar predictive results. Additional potential heating and cooling rates were determined in the lab with various heat sources and sinks to assess the ability of lizard body temperatures to vary in the short term and to confirm the accuracy of our field readings. Chase studies in the lab showed that there was no significant change in the internal body temperatures of the lizards if they were chased to and from heat sources and

sinks over a ten-minute period. The lizards appeared to be unable to maintain preferred laboratory temperatures precisely in the field.