

Research article

Body surface temperature and length in relation to the thermal biology of lizards

Daniel Garrick*

Canterbury Christ Church University, Canterbury, UK.

* **Corresponding author:** Flat 4, 89 Henver Road, Newquay, Cornwall TR7 3DJ, UK. Email: daniel_garrick@hotmail.co.uk**Supervisor:** Georges Dussart, Canterbury Christ Church University, Canterbury, UK.

This study investigated body surface temperature (T_{bs}) in 22 lizards of 18 species. The difference between T_{bs} and ambient temperature (T_a) was correlated with size. The greater $T_{bs} - T_a$ differentials, which were recorded in larger lizards, may occur as a result of heat transfer from the core to surface in prevention of overheating. The structure of the integument may contribute to heat dissipation. Heliothermy and thigmothermy as forms of thermoregulation were also incorporated into the data set. Heliothermic lizards showed a positive correlation between length and $T_{bs} - T_a$. Thigmothermic lizards, however, exhibited a negative correlation. Differences in size and rate of conductive heat transfer are put forward as possible reasons for the negative correlation.

Key words: thigmothermy, heliothermy, lizard, length.

Lizards, like most reptiles, are ectothermic. Ectothermy is the reliance on external heat sources to increase body temperature.^{1, 2} Thus lizards gain heat, principally, from their environment. To achieve optimum body temperature lizards perform different thermoregulatory behaviours. Thermoregulation is a well-documented area of reptile biology.^{3–5}

The use of thermoregulation to achieve and maintain optimum body temperature has contributed to the great diversity of lizards and even allowed colonization of temperate regions. For example, through simple body posturing, some species within the South American genus *Liolaemus* can attain body temperatures 30°C above the ambient temperature.⁶ Such a high differential, though uncommon, emphasizes the diversity of thermal relations among lizards.

Heliothermy and thigmothermy are further means of ectothermal thermoregulation.⁷ Heliothermy is heat gain by short wavelength solar radiation. Thigmothermy involves heat conduction to the reptile body by direct contact with a warm substratum.⁸ In practise, heliothermy and thigmothermy enable lizards to compensate for the thermal conditions of the habitat.⁹ Heliothermy and thigmothermy in lizards are therefore related to habitats and life-history strategies.

Heliothermy is a well-documented area in lizard biology.¹⁰ A principal reason for this bias is that diurnal basking lizard species are often the dominant vertebrates in hot arid environments and data on these animals are relatively easy to obtain. In contrast, Belliure and Carrascal⁸ suggest thigmothermy is a less well-studied aspect of animal thermal relations.

In general, thigmothermy is practised by species that have limited access to solar radiation.¹¹ Most studies of lizard thigmothermy have considered diurnal species.^{12, 13} Among diurnal lizards, thigmothermy is normally practised by species in forest environments where incoming solar radiation is impeded by the tree canopy. Morgan¹⁴ suggests that in such environments, thermally discrete microclimates are important. In contrast thigmothermic behaviour is relatively more important for nocturnal lizards, which do not receive any solar radiation input.

Previous studies of thermal interactions between lizard and environment have predominantly used the internal body temperature (T_b) (i.e. cloacal) and ambient temperature (T_a) differential.^{12, 15–17} Auffenberg¹⁵ and Stevenson¹⁶ related body temperature to size. These authors concluded that larger size conferred a greater $T_b - T_a$ differential due to thermal inertia. Thermal inertia is based upon the physical properties

of heat dissipation whereby larger objects retain heat for longer than smaller objects due to reduced surface-to-volume scaling. Such a phenomenon has been demonstrated in extant crocodylian species and has been proposed for elevated temperatures in large dinosaur species.^{2, 18, 19}

In contrast with previous work, this paper investigates radiant heat transmission using body surface temperature (T_{bs}). Cowles²⁰ suggested that the dermal surface of reptiles could act as a heat collector and dispenser. Therefore the question arises as to whether the previous identified relationships between core and ambient temperatures are similar to the differentials between T_{bs} and T_a ? The following experiment aims to investigate the correlation between length and $T_b - T_a$ differential. A further aim is to gain a greater understanding of heliothermy and thigmothermy in a range of lizard species.

Materials and methods

Prior to the main experiment, a preliminary study was carried out. Data were collected from three individual lizards of three species of differing size. The preliminary study was used to determine first, how readings would be recorded and secondly, the general protocol for the main experiment. The study also determined whereabouts on the body it was possible to collect temperatures accurately without the need for physical contact.

Data collected in the study were obtained from captive lizards maintained indoors under artificial conditions. Environments of captive lizards are mostly constant since heat sources and photoperiods are regulated. For the investigation undertaken here, this is an advantage since it allows a fair comparison of inter-specific effects.

Body surface temperature (T_{bs}) – ambient temperature (T_a) differential

Data were obtained from four private and zoological institutions in the UK and Germany (Table 1). Overall data for the main experiment were collected from 22 individual lizards representing 18 species in 6 families (Table 2). Data acquisition took place in September 2006 between

Table 1. Abbreviations used in text

Symbol	Definition
LF	Lower fore leg body site
LH	Lower hind leg body site
MBL	Mid-body lateral body site
T	Mid-caudal site
T_a	Ambient temperature
T_b	Body temperature
T_{bs}	Body surface temperature

Table 2. Key to list of collections used in study

Collection	Abbreviation
Private collection	P
Terrazoo Rheinberg	T
Zoo Duisburg	ZD
Zoom Erlebniswelt	ZE

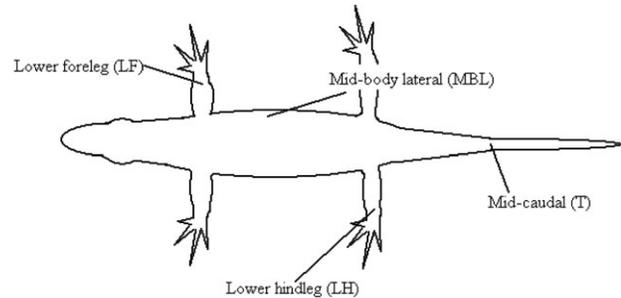


Figure 1. The four anatomical sites used for data collection in experiment.

13:00–16:00 hours. All measurements were taken indoors within enclosures.

Temperature was measured using a DT-8812 infrared non-contact thermometer. The thermometer is laser pointed and provides measurement collection at a distance to spot ratio of 8:1. The resolution is -20°C to 200°C in 0.1°C intervals, with a display accuracy of $\pm 2.0\%$. Temperature readings were recorded in degree Celsius ($^{\circ}\text{C}$). Measurements were taken within 200 mm of study animal. Each measurement recorded the T_{bs} at a predetermined anatomical site. The four sites chosen for data collection were mid-body lateral (MBL), lower fore leg (LF), lower hind leg (LH) and mid-caudal (T) (Figure 1). To get a temperature reading the thermometer laser was aimed at a point ~ 20 mm above the chosen anatomical site (as specified by manufacturers). Five consecutive readings were taken at each site. T_a was also measured by five consecutive readings. For the purpose of the experiment T_a was, as defined by Pough and Gans,⁷ the mean air temperature outside the boundary layer in the immediate vicinity of the lizard (i.e. within 300 mm radius of study animal). There was a 20-s delay between each reading. Between sites and T_a readings there was a delay of 3 min. This delay allowed the infrared sensor to equilibrate. Most of the study animals (90%) were exposed within enclosure when readings were taken. However, readings from two individuals were taken while sheltered (see Table 3). There was no physical contact with the study animal during data collection.

Heliothermy and thigmothermy

The protocols described above were used for the measurement of heliothermic and thigmothermic species. Species

Table 3. Individuals measured in study with $T_{bs} - T_a$ differentials and heliothermic/thigmothermic categorization. Note both sheltered and non-sheltered individuals are included in this table. Heliothermic thigmothermic classification is prior to output of discriminant analysis (see Materials and Methods). Abbreviations for collection are given in Table 2

Common name	Scientific name	Family	Length (mm)	MBL $T_{bs} - T_a$ Differential	Heliothermic/thigmothermic	Collection
Frilled Dragon	<i>Chlamydosaurus kingii</i>	Agamidae	550	2.6	H	ZD
Frilled Dragon	<i>Chlamydosaurus kingii</i>	Agamidae	600	3	H	T
Collared Lizard	<i>Crotaphytus collaris</i>	Iguanidae	200	1.2	H	P
Spiny-tail Iguana	<i>Ctenosaura similis</i>	Iguanidae	750	4.2	H	P
Rhinoceros Iguana	<i>Cyclura cornuta</i>	Iguanidae	1500	5.1	H	T
Leopard Gecko	<i>Eublepharis macularis</i>	Gekkonidae	220	0.4	T	P
Canary Island Lizard	<i>Gallotia stehlini</i>	Lacertidae	450	2.3	H	P
Canary Island Lizard	<i>G. stehlini</i> (shelter)	Lacertidae	400	1.3	H	P
Tokay Gecko	<i>Gekko gecko</i>	Gekkonidae	250	0.1	T	ZE
Fat-tailed Gecko	<i>Hemithetheconyx caudicinctus</i>	Gekkonidae	220	0.2	T	P
Green Iguana	<i>Iguana iguana</i>	Iguanidae	750	3.7	H	ZE
Green Iguana	<i>I. iguana</i>	Iguanidae	1800	2.5	H	ZD
Eyed Lizard	<i>Lacerta lepida</i>	Lacertidae	100	0.7	H	P
Star Agama	<i>Laudakia stellio brachydactylus</i>	Agamidae	200	1.4	H	P
Frog-eyed Gecko	<i>Teratoscincus scincus</i>	Gekkonidae	150	0.6	T	P
Blue-tongued Skink	<i>Tiliqua gigas</i>	Scincidae	400	2.7	H	ZD
Blue-tongued Skink	<i>T. gigas</i> (shelter)	Scincidae	350	0.8	H	ZD
Shingleback Skink	<i>Trachydosaurus rugosus</i>	Scincidae	350	2.5	H	T
Moroccan Uromastyx	<i>Uromastyx acanthinurus</i>	Agamidae	300	2.6	H	ZE
Saharan Uromastyx	<i>Uromastyx geyri</i>	Agamidae	400	2.3	H	P
Ridge-tailed Monitor	<i>Varanus acanthurus</i>	Varanidae	550	3.2	H	T
Gould's Monitor	<i>Varanus gouldii</i>	Varanidae	1800	4.3	H	T

were categorized as heliothermic or thigmothermic in accordance to whether a species was diurnal (heliotherm) or nocturnal (thigmotherm). No further thermoregulatory categories were accounted for.

Statistical methods

Statistical analyses were performed in accordance to the protocols described in Zar.²¹ The correlation method used throughout the experiment was non-parametric Spearman's Rank. Multiple regression analysis (performed through Microsoft Excel) was used in conjunction with Spearman's Rank correlation. One-way ANOVA (as provided by MINITAB) was used to analyse site $T_{bs} - T_a$ differential versus length. Data input for the one-way ANOVA was preceded by an F_{max} test to check homogeneity of variance. The F_{max} test is used to screen samples for normal distribution of data. Discriminant analysis was provided by MINITAB. This method is used to separate sampling units into their true groupings. Data input involves pre-classification of sampling units. In the case of my study pre-classification comprised two units: heliothermic or thigmothermic. Each individual's unit was plotted with $T_{bs} - T_a$ differential.

Results

Overall data collection: site body surface temperature (T_{bs}) versus ambient temperature (T_a)

First, the temperature relations of the four anatomical sites on the reptile body were compared with each other for the 22 lizards (Figure 2). Figure 2 shows close correlations between T_{bs} and T_a for all four sites. All anatomical sites have similar gradients. Coefficients (r^2) for the sites range from 0.946 to 0.974. Such results suggest a positive correlation between T_{bs} and T_a at each of the sites.

Overall, LH exhibited the lowest temperature (Figure 1). Proportionately, 27% LH readings were lower than T_a . In contrast, 22% of T and 9% of LF readings were lower than T_a . MBL showed no readings lower than T_a (0%). Therefore, attention was focused on MBL as it more closely represents the animal's internal temperature.

Inter-family comparison

The 18 different species measured represent 6 different families (Figure 3, Table 2). Data for each anatomical site for each individual were averaged and categorized by family.

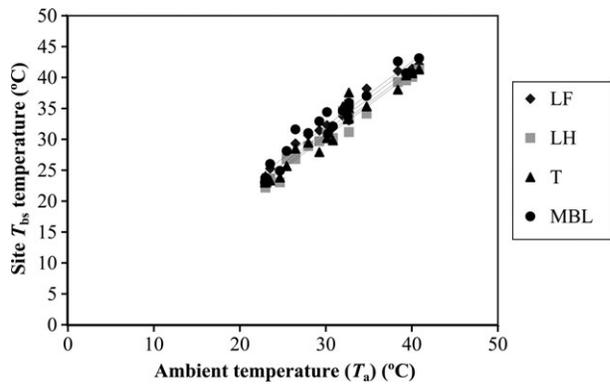


Figure 2. Mean site temperature for 22 individual lizards against the mean ambient temperature. r^2 values are given as LF: 0.974, LH: 0.966, MBL: 0.946, T: 0.946 (see Table 1 for key to abbreviations).

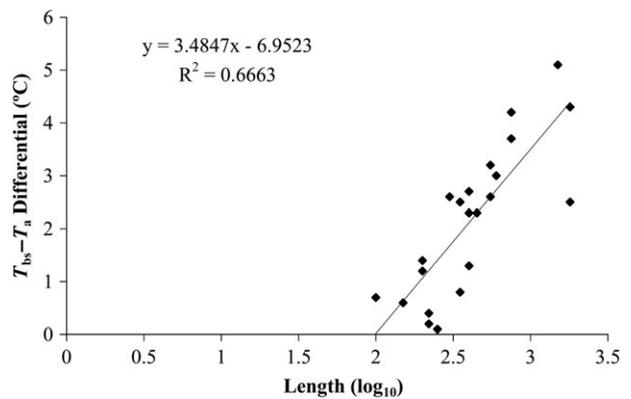


Figure 4. $T_{bs} - T_a$ differentials, from 22 individual lizards, against length (\log_{10}).

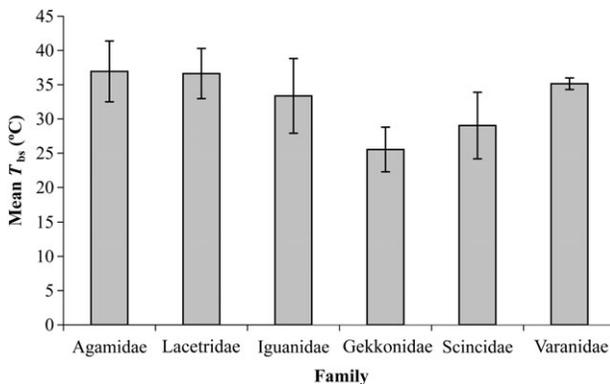


Figure 3. Comparison of mean T_{bs} (for all four anatomical sites) between the six lizard families used in study. Standard deviation is given as 4.57.

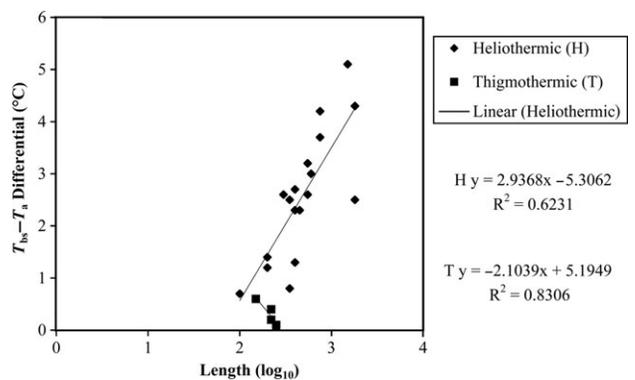


Figure 5. Comparison of the 18 heliothermic and 4 thigmothermic species measured in study showing $T_{bs} - T_a$ differential against length (\log_{10}).

Figure 3 shows that the Gekkonidae exhibited the lowest mean T_{bs} (25.5°C), whereas the Agamidae exhibited the highest mean T_{bs} (36.9°C).

Body surface temperature (T_{bs}) – ambient temperature (T_a) differential versus length

One-way ANOVA analysis showed MBL to be the anatomical site with the greatest $T_{bs} - T_a$ differential (Figure 4). Other anatomical sites displayed more variable readings and $T_{bs} - T_a$ differential between all four sites fluctuated considerably. One-way ANOVA showed significant difference ($P < 0.001$). The MBL data were used to give $T_{bs} - T_a$ differential as the independent variable, to be compared with \log_{10} length. Figure 4 indicates a positive correlation between $T_{bs} - T_a$ differential and \log_{10} length ($r^2 = 0.666$). Multiple regression analysis of the data set gave F as 39.9, thus indicating a strong signal-to-noise ratio (regression MS/residual MS). The given P -value from the regression analysis was < 0.001 .

Heliothermy and thigmothermy

Eighteen heliothermic lizards and four thigmothermic lizards were studied in accordance to the prior classification described in Materials and Methods (see Table 2 for individuals; Figure 5). Figure 5 shows a positive correlation between $T_{bs} - T_a$ differential and length for the heliothermic species data ($r^2 = 0.623$). In contrast, the thigmothermic species data set shows a negative slope ($r^2 = -0.830$).

To assess level of confidence in determining heliothermy and thigmothermy in the study species, a discriminant analysis was performed using $T_{bs} - T_a$ differential from MBL readings. Discriminant analysis showed a confidence level of 77% correct classifications. Five misclassifications resulted in species pre-classified as heliothermic being classified as thigmothermic. The sheltered individuals (*Tiliqua gigas*, *Gallotia stehlini*) measured in the study were both incorrectly classified. The further misclassifications were *Lacerta lepida*, *Crotaphytus collaris* and *Laudakia stellio brachydactylus*. No thigmothermic species were misclassified.

Discussion

Overall, the data set suggests that anatomical T_{bs} is associated with T_a (Figure 2), which is congruent with the established concept that lizards are ectothermic.²

Body surface temperature (T_{bs}) – ambient temperature (T_a) differential versus length

Central to the study was the comparison of $T_{bs} - T_a$ differential (from MBL reading) with length. The relationship between length and $T_{bs} - T_a$ differential might be explained by the role of integument. Licht and Bennett²² compared a scaleless snake and a normal snake and suggested that reptile integument was not a significant heat insulator. Scales are undoubtedly important to radiative and conductive heat exchange. However, if convective heat is lost through an integument it could suggest endogenous heat production. Such heat production has been demonstrated for some reptile species. For example, digestion is known to induce both a faster metabolic rate and increased body temperature in some species.^{23, 24} Brattstrom (cited in Auffenberg¹⁵) notes that the integument of the varanid *Varanus varius* was only poorly effective at retarding heat loss and Stevenson¹⁶ includes thermal conductance between core and surface layer in a mathematical model of thermal balance in ectotherms.

Readings from the MBL anatomical site exhibited a mean $T_{bs} - T_a$ differential of 2.16°C, which represented a thermal difference of 36.8%, 64.9% and 83.2% greater than the other three sites. One-way ANOVA of site $T_{bs} - T_a$ differentials showed significant variation ($P < 0.001$) between all four sites. The MBL site is located on the trunk of the lizard. The proximity of MBL to body organs and thus potential endogenous heat sources may be the reason for the greater $T_{bs} - T_a$ differentials recorded at this anatomical site.

Bartholomew²⁵ suggested that thermal conductance is so great in lizards that endogenous heat is lost at a rate that is proportional to its production. In small lizards, endogenous heat production is insignificant due to the rapid dynamics of heat gain and loss as a result of greater surface-to-volume ratios. However, in large lizards endogenous heat can be significant.^{15, 25, 26} In this present study, *Varanus gouldii* was one of the largest species and it exhibited a $T_{bs} - T_a$ differential of 4.3°C. The greatest $T_{bs} - T_a$ differential, of 5.1°C, was recorded from the iguanid *Cyclura cornuta*. Although the latter species is shorter than *V. gouldii*, it is of greater bulk and thus may suggest mass to be a factor in heat exchange. Mass was not taken into account in this study, but could be a consideration for future lines of investigation.

Greater $T_b - T_a$ differential in large ectotherm species is often attributed to thermal inertia.^{18, 27} The Komodo Monitor (*Varanus komodoensis*) is the world's largest extant lizard species. Auffenberg¹⁵ accredits $T_b - T_a$

differentials in *V. komodoensis* to physiology. The large differentials recorded in *V. gouldii* and *C. cornuta* could therefore indicate the existence of some form of physiological heat production in these species. With thermal inertia, greater differentials in larger species might reflect transfer of internally generated heat from body core to surface. Heat dissipation through the integument may help prevent larger species from overheating.

If $T_b - T_a$ differential is generally correlated with size it could counteract short-term changes in T_a . Small species need to actively bask for a fraction of the time required for large species²⁸. Therefore small lizards are able to resume activity within much shorter time frames than larger species. To counteract an inevitable greater rate of cooling, smaller lizards perform short-term intermittent patterns of thermoregulation and activity throughout the day.

Bergmann's rule states that animals at higher latitudes are generally larger than those in the tropics.²⁹ In contrast, Ashton and Feldman³⁰ observe the opposite for snakes and lizards. Smaller size and therefore greater rate of heat gain would be of greater benefit at higher latitudes due to increased seasonal variation in temperatures. Thus there may be a larger versus smaller trade-off in lizards.

One of the two largest lizards (1800 mm) in my study, *Iguana iguana*, displayed a $T_{bs} - T_a$ differential of 2.5°C. In accordance with the other data collected here, a lizard of this size should have a bigger $T_{bs} - T_a$ differential. To put the result into context, a smaller (750 mm) sub-adult individual of *I. iguana* demonstrated a $T_{bs} - T_a$ differential of 3.7°C. The reason for the disparity may lie in the conditions in which the large individual was housed. The large *I. iguana* was housed in a large, open display as part of a multi-species exhibit in a zoo. No heat sources were provided and T_a fluctuated with T_a in the building. Avery¹⁰ states that iguanids, in general, are active at high constant temperatures. Wild adult *I. iguana* bask prominently and thus raise their T_b . Therefore without access to any direct radiative or conductive heat source in the zoo, the study individual would not be able to raise its T_b . In addition, the surrounding T_a of the large *I. iguana* was one of the lowest (23.5°C) in the data set. Thus it is possible that at certain temperatures T_{bs} conforms more to T_a . If such a phenomenon does occur, a smaller T_{bs} and T_a differential would result in reduced heat loss from core. Reduced heat loss at a lower T_a supports the suggestion that integument dissipates heat in large lizards when under periods of high T_a .

Heliothermy and thigmothermy

An objective of the study was to compare heliothermy and thigmothermy in lizards. The results showed that $T_{bs} - T_a$ differential in heliothermic species was positively correlated with length. Thigmothermic species, on the other hand seemed to show a negative correlation, though there were relatively few data.

Bennett³¹ correlated maximal locomotor capacity in lizards with T_b . Bennett concluded that species performed at their peak at higher T_a (higher than that would be experienced in the wild for some). Bennett's results suggest heliothermy could enhance lizard performance. Rummery *et al.*¹³ view heliothermy as a high cost method of raising body temperature. For example, diurnal species which often bask prominently in open areas to maximize radiative heat gain are exposed to increased risk of predation. Large heliothermic species are at less risk of predation. Also, because of their large size, their higher T_b means that relatively less time is spent basking. Most lizard species, however, are of small to moderate size and therefore heliothermy is risky.

Nocturnal lizards face different constraints since they cannot thermoregulate in the classical sense. Some nocturnal species use protected basking where the protection is afforded by a crevice or thick vegetation that does not impede solar radiation.¹⁰ Protected basking therefore, is used by some lizard species that remain inactive during the day but become active at night using the heat gained while at rest. Equally, some species use camouflage to enable discreet basking. For the purpose of these analyses, nocturnal lizards were categorized as thigmothermic. All the thigmothermic lizards in this study were geckos. Geckos control T_b actively through selection of substrata and passively through activity times (according to location or season).¹⁰ Inter-family comparison shows that the Gekkonidae exhibit the lowest mean overall T_{bs} of all six families in the study. Also, all geckos recorded low $T_{bs} - T_a$ differentials and were of relatively small size (<250 mm). The negative correlation between $T_{bs} - T_a$ differential and length seen in the study could suggest that geckos might get a metabolic benefit from smaller size.

Thermal conductance is greater during heating than in cooling.³² However, larger lizards require a longer period of contact with the substratum to reach their optimum body temperature. Therefore smaller size enables optimum body temperature to be reached in a shorter time frame. The same principle applies to heliothermic species and radiative heat gain.

The discriminant analysis showed five misclassifications. Sheltered individuals of *T. gigas* and *G. stehlini* were among the incorrectly classified taxa. In contrast, non-sheltered individuals of these species were classified correctly as heliothermic. Both sheltered and non-sheltered individuals of the same species were within the same enclosures. However, temperature measurements from one of each species were taken from individuals hiding in an enclosure refuge.

Sheltered individuals of *T. gigas* and *G. stehlini* showed markedly low $T_{bs} - T_a$ differentials compared with non-sheltered individuals. Regal³³ stated that lizards seek low temperatures when not active. Data obtained from the

present study suggest that low temperature is more important than shelter, which would then be considered coincidental with low T_a . Shelters are often less influenced by short-term environmental temperature fluctuations and thus can provide stable microclimates.¹⁷ Therefore, it is probable that shelters are used to maintain selected body temperature through intermittent use.

Adolph⁴ notes that some terrestrial sheltered microhabitats are warmer than exposed arboreal perches. In relation to the present study the statement is not true, as recorded T_a was much greater outside of the shelter (2.4–3.9°C). However, such a situation would be expected under captive conditions where oscillations in T_a are almost non-existent. Natural habitats, however, offer a more varied spatial distribution of differing thermal microclimates. Therefore wild lizards are presented with greater opportunities to exert control, which would lead them to establish their optimum body temperature.

In the discussion of heliothermy and thigmothermy, it should be remembered that neither are definitive means of thermoregulation. Pough *et al.*²⁶ states that heliothermy and thigmothermy are ends of a spectrum in thermoregulation. Within heliothermy, further categorizations include whether a species performs shuttling or posturing thermoregulatory behaviours. Such behaviours were not accounted for the present study.

In summary, the results suggest that radiant heat transmission from the integument is greater in larger individuals. Exactly why this occurs is unknown and thus requires further investigation.

One possibility is that the integument of larger lizards shields them more efficiently than smaller bodied species from radiative heat gain, thus preventing the overheating of bodies that already possess greater $T_b - T_a$ differentials, because of thermal inertia. Therefore, the results obtained could simply be attributed to heat reflecting from the integument rather than transfer from the core. However, this hypothesis does not encompass the younger stages of growth when maximizing radiative heat gain would be imperative.

This study could be improved by examining more individuals and species. A starting point for further study could use measurements of species larger than those in this study. As mentioned earlier, mass could also be measured to complement length in order to give a better picture of individuals' volume.

A second line of investigation could be to compare dorsal T_{bs} and ventral T_{bs} . Tercafs³⁴ notes differences in radiative transmission between dorsal and ventral integuments. Such a comparison could improve our knowledge of the role of conduction in lizard thermal relations. Also substratum temperature could be included in a future study and integuments of a selection of species could be examined.

Most of the species studied here (82%) were heliotherms. The limited number of thigmothermic species for this group means that no strong conclusions can be drawn regarding the relationship between length and $T_{bs}-T_a$ differential. However, the results raise issues for future study. For example, does $T_{bs}-T_a$ differential decrease further with greater length in thigmothermic lizards? Also how does the thermal performance of diurnal thigmothermic species, such as those present in deep forest habitats, compare with nocturnal species? The dearth of information on lizard thigmothermy is an incentive to continue the line of investigation.

Funding

This project was self funded, although Canterbury Christ Church University did provide some funding for equipment.

Acknowledgements

The author would like to thank the invaluable assistance of Stefan Terlinden who provided opportunity to collect data in Germany. Equal gratitude is bestowed to staff at Zoo Duisburg, Zoom Erlebniswelt at Gelsenkirchen and Terrazoo Rheinberg who permitted use of their lizards in the study. In addition the author thanks Chris Davies for allowing his private collection to be used for data collection. Finally, I would like to thank Professor Georges Dussart for his helpful guidance throughout the project.

References

- Nelson DO, Heath JE, Prosser CL (1984) Evolution of temperature regulatory mechanisms. *Am Zool* 24: 791–807.
- Pough FH, Janis CM, Heiser JB (2005) *Vertebrate Life*, 7th edn. New Jersey: Pearson Education, Inc.
- Gans C, Pough FH (1982) Physiological ecology: its debt to reptilian studies, its value to students of reptiles. In C Gans, eds, *Biology of the Reptilia*. New York: Academic Press, pp. 1–13.
- Adolph SC (1990) Influence of behavioural thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* 71: 315–327.
- King D, Green B, Herrera E (1994) Thermoregulation in a large Teiid lizard, *Tupinambis teguixin*, in Venezuela. *Copeia* 3: 806–808.
- Schmidt-Nielsen K (1997) *Animal Physiology*, 5th edn. Cambridge: Cambridge University Press.
- Pough FH, Gans C (1982) The vocabulary of reptilian thermoregulation. In C Gans, eds, *Biology of the Reptilia*. New York: Academic Press, pp. 17–23.
- Belliure J, Carrascal LM (2002) Influence of heat transmission mode on heating rates and on the selection of patches for heating in a Mediterranean lizard. *Physiol Biochem Zool* 75: 369–376.
- Belliure J, Carrascal LM, Díaz JA (1996) Covariation of thermal biology and foraging mode in two Mediterranean Lacertid lizards. *Ecology* 77: 1163–1173.
- Avery RA (1982) Field studies of body temperatures and thermoregulation. In C Gans, eds, *Biology of the Reptilia*. New York: Academic Press, pp. 93–166.
- Kearney M, Predavec M (2000) Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology* 81: 2984–2996.
- Huey RB, Webster TP (1975) Thermal biology of a solitary lizard: *Anolis marmoratus* of Guadeloupe. *Ecology* 56: 445–452.
- Rummery C, Shine R, Houston DL et al. (1995) Thermal biology of the Australian forest dragon, *Hypsilurus spinipes* (Agamidae). *Copeia*: 818–827.
- Morgan KR (1988) Body temperature, energy metabolism, and stamina in two Neotropical forest lizards (Ameiva, Teiidae). *J Herpetol* 22: 236–241.
- Auffenberg W (1981) *The Behavioural Ecology of the Komodo Monitor*. Gainesville: University Presses of Florida.
- Stevenson RD (1985) Body size and limits to the daily range of body temperature in terrestrial ectotherms. *Am Nat* 125: 102–117.
- Mautz WJ (1994) Thermal biology and microhabitats of Xantusiid lizards. In PR Brown, JW Wright, eds. *Herpetology of the North American Deserts*. Excelsior: Southwestern Herpetologists Society, pp. 227–238.
- Reid REH (1997) Dinosaurian physiology: The case for “intermediate” dinosaurs”. In JO Farlow, MK Brett-Surman, eds, *The Complete Dinosaur*. Bloomington: Indiana University Press, pp. 449–473.
- Gillooly JF, Allen AP, Charnov EL (2006) Dinosaur fossils predict body temperatures. *PLoS Biol* 4: 0001–0003.
- Cowles RB (1958) Possible origin of dermal temperature regulation. *Evolution* 12: 347–357.
- Zar JH (1996) *Biostatistical Analysis*. New Jersey: Prentice Hall.
- Licht P, Bennet AF (1972) A scaleless snake: tests of the role of reptilian scales in water loss and heat transfer. *Copeia*: 702–707.
- Marcellini DL, Peters A (1982) Preliminary observations on endogenous heat production after feeding in *Python molurus*. *J Herpetol* 16: 92–95.
- Tattersall GJ, Milsom WK, Abe AS et al. (2004) The thermogenesis of digestion in rattlesnakes. *J Exp Biol* 207: 579–585.
- Bartholomew GA (1982) Physiological control of body temperature. In C Gans, eds, *Biology of the Reptilia*. New York: Academic Press, pp.167–211.
- Pough FH, Andrews RM, Cadle JE et al. (2004) *Herpetology*, 3rd edn. New Jersey: Pearson Education, Inc.
- Bakker RT (1986) *The Dinosaur Heresies*. New York: William Morrow and Company, Inc.
- Díaz JA (1994) Field thermoregulatory behaviour in the western Canarian lizard *Gallotia galloti*. *J Herpetol* 28: 325–333.
- Wilmer P, Stone G, Johnston I (2005) *Environmental Physiology of Animals*. Oxford: Blackwell.
- Ashton KG, Feldman CR (2003) Bergmann’s rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57: 1151–1163.
- Bennett AF (1987) Evolution of the control of body temperature: is warmer better? In P Dejours, L Bolis, CR Taylor, et al., eds. *Comparative Physiology: Life in Water and on Land*. Padova: Fidia Research Series, IX-Liviana Press. pp. 421–431.
- Avery RA (1979) *Lizards: A Study in Thermoregulation*. London: Edward Arnold.
- Regal PJ (1967) Voluntary hypothermia in reptiles. *Science New Series* 155: 1551–1553.
- Tercafs RR (1963) Transmission of ultra-violet, visible and infra-red radiation through the keratinous layer of reptile skin (Serpentes and Sauria). *Ecology* 44: 214–218.

Submitted on 30 September 2007; accepted on 28 January 2008; advance access publication 17 April 2008