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TECHNICAL REPORT

Field studies of reptile thermoregulation: how well do physical models predict operative temperatures?

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Summary

1. Field-based studies on reptile thermoregulation increasingly rely upon physical models to estimate operative temperatures. Some investigators use models that mimic the size, shape, colour and posture of their study species, but such details may have little influence on thermal regimes (and hence, complex models may be a waste of time and money).
2. Temperatures were measured at 10-min intervals inside 48 hollow copper-pipe models exposed to natural weather conditions over a 27-day period, in a factorial design to examine the effects of model attributes on thermal profiles.
3. These data clarify the ways in which model size, colour (reflectance), orientation and degree of contact with the substrate affect (a) mean, minimum and maximum temperatures, and (b) the number of hours per day that the models exceed specified thermal thresholds. Also examined are (c) interactions between model attributes in these respects, and (d) the ways in which such effects depend upon local weather conditions.
4. Model temperatures were affected by all of the attributes tested, but with few interactions between these effects. Although statistically significant, the effects of model attributes upon operative temperature regimes were generally minor (<5% of mean values).
5. Guidelines for the use of physical models in future research are provided.

Key-words: Biophysics, copper models, ectotherm, methodology, weather

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Introduction

Ectothermic animals can control their body temperatures, and this control may have important consequences for the animal's ability to exploit environmental resources (e.g. Cowles & Bogert 1944). In recent years, research on the thermal biology of reptiles and amphibians has been revolutionized by new conceptual approaches (e.g. Heath 1964; Grant & Dunham 1988; Hertz, Huey & Stevenson 1993; Christian & Weavers 1996) and methodological advances (Bakken & Gates 1975; Bakken 1992). Both of these developments involve the idea of operative temperature (T_e), defined as the temperature of an inanimate object of zero heat capacity with the same size, shape and radiative properties as an animal exposed to the same microclimate (Bakken & Gates 1975). Operative temperature provides a more meaningful measure of thermoregulatory opportunities and challenges than simple measures of air or ground temperatures, because it integrates heat exchange across multiple pathways (notably, radiation, convection and conduction). Data on operative temperatures are used to calculate variables such as potential activity times (Porter *et al.* 1973; Grant & Dunham 1988) and thermoregulatory effectiveness (Hertz *et al.* 1993; Bauwens, Hertz & Castilla 1996; Christian & Weavers 1996; Kearney & Predavec 2000).

Despite frequent measurement of operative temperature in the field, the techniques for making such measurements have received surprisingly little attention. A wide variety of approaches have been adopted, ranging from mathematical modelling of energy fluxes (Porter *et al.* 1973; Roughgarden, Porter & Heckel 1981; Christian & Weavers 1996), to the use of physical models that closely mimic the study organism in size, colour, posture and heat capacity (Adolph 1990; Hertz 1992a,b; Bauwens *et al.* 1996). The most popular technique has involved hollow-walled copper tubes with very low heat capacity (which thus respond rapidly to changes in radiation levels, etc.), but studies have differed in the degree of complexity of such models. Some researchers have gone to great trouble and expense to manufacture lifelike models that mimic aspects such as colour, posture and scale microtopography (based on casts of dead animals) (Porter *et al.* 1973; Hertz 1992b). Such realism is expensive to attain, and does it really matter? Recently, Vitt & Sartorius (1999) suggested that such models display similar thermal regimes to

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data-loggers placed in the same location. Because this issue has obvious logistical implications for research on reptile thermoregulation, we have extended the study by Vitt & Sartorius (1999) to examine the degree to which various attributes of simple physical models (size, colour, orientation, degree of contact with the substrate) influence operative temperature regimes.

Our study was designed to provide guidance for field studies. Thus, our focus is not the thermal characteristics of models *per se*, but what they can tell us about the methodological decisions facing fieldworkers. For this reason, we have made the following decisions:

1. Relied primarily upon physical models rather than mathematical models. Thermal environments are complex, and effects are not always easily predicted from intuition or from simple theoretical considerations. For example, Bakken & Gates (1975) found that physical size affected thermal regimes very differently depending on whether the model was on the ground or suspended in the air.
2. Selected a subset of independent variables that relate directly to the decisions that need to be made by fieldworkers. Thus, our models were simple, resembled lizards in overall size and shape, and differed from each other in attributes that are easily manipulated by the researcher.
3. Selected the same dependent variables as those derived by fieldworkers using physical models. The most obvious such variable is temperature *per se* (as analysed by Vitt & Sartorius 1999), which researchers use for calculations of parameters such as the effectiveness of thermoregulation (by calculating thermal differentials between models and reptiles: Hertz *et al*. 1993). However, thermal models are also used to estimate the duration of time per day when particular body temperatures are available to the study organism. Activity periods of reptiles may be restricted to windows of time when operative temperatures exceed some minimum level or fall below some upper level (Porter *et al*. 1973; Porter & James 1979; Grant & Dunham 1988). Thus, we have calculated the duration of 'potential activity periods' based on a range of thermal thresholds.
4. Emphasized the magnitude of error that model attributes might introduce into such calculations, rather than whether or not a particular effect is statistically 'significant'. Statistical tests can tell us which effects are real and which are not, but from a logistic standpoint, the critical issue is the magnitude of such effects.

Materials and methods

Physical models were constructed from hollow copper pipes. Both ends of each model were sealed by plastic caps, and a hole was drilled in the side of each model to allow entry for a thermocouple probe from a Campbell CR10 Data-Logger (Campbell Scientific, Logan, UT, USA). The data-logger was calibrated prior to use against a calibrated reference thermometer (accuracy ±0·1 °C), and was set to record temperatures every 10 min throughout the study (note, however, that only a single data point per model was used in our statistical analyses, to avoid pseudoreplication). The sensing tip of each data-logger probe was positioned exactly in the centre of the lumen of each model. All of the models were placed out in a regular array in an open grassy area, far enough away from trees to preclude shadows. The models were placed individually on 30×30 cm^2 concrete pavers which were arranged in a 6×8 grid. Each paver was covered by a 2-cm depth of river sand.

The models differed in four attributes:

1. *Size* – either large (246 mm long × 60 mm diameter, 1·22 mm thick) or small (60 mm long × 15 mm diameter, 1·02 mm thick).
2. *Solar reflectance* – either high (painted with Krylon no. 2003 Jade Green, reflectance 45%) or low (painted with Krylon no. 1318 Grey Primer, reflectance 7·3%).
3. *Orientation to the midday sun's rays* – either at right-angles (east–west) to maximize exposure, or parallel (north–south) to minimize exposure.
4. *Degree of contact with the substrate* – either firmly embedded (10 mm into sand) or placed on top of the sand. This procedure resulted in about 40% *vs* 20% of the model's surface area being in contact with the ground for large models, and about 50% *vs* 30% for small models.

These attributes were selected to mimic a wide range of the reptile species commonly studied using operative-temperature models. The models were relatively lizard-like in overall shape (4 : 1 ratio of length to diameter). Their reflectances spanned the range from above the highest reptile reflectance that we found in published literature (40% for *Diposaurus dorsalis*: Porter & Gates 1969) to near the lowest (4·2% for *Sceloporus occidentalis*: Porter 1967). The orientations and degree of substrate contact spanned the ranges likely to be encountered with surface-active reptiles.

The factors were used orthogonally, to create three replicates of each possible combination of the above factors (total of 48 models). For example, there were three small light-coloured models set out at right angles to the midday sun's rays and in firm contact with the ground. The position of models within the array was random with respect to treatment. An automatic weather station (Macquarie University, Sydney, Australia: 33°46′S, 151°7′E, 55·0 m above sea level; web site http://atmos.es.mq.edu.au/~aws2/) <1 km from our study site provided readings of air temperatures, wind speeds and net radiation at 15 min intervals.

Temperatures were monitored inside the models, and associated weather conditions, for 27 days (9–17 November 1999, and 20 November to 7 December 1999). Our analysis was oriented around three main questions:

1. To what degree do a model's attributes (size, colour, orientation and degree of contact with the substrate) affect its mean, maximum and minimum temperature, and the amount of time each day that it exceeds some arbitrary thermal threshold?
2. Are interactions between the model attributes significant in this respect? For example, the effect of colour might depend upon the model's size or orientation (Stevenson 1985b).
3. Does the relative importance of such effects vary with weather conditions (in which case, researchers in different climatic zones may need to pay more or less attention to particular attributes)?

To avoid pseudoreplication, all of our statistical analyses are based on only a single data point from each model. Additional detail and statistical results are available from the authors, by request.

Results

Our study spanned late spring and early summer conditions in Sydney, a time of peak lizard activity. Weather data were available for 26 of the 27 days; data were not gathered on one day (9 November) when the system malfunctioned. Mean daily air temperatures ranged from 13·8 to 23·1 °C (mean = 18·2 °C), with maxima from 16·9 to 29·9 °C and minima from 9·1 to 17·4 °C. Mean net radiation ranged from 41·6 to 194·8 W m^{-2}. Wind speeds averaged 1·2–3·7 m s^{-1} over the study period.

DETERMINANTS OF MODEL TEMPERATURES

Statistical tests

The mean temperatures exhibited by our copper models were influenced by three of the four variables that were manipulated (size, colour, degree of contact with the substrate) but not by the fourth (orientation). Model attributes also modified the duration of time per day when operative temperatures exceeded some critical level. Durations of time above several thermal levels were calculated. Changes to the model's attributes modified these durations, but in a complex way.

Following Bonferroni correction, the size of the model affected all variables that were tested ($P < 0{\cdot}05$ for mean, maximum and minimum temperature, and time spent above 10, 15, 20, 25, 30, 35 and 40 °C). The model's colour affected its mean and maximum temperature, as well as the amount of time it spent above moderate to high thermal thresholds (25, 30, 35 and 40 °C). The degree of contact between the model and the substrate influenced all variables except time spent above thresholds of 30 and 35 °C. The model's orientation affected time above high-temperature thresholds (30, 35 and 40 °C). A significant interaction was also found between the effects of size and colour, whereby colour had little effect on the temperatures inside small models, but a substantial effect on large models (Fig. 1; see below). This interaction term was significant for mean and maximum temperature, as well as for time periods above 25, 30, 35 and 40 °C. Overall, maximum temperatures showed the same pattern as mean temperatures, whereas colour did not influence minimum temperature.

Magnitude of effects

Despite their statistical significance, most of the effects described above were relatively minor. The maximum temperature attained by the model was the most sensitive parameter in this respect, with small models reaching temperatures an average of 3·7 °C higher than otherwise identical large models (Table 1). The effects on other variables involved were <1 °C in average values for temperature readings, and were ≤36 min (0·6 h) per day for the duration of time above particular threshold temperatures (Table 1).

It is difficult to make direct comparisons of the magnitude of effects on different variables, because of differences in mean values. Despite the low absolute magnitude of discrepancies among models (above), they may be significant if the dependent variable involved itself has a low mean value. Figure 2 demonstrates this effect, by displaying effect sizes as a proportion of the overall mean value for that dependent variable. Because only a short amount of time was spent above high-temperature thresholds, even a small change to that time period introduced a substantial change when calculated on a proportional basis. In contrast, the models were above low-temperature thresholds most of the time, and so model attributes had little proportional effect on such variables (Fig. 2). The other primary message from Fig. 2 is to reinforce the result that most effects of model attributes on thermal regimes were minor (<5%), despite the statistical significance of many of them.

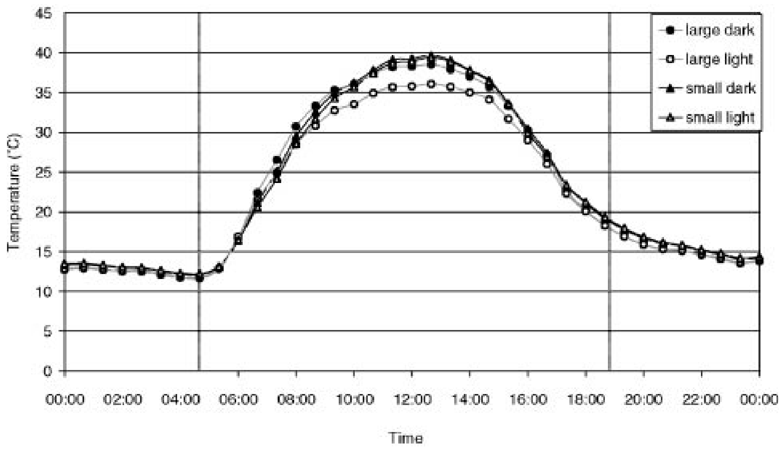

Fig. 1. Daily thermal profiles of models differing in size and colour averaged over the 27-day study period. Broken vertical lines indicate approximate times of sunrise and sunset.

Table 1. Values of mean, maximum and minimum model temperature as well as time spent at or above particular thermal thresholds, averaged over 27 days, for models differing in size, colour, contact with the substrate and orientation to the midday sun's rays. The absolute differences between these values for each model attribute are also indicated, with statistically significant differences in boldface

					Mean daily hours						
Factor	Level	Mean temp.	Maximum temp.	Minimum temp.	≥10 °C	≥15 °C	≥20 °C	≥25 °C	≥30 °C	≥35 °C	≥40 °C
Size	Large	22·7	53·1	6·9	23·0	17·2	11·7	8·8	6·4	4·4	2·6
	Small	23·5	56·8	7·3	23·5	17·7	12·1	8·9	6·6	4·7	3·1
	Difference	**0·8**	**3·7**	**0·4**	**0·5**	**0·5**	**0·5**	**0·1**	**0·2**	**0·3**	**0·5**
Colour	Dark	23·3	55·9	7·0	23·1	17·4	11·9	9·0	6·7	4·8	3·2
	Light	22·9	53·9	7·2	23·4	17·6	11·9	8·7	6·3	4·3	2·6
	Difference	**0·4**	**2·0**	0·2	0·2	0·2	0·0	**0·3**	**0·4**	**0·5**	**0·6**
Contact	High	23·3	55·7	7·5	23·5	17·7	12·1	8·9	6·6	4·6	3·0
	Low	22·8	54·1	6·7	23·0	17·2	11·7	8·8	6·5	4·4	2·8
	Difference	**0·5**	**1·6**	**0·8**	**0·5**	**0·5**	**0·4**	**0·2**	0·1	0·2	**0·2**
Orientation	Parallel	22·9	54·5	7·1	23·2	17·5	11·9	8·8	6·4	4·4	2·8
	Normal	23·2	55·3	7·1	23·2	17·5	12·0	8·9	6·7	4·7	3·0
	Difference	0·3	0·8	0·0	0·0	0·0	0·1	0·2	**0·3**	**0·3**	**0·3**
Overall mean		23·1	54·9	7·1	23·2	17·5	11·9	8·8	6·5	4·5	2·9

INTERACTIONS BETWEEN MODEL ATTRIBUTES

Surprisingly, only one interaction among model attributes had a significant effect on thermal regimes. The colour (reflectance) of a model influenced mean and maximum (but not minimum) temperatures more in large models than in small models (Fig. 1). The same effect was evident for the duration of time spent above high-temperature thresholds (see above). Throughout our analyses, higher-order interactions were rarely significant, even without Bonferroni correction. Indeed, the interaction between the model's size and colour was the only such significant effect. The lack of significant higher-order interactions greatly simplifies interpretation of our results.

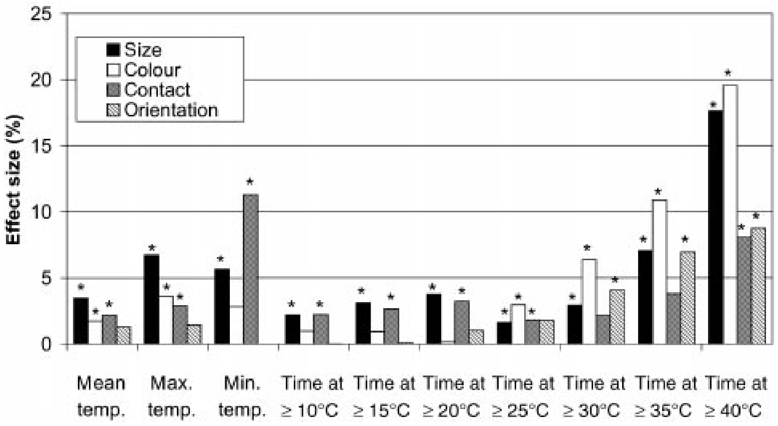

Fig. 2. Effects of different model attributes on mean, maximum and minimum model temperature as well as time spent at or above particular thermal thresholds, expressed as a percentage of the overall mean for each dependent variable. Statistically significant effects are indicated by an asterisk.

EFFECTS OF WEATHER CONDITIONS ON MODEL TEMPERATURES

Clearly, local weather conditions will modify model temperatures. Do these effects depend upon model attributes? For example, will temperatures inside large models be more or less sensitive to maximum air temperatures (or wind speed, etc.) than will temperatures inside small models? To examine this issue, the mean value was taken for each dependent variable (e.g. maximum temperature) for each day for each model. The mean value for models differing in one attribute (e.g. all large models *vs* all small models) could then be calculated. The disparity between these two values offers an index of the effect of the variable in question, and this score was regressed against daily means of the four weather variables recorded during our study, treating each day as an independent replicate. A multiple linear regression design was used whereby all four weather variables were analysed simultaneously, allowing us to examine the effects of each weather variable independently of all the others.

Even after Bonferroni correction, all of the dependent variables except time spent at or above 15 and 20 °C were affected by at least one of the weather variables, and all weather variables affected at least one of the dependent variables (results available from data archives). That is, the way in which a particular model attribute affected thermal regimes was itself sensitive to weather conditions. Daily changes in maximum and minimum air temperatures generally had less effect in this respect than did changes in wind speed or radiation intensity (3, 4, 9 and 14 significant results, respectively, out of 40 such tests in each case). The dependent variables most sensitive to radiation and wind speed were mean and maximum model temperatures and the durations of time spent above the higher thermal thresholds. In particular, these dependent variables

Table 2. Extremes (maximum and minimum) of daily disparities between models that differed in size, colour, contact and orientation, calculated for mean, maximum and minimum model temperature as well as time spent at or above particular thermal thresholds. Also indicated are the relative differences in the magnitudes of these disparities, expressed as a percentage of the overall mean for a particular dependent variable

	Size			Colour			Contact			Orientation		
Dependent variable	Max.	Min.	Rel. diff.	Max.	Min.	Rel. diff.	Max.	Min.	Rel. diff.	Max.	Min.	Rel. diff.
Mean temperature	1·2	0·2	4·7	0·7	0·1	2·3	0·8	0·2	2·6	0·6	0·1	2·5
Max. temperature	4·2	0·3	7·1	2·6	1·1	2·8	2·1	0·1	3·6	1·1	0·0	1·9
Min. temperature	1·0	0·3	8·9	0·4	0·1	3·5	0·9	0·3	8·2	0·2	0·0	2·1
Time ≥10 °C	2·3	0·0	9·7	0·7	0·0	3·0	2·1	0·0	9·1	0·4	0·0	1·6
Time ≥15 °C	2·1	0·0	11·9	0·6	0·0	3·2	1·2	0·0	6·8	0·2	0·0	1·3
Time ≥20 °C	1·2	0·0	10·3	0·6	0·0	5·4	0·8	0·0	6·3	0·4	0·0	3·0
Time ≥25 °C	0·8	0·0	9·6	0·8	0·0	8·5	0·8	0·0	8·7	0·4	0·0	4·4
Time ≥30 °C	1·4	0·0	21·5	0·9	0·0	13·8	1·1	0·0	16·3	0·5	0·0	8·3
Time ≥35 °C	1·1	0·0	24·1	0·9	0·0	20·5	0·6	0·0	13·0	0·6	0·0	13·9
Time ≥40 °C	1·9	0·0	65·6	1·4	0·0	49·1	0·9	0·0	31·6	0·7	0·0	25·1

were positively related to radiation and negatively related to wind speed. The effects of model attributes on these variables were most pronounced on sunny days and least pronounced on windy days.

Table 2 shows the extremes of daily disparities between models that differed in a single attribute (e.g. large *vs* small, light *vs* dark), to provide an indication of the potential magnitude of the effects of daily weather conditions in this respect. Again, maximum temperature was the variable most sensitive to weather conditions, with the mean daily disparity between large and small models ranging from 0·3 to 4·2 °C over the study period. The effect of model attributes on other dependent variables was in the order of 0·1–2 °C for temperature readings and 0–2 h per day for the duration of time above particular threshold temperatures.

To facilitate direct comparisons of the magnitude of weather effects on different dependent variables, the range of the daily disparities between models of different attributes as a proportion of the overall mean for a particular dependent variable can be calculated. Weather conditions introduced relatively little variation in the disparity between models of different attributes in terms of temperature readings. For 12 such calculations (size, colour, degree of contact and orientation *vs* mean, maximum and minimum temperature), the calculated daily disparity was <10% in all cases, and <5% in 9 of the 12. Similar results were obtained for the amount of time spent per day above lower temperature thresholds, but not for the amount of time spent above the higher-temperature thresholds (Fig. 3). Thus, studies of organisms with high thermal thresholds for activity may need to use models that mimic the animal's attributes very closely.

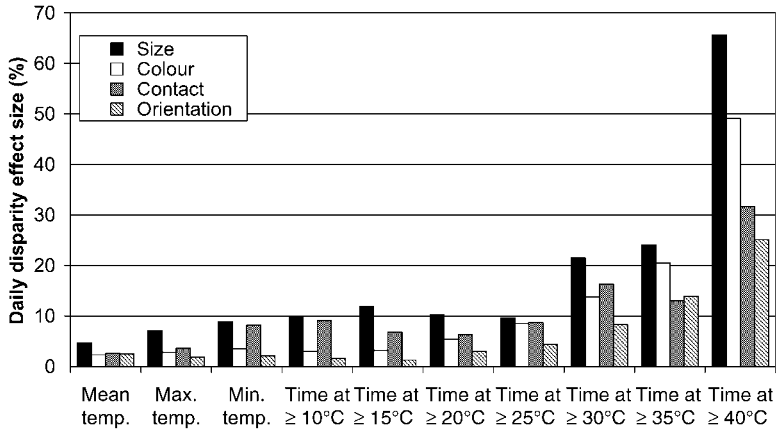

Fig. 3. Effects of different model attributes on the degree to which day-to-day variation in weather conditions affected mean, maximum and minimum model temperature as well as time spent at or above particular thermal thresholds. In each case, the effect size is expressed as a percentage of the overall mean for each dependent variable.

Discussion

Our discussion is based around two questions: (1) why did changes in physical attributes affect temperatures inside our models, and (2) what kinds of physical models should be used to measure operative temperatures?

DETERMINANTS OF MODEL TEMPERATURE

Our results are explicable in terms of previous, more detailed analyses of the physical processes driving thermal variation. The temperature within a model depends upon the balance between heat exchange via convection (combined effect of air temperature and wind), radiation (solar radiation and thermal radiation emitted from surrounding surfaces) and conduction (heat flow through solid surfaces in contact with the model: Bakken *et al.* 1985). The attributes of the model that were manipulated (size, colour, orientation, degree of substrate contact) differentially influenced these processes, resulting in significant effects on the model's internal temperature.

The actual causal pathways are complex, as illustrated by the effect of model size, the factor with the largest thermal effect. *A priori*, we might expect larger models to reach higher temperatures than smaller models, because their thinner boundary layer (and thus higher convection coefficient) should couple them more strongly to radiation than to air temperature (Gates 1980). This was not the case. Smaller models reached higher temperatures, probably because of effects involving the supporting surface. For small models, the temperature of the supporting surface can have dramatic effects on internal temperature (Bakken 1989). The supporting surface may influence model temperature via reflected solar radiation and thermal radiation, conduction or convection via the boundary layer of this surface. This latter effect may have been the most important, with large models extending further above the surface boundary layer and so experiencing higher wind speeds and cooler air temperatures (Bakken & Gates 1975). On windy days the surface boundary layer is much reduced, leading to a reduced disparity between models of different attributes.

The physics of heat transfer also explain another major result from our study: the strong interaction between the effects of model size and colour (Fig. 1). Colour affected large models more strongly than it did small models. As mentioned above, the thicker boundary layers of small objects couple them more strongly to air temperature than to radiation, which would cause them to be less sensitive to differences in colour than large objects. The strong effects of size and the relatively insignificant effects of colour for small models, and of orientation in general, are consistent with theoretical analyses (Stevenson 1985a,b) and indicate that radiation primarily influenced model temperature via its effects on the supporting surface rather than directly (Bakken 1989). Thus, the orientation of the supporting surface may be more important than the orientation of the model itself in determining thermal profiles.

The fact that colour affects temperature in large animals but not small ones (Fig. 1) poses significant biological questions. For example, black heads on small snake species have been interpreted as adaptations to accelerate heating of the brain (e.g. Shine 1991; Ehmann 1992; Greer 1997), but this inference is inconsistent with our data. The head of a small snake (such as *Tantilla* or *Furina*) would be too small for its rate of heating to be affected by colour. Thus, alternative explanations are needed (for example, melanin might protect against UV radiation). Second, this interaction between size and colour suggests a reason why seasonal and diurnal colour change is more prevalent in larger reptiles than in smaller ones. For example, seasonal shifts in dorsal colour have been described in several species of large Australian elapid snakes (e.g. *Pseudonaja* – Banks 1981; *Acanthophis* – Johnston 1996) but not in smaller taxa. Similarly, day–night shifts in colour are frequently reported in large pythons, but not in smaller snakes (e.g. Shine 1991). It may be generally true that larger species (of both insects and reptiles) tend to have higher reflectances and a greater capacity for colour change (Parry 1951; Norris 1967).

IMPLICATIONS FOR FUTURE STUDIES

Broadly, our results support those of Vitt & Sartorius (1999), and thus are encouraging for fieldworkers. Various attributes of copper models do indeed modify thermal regimes, but the effects are relatively minor. Shifts of <1 °C in mean temperature, or <10 min in the amount of time per day above a particular thermal threshold, are likely to be trivial compared to the accuracy of data-loggers, or the temporal shifts in local weather conditions over the course of a field study. That is, estimates of operative temperatures in the environment will depend more on the vagaries of local weather conditions, than on the details of model construction.

There are caveats to this general conclusion, however, as follows:

1. If studying large animals, use large models and try to mimic reflectances closely.

2 If your focus is temperature (to use in calculations of thermoregulatory precision, etc. as per the methods Hertz *et al.* 1993), then be aware that local weather conditions may modify the ways in which model attributes (size, colour, etc.) influence your measures of operative temperature. This factor will be less important if you are simply using the models to identify durations of time above particular thermal thresholds.

3. The size of the model is the most important determinant of its thermal profile, with the degree of contact with the ground being next most important overall. Orientation to the midday sun's rays may be least important (although its effect will be stronger at higher latitudes than our study site, and during the morning and afternoon rather than at midday).

4. If your study organism has a low thermal minimum for activity, then your estimates of the duration of time above that minimum will be sensitive to the model's degree of contact with the ground. For higher thermal thresholds, the model's colour and orientation become more important.

5. Because copper models have a low thermal inertia, they will be poor predictors of the time of day at which a reptile (especially, a large reptile) would exceed (and later, fall below) particular thermal thresholds. Nonetheless, the models will provide a reasonable estimate of the total amount of time per day that operative temperatures exceed that threshold, so long as it is relatively low. The amounts of time spent above very high thresholds would be much greater for the model than for a real animal, because of the difference in thermal time constants.

6. Investigators should be aware of the role of the boundary layer: where and how you place your models may be more important than getting the reflectivity just right (especially for small animals). Bakken (1989) showed that even a small gap between a lizard model and a tree trunk could significantly alter operative temperatures inside the model.

7. Our results were obtained under spring–summer conditions in Sydney. Under different climatic circumstances (e.g. lower temperatures, stronger winds), model attributes may affect thermal regimes more substantially. It would be of interest to replicate our study under other conditions. We predict that the effects of model attributes will be more important in cooler climates, but that such effects will generally be fairly small.

8. Our models were very simple, ignoring aspects such as limbs, posture and scale architecture that can possibly influence thermal regimes. We urge caution in the use of simple models, but also suggest that additional studies on the effects of such traits are long overdue.

Acknowledgements

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