

PERSPECTIVES

How to avoid errors when quantifying thermal environments

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Summary

1. Modelling thermal environments at high resolution becomes simpler when using operative temperature, which condenses microclimate and morphology into an index of thermal stress. Operative temperature can be mapped using large numbers of ‘operative temperature thermometers’, hollow models that duplicate external properties of the animal.
2. As climatologists predict that air will warm by 2–4 °C by 2100, biologists must be able to distinguish climate change from systematic errors in operative temperature of the same magnitude.
3. A systematic error in operative temperature of 2 °C or a similar amount of climate warming can change predicted surface activity and indices of habitat quality, thermoregulatory precision and predation risk by 5–12%, and in some cases more than 30%.
4. As construction details of operative temperature thermometers can affect their accuracy by 2 °C or more, biologists should use detailed physical models calibrated against living animals over potential ranges of postures, orientations and microclimates.
5. Water-filled models do not measure operative temperature correctly, fail to capture thermal extremes and are an unnecessary complication as one can easily compute the body temperature of moving or stationary animals from body mass and the spatio-temporal distribution of operative temperatures.

Key-words: climate change, microclimate, operative temperature, operative temperature thermometer, thermal heterogeneity, thermal map, thermoregulation

Introduction

Although environments have always been changing, human activities have accelerated rates of change by destroying habitats, driving climates and facilitating invasions. To predict the biological impacts of environmental change, researchers have modelled the fundamental niches of animals using information about physiology, behaviour and morphology (Kearney & Porter 2009; Buckley *et al.* 2010; Kearney *et al.* 2010). Climate change is of particular interest because it has direct and indirect effects on every species (Parmesan 2006; Araújo & Luoto 2007; Schweiger *et al.* 2008; Berg *et al.* 2010; Van der Putten, Macel & Visser 2010; Pateman *et al.* 2012).

Often, the impacts of climate change have been inferred from large-scale meteorological data (Root & Schneider 1993; Buckley 2008; Kearney & Porter 2009; Buckley *et al.* 2010; Kriticos & Leriche 2010). Unfortunately, the body

temperatures of animals do not correlate well with climatic variables such as air temperature (Porter & Gates 1969; Gates 1980; Helmuth *et al.* 2010). The environmental factors that combine to determine body temperature (air and surface temperatures, solar radiation, wind, tides, precipitation, etc.) do not always occur in the same relationship with one another. Furthermore, the direct interaction between organisms and their environment usually occurs at very small scales; for example, submeter variations in slope and aspect change the temperatures of intertidal mussels by 6–13 °C (Helmuth & Hofmann 2001; Fitzhenry, Halpin & Helmuth 2004). Comparable or greater variation in body temperature results from changes in posture and orientation of the focal animal and the nature of the supporting surface (Pearson 1954; DeWitt 1971; Tracy, Tracy & Dobkin 1979; Bakken 1989). When these variations span the range of preferred body temperatures with sufficient margins, they facilitate behavioural thermoregulation and make detailed knowledge of thermal conditions unimportant. However, at temporal or

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geographical limits, with reduced thermal margins, small variations in temperature determine whether animals have sufficient time and space for the activities that ensure their survival. Thus, efforts to predict impacts of environmental change on the distribution and abundance of animals demand models with many independent variables (Buckley 2008; Kearney & Porter 2009), mapped at fine spatial and temporal resolutions (Helmuth & Hofmann 2001; Helmuth *et al.* 2002; Sears, Raskin & Angilletta 2011; Kearney, Matzelle & Helmuth 2012).

Indices that summarize climatic parameters simplify efforts to map thermal environments. One such index – referred to as either operative environmental temperature or operative temperature (Bakken 1981, 1992) – is particularly useful. By combining properties of a microenvironment (e.g. temperatures, radiation, wind) with properties of an organism (e.g. size, shape, posture), this index tells us whether that organism, given its current temperature, would gain or lose heat in that microenvironment. (Herrington, Winslow & Gagge 1937; Winslow, Herrington & Gagge 1937; Bakken & Gates 1975; Bakken 1976a, 1981, 1992). Operative temperature (T_e) can be computed for a microclimate given properties of the animal that determine how air temperature, wind speed and electromagnetic radiation affect heating or cooling:

$$T_e = T_a + \Delta T \quad \text{eqn 1}$$

The starting point is air temperature, T_a (°C), and the variable ΔT is the difference between operative temperature and air temperature caused by solar and thermal radiation, as modified by convection:

$$\Delta T = \frac{(Q_a - A_e \sigma \varepsilon T_r^4)}{H + R} \quad \text{eqn 2}$$

where T_r is the surface temperature of the animal, Q_a is the total electromagnetic radiation absorbed by the animal (W animal^{-1}), A_e is the animal's effective area exchanging thermal radiation (Halliday & Hugo 1962), σ is the Stefan–Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$), ε is the thermal emittance ($0 < \varepsilon < 1$), and H is the convective conductance of the animal ($\text{W animal}^{-1} \text{ }^\circ\text{C}^{-1}$). Similarly, the radiative conductance of the animal is $R = 4A_e \sigma \varepsilon T_a^3$ ($\text{W animal}^{-1} \text{ }^\circ\text{C}^{-1}$).

Unfortunately, one cannot use meteorological data and biophysical equations to map operative temperatures at the scale experienced by most organisms. The climatic variables required to calculate operative temperatures over large areas are known only at coarse spatial and temporal resolutions. Researchers have had some success combining meteorological (Wethey *et al.* 2011) or micrometeorological (Porter *et al.* 1973) data with mathematical models to predict operative temperatures of animals in standardized positions and simple habitats. But often, data taken within decimetres of small animals (Roughgarden, Porter & Heckel 1981) inadequately capture the effects of air temperatures and wind speeds near the surface of an animal (Bakken 1989). Thus, one should not use measured or

modelled microclimatic variables to compute operative temperature for animals smaller than an array of meteorological instruments (e.g. Roughgarden, Porter & Heckel 1981; Van Damme, Bauwens & Verheyen 1987; Grigg & Seebacher 1999; Seebacher, Grigg & Beard 1999).

Fortunately, physical models of an animal can be used to integrate microclimatic and organismal properties without complex computations (Bakken & Gates 1975; Bakken, Santee & Erskine 1985; Bakken 1992; Dzialowski 2005). The use of such models as operative temperature ‘thermometers’ results from the observation that operative temperature can be defined as the temperature of an object with the same external properties (e.g. size, shape, colour and texture) as those of the organism minus its capacity to produce or store heat (Bakken & Gates 1975). Because the size of the sensor equals the size of the animal, spatial and temporal variations in operative temperature can be mapped at the exact resolution needed to visualize thermal resources (Bakken & Gates 1975; Grant & Dunham 1988; Hertz 1992; Angilletta 2009b; Wethey *et al.* 2011). Operative temperature thermometers are relatively inexpensive to construct in large numbers (e.g. Hertz 1992; Bauwens, Hertz & Castilla 1996; Gifford, Clay & Powell 2012). For solid models (Fitzhenry, Halpin & Helmuth 2004) or hollow ones (Appendix S1, Supporting information), temperature recorders such as Thermochrons[®] (Maxim Integrated Products, Sunnyvale, CA, USA) can be built into the model, eliminating the need for wires that communicate with recording devices. This design enables one to distribute models independently throughout an environment. Thus, physical models that sense operative temperatures provide a particularly useful way to explore the spatiotemporal structure of the environment and to validate high-resolution thermal maps (e.g. Helmuth *et al.* 2010; Kriticos & Leriche 2010; Sinervo *et al.* 2010; Sears, Raskin & Angilletta 2011; Wethey *et al.* 2011; Kearney, Matzelle & Helmuth 2012). Thermal maps on organismal scales enable one to project population dynamics on larger scales (Hertz 1992; Sears, Raskin & Angilletta 2011). In the light of global climate change, such maps will help not only researchers interested in basic ecological problems but also managers who design refuges and parks for threatened species (e.g. Lelievre *et al.* 2012).

Small systematic errors reduce the value of operative temperature thermometers

To be effective, operative temperature thermometers must be designed and used to minimize errors (Bakken, Santee & Erskine 1985; Bakken 1992; Bakken *et al.* 2000; Dzialowski 2005). Given the frequent use of physical models with simple geometries, such as cylinders, discs or spheres (e.g. Van Berkum, Huey & Adams 1986; Wills & Beaupre 2000; Grbac & Bauwens 2001; Stokes & Meek 2003; Sinervo *et al.* 2010; Gifford, Clay & Powell 2012), many researchers must feel that the design of these models does not greatly affect accuracy, especially if errors are small

compared with daily or spatial variation in operative temperature. This argument, which confuses random and haphazard errors, is valid only if the errors are normally (or at least predictably) distributed about the true value of operative temperature. In such cases, either parametric statistics (Hertz 1992) or randomization tests (Wills & Beaupre 2000) may be used to compare samples.

Unfortunately, systematic errors can result from either design or placement of operative temperature thermometers. Basic physics (Gates 1980; Incropera & DeWitt 2001) guarantees that, all else being equal, the presence of solar radiation will cause a black model to read warmer than a white one. A model shaped like a lizard will typically respond to changes in air temperature and wind speed more than will a cylindrical model of the same volume; this phenomenon occurs because the average dimension of the cylindrical model exceeds that of the lizard model. No amount of sampling will eliminate such systematic errors, which will appear to be real differences among thermal qualities of habitats or inferred thermoregulatory performances of species. The question is, then, 'Are likely systematic errors sufficient to alter one's conclusions?' This question becomes especially important when one recognizes that systematic errors in operative temperature as small as 2–4 °C could be confounded (compare eqn 1) with a similar change of global air temperature that might occur by 2100 (IPCC 2008).

We can infer the significance of systematic error from a simple simulation (see Appendix S2, Supporting information). To ensure realistic parameters for this simulation, we used operative temperatures recorded on a summer day at a site in Chaves Co., New Mexico, USA, when lizards of six species were active. Data were recorded for a day using four hollow copper models placed in sites with different slope, aspect and shade (Fig. 1). Additionally, we assumed that lizards could access a refuge that provided an operative temperature equal to the air temperature (1 m above the ground). We defined hypothetical lizards

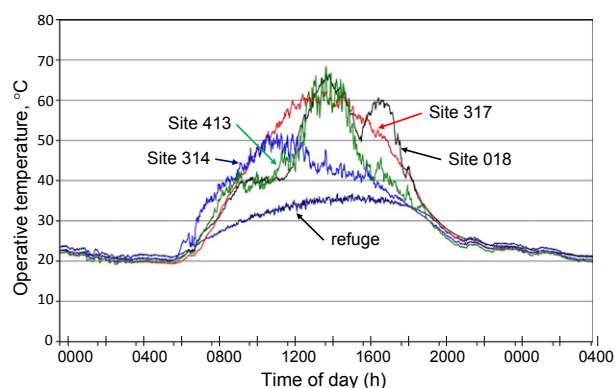


Fig. 1. Operative temperatures recorded by four hollow copper electroformed lizard models at four different sites on the ground and in a refuge. Data were recorded in New Mexico in June on a day when lizards of at least six species were active. These data can be found in Appendix S2 and were used to compute the results in Tables 1–3.

of three body masses (time constants were 5, 20 and 80 min) that attempted to regulate body temperatures within a specified range (either 34–38 °C or 32–36 °C).

We simulated five home range scenarios. In four scenarios, lizards were restricted to a surface home range with a uniform operative temperature as defined by one of the 4 models in Fig. 1. A lizard would stay in a refuge as long as its body temperature remained within the preferred range. Otherwise, the lizard would shuttle between the surface and the refuge whenever its body temperature fell outside the preferred range. When the operative temperature on the surface fell below the preferred range of temperatures, the lizard would enter the refuge and remain there until the surface environment warmed sufficiently. The fifth scenario tested the hypothesis that large habitat variation in operative temperature can negate the effects of much smaller systematic measurement errors by facilitating behavioural thermoregulation. We assumed that the home range contained all microhabitats defined in Fig. 1, which at any one time vary in operative temperature about 10 times more than the systematic error. This computation assumed that the lizard was perfectly aware of its thermal environment and could access the refuge or any microhabitat within its home range. When active on the surface, the lizard would select the microhabitat with the operative temperature that was closest to its preferred range of temperatures. In all other respects, lizards in this scenario behaved as they did in the other four scenarios. The preferred ranges of body temperatures were chosen to yield two behavioural patterns. The preference for 34–38 °C resulted in continuous activity, because the refuge was always cooler than preferred temperatures. The preference for 32–36 °C resulted in bimodal activity, because the refuge provided operative temperatures within the preferred range during the middle of the day.

To examine the consequences of systematic error in operative temperature, we computed indices of habitat quality and thermoregulatory performance, using operative temperature as recorded or operative temperature with a systematic ± 2 °C error. This magnitude of error seems conservative given empirical estimates of potential errors and projected increases in mean global temperature (IPCC 2008). The index of habitat quality was the mean absolute deviation of operative temperature from the preferred body temperature (d_c). We computed their effectiveness of thermoregulation E (Hertz, Huey & Stevenson 1993) using the operative temperature on the surface as the null hypothesis:

$$E = 1 - d_b/d_c \quad \text{eqn 3}$$

where d_b equals the absolute difference between the body temperature and the preferred body temperature, and d_c equals the average absolute difference between the operative temperature and the preferred body temperature. Variations in this index have been proposed and are compared in Appendix S3 (Supporting information). The other thermal indices include the number of shuttling movements

and the time spent on the surface. More shuttling between the surface and the refuge should increase predation risk. More time on the surface should not only increase predation risk but also increase foraging success. Following Christian & Weavers (1996), we restricted computations to the active period. Results are presented in Table 1.

A systematic error in operative temperature as small as 2 °C can have a surprisingly large effect on indices of habitat quality and thermoregulation. In our example, an error of ± 2 °C typically impacted indices by 8–12%, but the impact equalled or exceeded 32% in some cases (Table 1). The effect of error varied markedly among the scenarios in which a lizard occupied a homogeneous home range, because each scenario involved a distinct diel pattern of operative temperature. Although the fifth scenario considered a heterogeneous home range with operative temperatures varying among patches by about 20 °C during much of the day, the average effect of an error

of ± 2 °C on the indices was about the same as for the other scenarios; for all time constants and target body temperatures of 34 °C and 36 °C, indices were impacted as follows: (i) habitat quality, 12.5–12.2% for the heterogeneous site vs. 12.8–12.3% for all sites; (ii) thermoregulatory effectiveness, 4.8–8.5% vs. 5.0–7.8%; (iii) time on surface, 16.8–4.2% vs. 8.8–4.0% and (iv) shuttling frequency 9.75–10.5% vs. 17.4–12.2% (see Appendix S2, Supporting information).

For those readers who wish to explore these patterns further or generate different scenarios, an Excel workbook containing the model can be found among the Supplemental Materials (Appendix S2, Supporting information). The first spreadsheet contains the operative temperatures used in our simulation. The next five spreadsheets contain code for computing these indices for the five scenarios. The last two spreadsheets summarize some results used in the text. Using this workbook, readers can perform their own

Table 1. Effects of errors in operative temperature of ± 2 °C on thermal indices for five scenarios, 4 with uniform operative temperature over the home range as plotted by one of the lines in Fig. 1 plus the refuge, and a complex scenario where the home range includes four microsites, each with one of the operative temperatures plotted in Fig. 1 plus the refuge. Indices are computed for each combination of scenario, time constant and target body temperature. Results are summarized over the five scenarios for each combination of time constant and target body temperature. Variation is measured relative to the value computed using the correct operative temperature

		$\tau = 5$		$\tau = 20$		$\tau = 80$	
		Value	Variation, %	Value	Variation, %	Value	Variation, %
Thermal quality of the habitat (d_e)							
$T_p = 34$ °C	Mean	11.9	12.8	11.9	12.8	11.9	12.8
	Max	16.8	19.8	16.8	19.8	16.8	19.8
	Min	6.6	8.9	6.6	8.9	6.6	8.9
$T_p = 36$ °C	Mean	10.5	12.3	10.5	12.3	10.5	12.3
	Max	15.3	20.1	15.3	20.1	15.3	20.1
	Min	5.6	8.8	5.6	8.8	5.6	8.8
Effectiveness of thermoregulation (E)							
$T_p = 34$ °C	Mean	0.854	4.0	0.852	4.5	0.815	6.4
	Max	0.908	6.8	0.905	10.5	0.886	9.8
	Min	0.744	1.7	0.743	2.1	0.721	2.7
$T_p = 36$ °C	Mean	0.81	6.9	0.82	7.3	0.77	9.3
	Max	0.90	14.7	0.89	15.3	0.86	17.7
	Min	0.64	3.5	0.66	3.4	0.62	4.1
Time on surface (min per day)							
$T_p = 34$ °C	Mean	216.9	5.3	198.4	9.3	203.5	11.9
	Max	278.0	18.2	228.0	18.6	240.0	27.3
	Min	153.0	2.0	145.0	0.5	165.0	0.0
$T_p = 36$ °C	Mean	297	3.4	293	2.9	296	5.7
	Max	384	9.1	377	8.6	369	13.5
	Min	213	0.3	208	0.0	218	0.6
Shuttling frequency (moves per day)							
$T_p = 34$ °C	Mean	84.7	13.6	30.1	12.2	15.8	26.5
	Max	105.0	23.5	51.0	29.6	42.0	57.1
	Min	61.0	2.4	19.0	0.0	5.0	0.0
$T_p = 36$ °C	Mean	128	12.4	45	10.6	21	13.5
	Max	159	20.9	67	22.9	58	26.7
	Min	93	6.7	29	0.0	9	0.0

calculations by manipulating the independent variables (e.g. the error in operative temperature, the time constant or the preferred range of temperatures).

The devil is in the details of operative temperature thermometers

Given that even small errors impact thermoregulatory indices enough to alter one's interpretation, biologists should strive to minimize systematic errors. Such errors result from poorly designing operative temperature thermometers but also from inadequately sampling thermal environments. First, we consider aspects of design such as colour, size, shape and heat storage capacity. Then, we turn to aspects of sampling such as placement, orientation and replication. These details about the design and use of operative temperature thermometers greatly affect our perceptions about thermal environments.

SIZE, SHAPE AND COLOUR

To accurately estimate operative temperature, a sensor must duplicate all relevant external properties of the animal (Bakken 1976a). As electroforming hollow models consume time and resources (Bakken & Gates 1975), some researchers have adopted simple geometric shapes, regarding the resulting errors as insignificant (e.g. Belliure & Carrascal 1996; Grbac & Bauwens 2001; Row & Blouin-Demers 2005; Sinervo *et al.* 2010; Wilms *et al.* 2011). Although colour matching is the same for a T_e thermometer of any geometry, the relative weightings of air temperature, wind speed, solar radiation and thermal radiation depend on geometry. Animals absorb solar radiation according to their cross-sectional area, but absorb diffuse thermal radiation and reflected solar radiation according to their effective radiating area, which is somewhat smaller than total exposed surface area (Halliday & Hugo 1962). Convection occurs at surfaces exposed to air and also varies with the local diameter and geometry of the object (Gates 1980; Incropera & DeWitt 2001). The relationships among these areas depend strongly on geometry; for example, a cylinder with a 4 : 1 ratio of length to diameter has surface area that exceeds by 36% that of a sphere with the same volume. A more lizard-shaped cone with a 8 : 1 ratio of base to height has a surface area that is 69% greater than that of the sphere. The ratio of projected area to total area is constant for a sphere; for a cylinder, cone or lizard, this ratio depends on whether solar radiation strikes parallel or perpendicular to the long axis (Tracy, Tracy & Dobkin 1979). Consequently, we have good reasons to expect that the shape of an animal significantly influences its operative temperature.

For a given geometry, the colour of the surface (or, more properly, its spectral absorptance) determines the fraction of incident radiation at each wavelength that will be absorbed. Therefore, the spectral absorbance of the operative temperature thermometer must approximate that of the animal (Bakken *et al.* 1978; Grant & Dunham 1988;

Hertz 1992; Walsberg & Wolf 1996; Dzialowski 2005). Two main factors may be overlooked. First, melanin and many other biological pigments become significantly less absorptive as the wavelength enters the near infrared range (Bakken *et al.* 1978; Gates 1980). As about half of direct solar radiation belongs to this range, one cannot assume that a visual match between colours equals a match between spectral absorptances. Second, the spectral irradiance (distribution of radiant power with wavelength) varies with the height of the sun above the horizon. Third, far more visible than near infrared radiation is filtered by vegetation (Gates 1980). If the spectral data are unavailable, the best alternative is to compare physical models and live animals, side-by-side, under all relevant spectral irradiance conditions (Bakken & Gates 1975; Grant & Dunham 1988).

How precisely must geometry and colour match the animal? Several teams of researchers have quantified the systematic errors that result from simplifying these features of operative temperature thermometers. Vitt & Sartorius (1999) compared the temperatures of electroformed models with the temperatures of two commercial devices: (i) a temperature logger with an external cylindrical thermistor probe of small diameter (Hobo Loggers[®], Onset Computer Co. Bourne, MA USA) and (ii) a disc-shaped temperature logger with an internal sensor (TidBits[®], Onset Computer Co. Bourne, MA USA). Such sensor–logger combinations eliminated the need for long runs of wire between sensors and a central data logger. Using three replicates for a single day at a single site, they observed a difference of less than 1 °C between the TidBits[®] and the hollow models, but Hobo Loggers[®] were less consistent. They concluded that these temperature loggers would work well when they are nearly the same size as the animal; however, they emphasized the importance of validating this approach for each application. By contrast, Fitzhenry *et al.* (2004) found that the temperatures of unmodified TidBits[®] differed by as much as 14 °C from the body temperature of live mussels, while anatomically accurate models were within 2 °C. Shine & Kearney (2001) found that the temperatures of hollow copper cylinders were only weakly affected by size, colour and position (effects ranged from 0.5 °C to 3.7 °C). In contrast, using carefully controlled conditions, Walsberg & Wolf (1996) found that electroformed models outperformed similarly sized models constructed from either copper or PVC cylinders; electroformed models yielded a steady-state temperature within 2.5 °C of a lizard's body temperature, whereas cylinders differed by as much as 6 °C. Our experience accords more with Walsberg and Wolf's findings than with Vitt & Sartorius (1999). In a field trial comparing 36 lizard models in three shape–size classes using four colours arranged in three replicate sets with the long axis oriented at azimuth angles of 0°, 120° and 240°, the average temperatures of electroformed models of different colours and sizes differed by as much as 10 °C, with differences of 2–4 °C within realistic ranges of size and colour (Fig. 2).

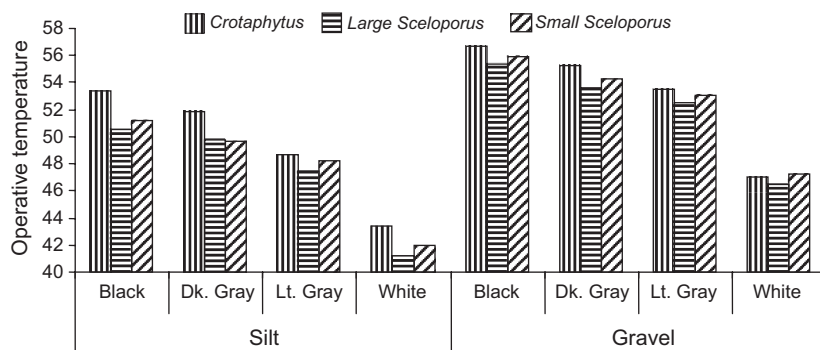


Fig. 2. Operative temperatures averaged from 10 AM to 4 PM recorded by electroformed models of three lizards of different size, shape and colour. Data were recorded in New Mexico at a valley site on silt soil and a hilltop site on gravel substrate for 2 days at each site, with the T_c thermometers resting loosely on the surface and repositioned between days. Overall temperature differences between sites were due to a gradual increase in air temperature during the 4-day study.

HEAT STORAGE CAPACITY

Operative temperature can change almost instantaneously, such as when the sun goes behind a cloud or when an animal moves into shade. Therefore, an ideal model would have zero heat storage to track operative temperature correctly through time. Hollow electroforms, which have low heat capacity, satisfy this requirement (Bakken & Gates 1975; Tracy & Christian 1986; Huey 1991; Hertz 1992; Sears *et al.* 2004). However, no real model has zero heat capacity, and heat storage can be significant for large models, which need thick walls to prevent another source of error, internal temperature gradients (Bakken 1992; O'Connor *et al.* 2000). A Z-transform can be used to estimate operative temperature from the temperature of a thick-walled model (Bartholomew, Vleck & Vleck 1981; O'Connor 2000); however, this procedure amplifies small errors in temperature (O'Connor 2000), and thus precludes the use of low resolution sensors (e.g. 8-bit Thermochrons®).

Particularly, large heat storage capacity has resulted when investigators used models filled with water to replicate the heat storage capacity of the focal animal (e.g. Robertson & Weatherhead 1992; King, Kuchling & Bradshaw 1998; Schwarzkopf 1998; Blouin-Demers & Weatherhead 2001; Stokes & Meek 2003; Oswald *et al.* 2008; Dubois *et al.* 2009; Lutterschmidt & Reinert 2012). Although most of these researchers interpreted the resulting values as operative temperatures, water-filled models will lag behind the true operative temperature and fail to capture thermal extremes throughout a day (Fig. 3). Thus, it is not possible to compare studies using water-filled models with studies using hollow models.

The significance of the distinction between the temperature of a hollow model and that of a water-filled model is conveniently explained using the concepts of stress and strain. In physics and engineering, stress designates an applied external force, whereas strain designates the response of the stressed system. By contrast, biologists have used stress and strain inconsistently and often synonymously.

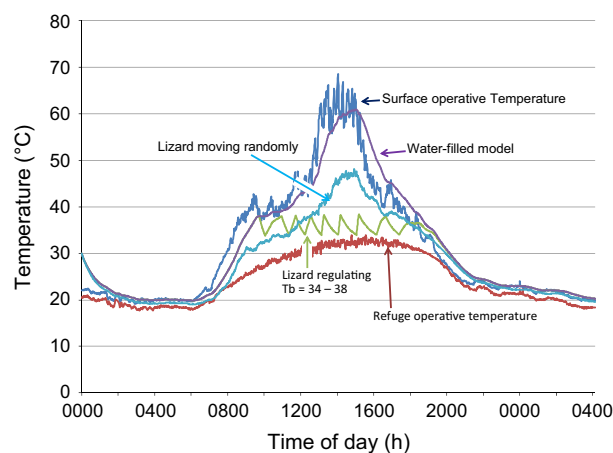


Fig. 3. Operative temperature recorded by a hollow electroform of a lizard positioned in two areas (on the surface and in a refuge) with computed temperatures that would be recorded by: T_{bw} , a water-filled model lizard. T_{br} , body temperature of a lizard moving randomly between the two areas. T_b , body temperature of a hypothetical lizard shuttling between the two areas to regulate $T_b = 36 \text{ °C} \pm 2 \text{ °C}$. The thermal time constant is $\tau = 40 \text{ min}$ for the lizards and water-filled model. The water-filled model temperature does not duplicate T_b of an active lizard and is not useful for calculating the T_b of moving lizards.

For example, stress often refers to phenotypes that result when organisms fail to respond adequately to external demands. Biologists describe a temperature as stressful only if that temperature produces limiting physiological strain (e.g. Santos, Castañeda & Rezende 2011). A more precise usage would consider only the environmental demand (e.g. high temperature) as stress, independently of whether the resulting strain limits the performance of an organism. The responses of a stressed organism (e.g. body temperature or the expression of heat shock proteins) are the resulting strains.

The tendency to confuse stress and strain reflects the close relationship between these concepts. Strain depends on properties of the stressed system, mathematically captured by a 'filter function'. For example, the force

generated by a muscle (a stress) can be measured by attaching the muscle to a flat metal spring. The bending of the spring during muscular contraction (strain) is measured by an electronic strain gauge. The filter function (stiffness) that relates force to bending is determined by calibrating the gauge with known stresses, such that the measured strain precisely reflects the applied stress. In a similar way, operative temperature reflects the thermal stress placed on an organism with specified external properties (Winslow, Herrington & Gagge 1937; Bakken & Gates 1975; Bakken 1976a). The external properties of the animal determine the impacts of air temperature, wind speed and radiation on the operative temperature. Any internal response, such as the body temperature of the animal derived from thermal stress through internal filter functions (e.g. behaviour, heat storage capacity, vasomotor response), is a thermal strain. Thus, the temperature of a water-filled model represents an index of thermal strain, not stress (Lutterschmidt & Reinert 2012).

The distinction between stress and strain might seem academic, given the entrenched usage in biology. After all, why should terminology in biology and physics agree as long as each field is internally consistent? We can think of two reasons. First, the increasing significance of interdisciplinary collaborations – which often involves such disparate fields as meteorology, fluid mechanics, heat transfer, physiology and ecology – foreshadows a need for consistent terminology. Second, and more importantly, imprecise terminology creates confusion within disciplines as well as between them; as noted earlier, researchers introduced systematic errors by measuring temperatures of water-filled models and presenting them as operative temperatures.

To illustrate the difference between thermal stress and thermal strain, we computed three indices of strain: (i) the temperature of a stationary water-filled model; (ii) the temperature of a hypothetical lizard moving randomly and (iii) the temperature of a lizard moving to regulate its temperature at $36^\circ \pm 2^\circ\text{C}$. These strain indices were computed using the data and procedures in Appendix S2 (Supporting information). Briefly, to compute the strain indices, we evaluated the exponential function sometimes referred to as ‘Newton’s law of cooling’ (Bakken & Gates 1975; Bakken 1976b; Dzialowski & O’Connor 2001; but see Bakken & Gates 1974):

$$T_b(t) = T_e(t) + [T_b(t - \Delta t) - T_e(t)] \exp(-\Delta t/\tau) \quad \text{eqn 4}$$

Here $T_b(t)$ is the body temperature at time t , Δt is the time interval between measures of operative temperature, and τ is the time constant, determined primarily by body mass. The sequence of operative temperatures appropriate to the movement model is represented by $T_e(t)$. We assumed that the lizard used dual set point temperatures and could choose between being on the surface or being in a nearby refuge. Thermal stress (T_e) and the three thermal strains (T_b) have been plotted in Fig. 3 to give a visual impression of the differences for a site with a uniform operative temperature and time constant.

In Table 2, we compare operative temperature and the calculated temperature of a water-filled model fixed on the surface for hypothetical reptiles with three different time constants exposed to the five scenarios used earlier. Depending on the time constant and the scenario, differences average 0.7–5.6 °C and can reach 4.5–15.9 °C (Table 2; details in Appendix S2, Supporting information). In contrast, when averaged throughout the day, the index of thermal quality computed with a strain index (the temperatures of water-filled models) differed little from that computed with operative temperatures (typically by 1–8%; Appendix S1, Supporting information); these indices were similar because a phase shift between operative temperature and the temperature of a water-filled model existed, such that differences partly averaged out over the course of the day. Differences could be much larger (50% or more) if indices were computed for morning data only or afternoon data only (Appendix S2, Supporting information).

The temperature of water-filled models might seem appropriate for estimating the temperature of a randomly moving animal (e.g. Lutterschmidt & Reinert 2012) for use in Seebacher & Shine’s (2004) modification of the effectiveness of thermoregulation E (see Appendix S3, Supporting information for a discussion of the differences among the various formulations of E). Seebacher & Shine (2004) argued that researchers interested in behavioural thermoregulation should compare observed body temperatures with the body temperature that would result from a random movement throughout the same environment combined with the organism’s capacity for heat storage, not to the operative temperature as proposed by Hertz, Huey & Stevenson (1993). However, the temperature of a moving animal depends strongly on thermal history (Christian, Tracy & Tracy 2006). Thus, a water-filled model, at best, estimates only the temperature of an animal rooted to the same spot with no cardiovascular response. This assumption could be valid for certain animals, such as sit-and-wait predators (Lutterschmidt & Reinert 2012) or sessile intertidal invertebrates (e.g. Helmuth 2002; Fitzhenry, Halpin & Helmuth 2004). More commonly, animals move between

Table 2. Absolute temperature difference between hollow and water-filled models fixed on the surface in the five scenarios as in Table 1 with operative temperatures plotted in Fig 1. Mean is the average over the five scenarios, and max is the largest value obtained in any scenario. In the complex habitat, data are the mean of all four hollow models vs. all four water-filled models

Site	$\tau = 5$		$\tau = 20$		$\tau = 80$	
	Mean	Max	Mean	Max	Mean	Max
Complex	0.5	1.8	1.6	3.6	5.4	8.5
018	0.7	3.6	2.3	7.4	6.4	13.5
412	1.0	4.5	2.2	9.0	6.4	15.9
314	0.6	2.8	1.2	4.3	3.8	9.4
317	0.6	1.8	1.8	3.5	6.3	10.2
Overall	0.7	4.5	1.8	9.0	5.6	15.9

sites with different spatiotemporal distributions of operative temperatures (Grant & Dunham 1988). Hence, body temperature will usually differ from the temperature of a water-filled model at a fixed location. Consequently, temperatures of water-filled models cannot generally predict body temperatures accurately. To illustrate, we compared the calculated temperature of a water-filled model fixed on the surface with the calculated temperature of a randomly moving lizard for the five scenarios used earlier. Average differences are around 7 °C, but can be up to 27 °C for some combinations of time constant and home range scenario (Table 3).

Because a time series of body temperatures can be estimated from a time series of operative temperatures (eqn 4), heavy and potentially leaky water-filled T_e thermometers are a largely unnecessary burden. The computation of body temperature is relatively insensitive to random errors in operative temperature; however, accuracy increases as Δt decreases, and Δt should always be smaller (0.1 or so) than the time constant (τ). Given a thermal map of the study site, either observed or predicted movements can be used to synthesize the time series of operative temperatures. Temperatures of a moving animal can then be estimated by plugging the time series of operative temperature, $T_e(t)$, into eqn 4.

Changes in parameters such as cardiovascular performance or wind speed may require the use of time series of time constants, $\tau(t)$, instead of a single value. Depending on species and habitat, variation in wind speed could also be important. Wind moves slowly at ground level, and the correlation between wind speed and convection coefficients in the field seems poor (Pearman, Weaver & Tanner 1972; Johnson 1975). Although variation in air temperature due to height above the surface and air movement strongly affects operative temperature (Bakken & Gates 1975), its effect on the time constant has received little study. One could model the effects of cardiovascular changes in heating and cooling time constants (Dzialowski & O'Connor 2001; Christian, Tracy & Tracy 2006). However, as wind effects on time constant are likely site specific and cardiovascular responses species specific, empirical field estimates of the time constant for the study site and species of interest are most appropriate.

Table 3. Absolute temperature difference between a randomly moving lizard and a stationary water-filled model in the five scenarios as in Table 1 with operative temperatures plotted in Fig 1. Data are presented as in Table 2

Site	$\tau = 5$		$\tau = 20$		$\tau = 80$	
	Mean	Max	Mean	Max	Mean	Max
Complex	3.4	11.9	3.3	8.7	2.9	5.8
018	9.1	25.8	8.7	20.6	9.0	14.6
412	7.0	27.0	7.5	17.5	7.6	15.3
314	5.6	17.7	6.0	13.3	5.6	9.6
317	9.5	26.7	9.5	17.6	8.9	13.1
Overall	6.9	27.0	7.0	20.6	6.8	15.3

So many dimensions, so few models

Because operative temperature integrates all relevant aspects of the thermal environment, it typically varies with 6 spatial coordinates: x , y and z , plus the azimuth, elevation and rotation of the animal (although rotation is often constrained by the supporting surface). The impact of these coordinates on operative temperature constitutes true variation in thermal stress, not random or systematic error. Therefore, each element of the set of accessible operative temperatures in a study area should be equally likely to be included in a sample, and samples should be large enough to make powerful statistical inferences. Two approaches are commonly used for sampling: (i) true random sampling (Hertz 1992) and (ii) area classification with equal sampling of each class followed by weighting for area or some other metric of utility to the animal (Tracy & Christian 1986; Grant & Dunham 1988; Huey 1991; Buckley 2010). The number of T_e thermometers needed for adequate sampling varies among habitats but is typically large (e.g. see Hertz 1992) given at least five spatial parameters to explore. Unfortunately, many studies (e.g. Sinervo *et al.* 2010) have used sample sizes too small to accurately characterize the study site (Clusella-Trullas & Chown 2011; Sears, Raskin & Angilletta 2011; Sinervo *et al.* 2011). Range limits appear to be constrained by the interaction of thermal habitat structure, animal physiology, social behaviour and predator-prey interactions, which together define a 'realized' thermal habitat structure of considerable complexity that must be fully explored to ensure reliable inferences (Grant & Dunham 1988; Buckley 2010).

Systematic errors in sampling design and placement of operative temperature thermometers will cause systematic errors in operative temperature. Orientation to the sun, as well as shade and light-coloured surfaces nearby, significantly impacts the absorbed radiation. The temperature, speed and turbulence of the air are affected by the height above the surface, surrounding rocks, vegetation and litter (Pearman, Weaver & Tanner 1972; Mitchell 1976; Gates 1980; Monteith & Unsworth 1990; Campbell & Norman 1998; Rockweit *et al.* 2012). For example, a series of cylinders with a 4 : 1 length/diameter ratio suspended 1 m above the surface, and thus exposed to the same wind speed, showed the expected monotonic positive relation between diameter and operative temperature (Bakken & Gates 1975). This pattern nearly disappeared when the same cylinders were placed on the surface, as the smaller cylinders experienced a lower average wind speed and higher average air temperature than the larger ones. Animals exploit such boundary layer effects to select appropriate operative temperatures for thermoregulation (DeWitt 1971; Muth 1977; Parker 1982; Chappell 1983). More complex boundary layer interactions have been demonstrated for perching lizards (Bakken 1989) and spotted owl nests (Rockweit *et al.* 2012).

As the size and geometry of an operative temperature thermometer determines where it can be placed, anatomically

accurate models can only occupy places that the focal organism can occupy. However, the rigidity of copper electroforms may exclude them from some positions available to live animals, and some thought should be given to how a flexible model could be designed to meet the other conditions for accuracy (Bakken 1992). While a geometric approximation (sphere, cylinder etc.) might be placed as would an anatomical model, naked ThermoChrons[®] (Vasconcelos, Santos & Carretero 2012), Hobo Loggers[®] (Wikelski & Carbone 2004) or TidBits[®] (Vitt & Sartorius 1999) are smaller than many animals and thus can be closer to a surface than can a real animal, where the air is warmer and moves more slowly. Therefore, the size and shape of the operative temperature thermometer play an important role in the sampling process.

To date, biologists using operative temperature thermometers have sampled the six spatial dimensions too coarsely or too haphazardly to construct accurate perceptions of the thermal environment (Dzialowski 2005). For instance, thermal constraints on activity of ectotherms have been modelled by bounding the range of microclimates. Specifically, one estimates the maximal and minimal operative temperatures of an environment, assuming that an animal can attain any temperature between these extremes. This simple approach enables one to use just a few models (Sinervo *et al.* 2011) or even to predict operative temperatures from first principles (Kearney & Porter 2004; Buckley 2008). However, environments consist of complex landscapes that can create substantial heterogeneity in operative temperature. On one hand, bounding the problem with minimal and maximal operative temperatures may overestimate thermal opportunities, because some areas or positions will be effectively inaccessible because of biotic factors or abiotic factors other than temperature. Thus, we can envision a measure of 'realized' thermal heterogeneity caused by these limitations. On the other hand, efforts to sample only minimal and maximal operative temperatures could lead to insufficient sampling, which underestimates the potential for behavioural thermoregulation (Clusella-Trullas & Chown 2011; Sears, Raskin & Angilletta 2011). High-resolution thermal maps are needed to compare the conclusions drawn from this simple approach with those drawn from more complex models of thermoregulation.

Conclusions

Given that modest systematic error in operative temperature can significantly impact indices of environmental quality and thermoregulatory performance, researchers should carefully consider the accuracy and responsiveness of operative temperature thermometers (Fig. 3, Table 1, Supporting information). The most useful estimates come from hollow models that mimic anatomical details of the study animal. This conclusion stems from comparisons of operative temperatures with body temperatures, a consideration of stress and strain, and simple simulations of an animal

thermoregulating in a heterogeneous environment. The use of water-filled or anatomically inaccurate models to estimate body temperature should be viewed with scepticism, unless one can show that these methods achieve a particular aim. For example, filled models would be appropriate when investigating the body temperatures of a sessile organism (Helmuth 2002; Fitzhenry, Halpin & Helmuth 2004; Helmuth *et al.* 2010). Likewise, anatomically inaccurate models might be adequate for application in which predictions are relatively insensitive to errors in operative temperature, for example when temperature is not a limiting resource. Unfortunately, the sensitivity of predictions to error depends on not only the true values of operative temperature but also the spatiotemporal distribution of operative temperatures as related to the behaviours of an animal. Thus, one can rarely know in advance whether the desired comparisons would be robust to errors in operative temperature. For this reason, we recommend the use of anatomically accurate models whenever possible. Procedures for making anatomically detailed hollow copper models with internal temperature recording are described in Supplemental Materials (Appendix S1, Supporting information and Figs S1 and S2, Supporting information).

Once the technical challenges of constructing accurate operative temperature thermometers have been met, these thermometers must be deployed in significant numbers over the relevant portion of the six-dimensional space to quantify thermal resources in a statistically valid design. Spatially explicit patterns of operative temperature, referred to as thermal maps, play a crucial role in understanding the costs and constraints associated with thermoregulation (Angilletta 2009a; reviewed by Angilletta 2009b; Sears, Raskin & Angilletta 2011). The growing need for highly resolved maps of large ranges has forced some biologists to calculate operative temperatures from biophysical principles rather than estimate them with physical models (Buckley 2008; Kearney & Porter 2009; Buckley *et al.* 2010; Kearney *et al.* 2010). Nevertheless, such calculations should ultimately be ground truthed with operative temperature thermometers (e.g. Wetthey *et al.* 2011) to inspire confidence in the predicted impacts of climate change. At the opposite end of the spatial scale, biologists who design and manage protected areas will benefit from maps of operative temperatures in natural habitats and anthropogenic shelters (Lelievre *et al.* 2012). Therefore, the technical issues that we have discussed will remain relevant for years to come.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Construction of electroformed T_e thermometers with internal logging of temperature.

Fig. S1. Steps in the construction of electroformed T_e thermometers with internal logging of temperature.

Fig. S2. An adapter for downloading data from electroformed T_e sensors with internal logging of temperature.

Appendix S2. This workbook in Microsoft Excel® provides computations of T_b given T_e 's in five microhabitats. Various models of movement were used (see text for details of movement models).

Appendix S3. Comparison of proposed indices of thermal quality and thermoregulatory effectiveness.