© 2024. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2024) 227, jeb246481. doi:10.1242/jeb.246481

COMMENTARY

Measurement of microclimates in a warming world: problems and solutions

Duncan Mitchell[1,2,*], Shane K. Maloney[1,2], Edward P. Snelling[1,3], Vinícius de França Carvalho Fonsêca[1,4] and Andrea Fuller[1]

ABSTRACT

As the world warms, it will be tempting to relate the biological responses of terrestrial animals to air temperature. But air temperature typically plays a lesser role in the heat exchange of those animals than does radiant heat. Under radiant load, animals can gain heat even when body surface temperature exceeds air temperature. However, animals can buffer the impacts of radiant heat exposure: burrows and other refuges may block solar radiant heat fully, but trees and agricultural shelters provide only partial relief. For animals that can do so effectively, evaporative cooling will be used to dissipate body heat. Evaporative cooling is dependent directly on the water vapour pressure difference between the body surface and immediate surroundings, but only indirectly on relative humidity. High relative humidity at high air temperature implies a high water vapour pressure, but evaporation into air with 100% relative humidity is not impossible. Evaporation is enhanced by wind, but the wind speed reported by meteorological services is not that experienced by animals; instead, the wind, air temperature, humidity and radiation experienced is that of the animal's microclimate. In this Commentary, we discuss how microclimate should be quantified to ensure accurate assessment of an animal's thermal environment. We propose that the microclimate metric of dry heat load to which the biological responses of animals should be related is black-globe temperature measured on or near the animal, and not air temperature. Finally, when analysing those responses, the metric of humidity should be water vapour pressure, not relative humidity.

KEY WORDS: Climate change, Globe temperature, Humidity, Shade, Wind speed

Introduction

Global warming already has had profound biological effects (see IPCC, 2022), especially in regions like the poles where the rate of warming is well above average (Rantanen et al., 2022). We can expect increases in the frequency and intensity of heatwaves (Domeisen et al., 2023; Perkins-Kirkpatrick and Lewis, 2020; Thompson et al., 2023), with potentially catastrophic thermal consequences. But exceeding the arbitrary threshold of 1.5°C in global mean surface temperature (Masson-Delmotte et al., 2022), in itself, will have little impact on the heat balance (or energy balance; see Glossary) of a lizard on a rock or a cow in a pasture.

The heat balance of terrestrial animals facing global warming depends on their rates of convective heat exchange with the air, conductive heat exchange with surfaces (typically solid or static liquid), radiant heat exchange (typically, but not always, also with surfaces but without physical contact), metabolic heat production and evaporative cooling. When scientists discuss the biological responses of terrestrial animals to global warming, they usually consider two metrics of the thermal environment: air (dry-bulb) temperature (see Glossary) and relative humidity (RH; see Glossary), either individually or combined in an index (e.g. de Castro Junior et al., 2023; Rahimi et al., 2021). Other than the fact that these metrics are reported routinely by meteorological services, the rationale for choosing them is not clear. Air temperature is rarely the main factor that defines heat load on terrestrial animals in warm environments: 'the impacts of climate change on species cannot be assumed to be proportional only to changing air temperature' (Gardner et al., 2024). Furthermore, there is no physiological process in vertebrates that is governed by RH, including evaporative cooling.

Meteorological services measure variables in the free-stream environment; that is, the environment undisturbed by surface structures. For example, wind speed and direction typically are measured on a 3 m or 10 m mast (e.g. National Centers for Environmental Information, USA, www.ncei.noaa.gov/access/monitoring/wind/, accessed 13 December 2023). By contrast, terrestrial animals interact with surfaces and air immediately adjacent to their bodies, with which they are in direct contact, and, at a distance, with the radiation sources and sinks that prevail at their location, some of which, such as night sky, can be remote. Their thermoregulatory responses are not responses to the regional climate or weather, but to their specific microclimate (Coleman and Downs, 2010; Kearney et al., 2021; Pincebourde et al., 2016; Varner and Dearing, 2014). Thus, analyses of heat balance and predictions of an animal's thermal responses require knowledge of those properties of the microclimate that affect the transfer of heat and water vapour (see Box 1).

In this Commentary, we discuss those properties of microclimates that affect the heat balance and thermoregulatory responses of terrestrial animals. The Commentary concentrates on hot microclimates, which will be most problematic in a warming world. We pay specific attention to the practices and problems related to the measurement of relevant microclimate properties. We conclude by proposing a simple, low-cost approach to microclimate measurements.

Measuring radiant heat transfer is critical and complex

Radiation versus convection as the main avenue of microclimate heat

The 'sensible' (Bakken, 1976) or dry (IUPS, 2001) heat transfer between an animal and its microclimate is the sum of radiant,

---

[1]Brain Function Research Group, School of Physiology, University of the Witwatersrand, Parktown, 2193, Johannesburg, South Africa. [2]School of Human Sciences, University of Western Australia, Perth, WA 6009, Australia. [3]Department of Anatomy and Physiology, and Centre for Veterinary Wildlife Research, University of Pretoria, Pretoria 0110, South Africa. [4]Animal Biometeorology Laboratory, São Paulo State University, Jaboticabal, SP - CEP 01049-010, Brazil.

*Author for correspondence (duncan.mitchell@wits.ac.za)

D.M., 0000-0001-8989-4773; S.K.M., 0000-0002-5878-2266; E.P.S., 0000-0002-8985-8737; V.d.F.C.F., 0000-0001-5842-1041; A.F., 0000-0001-6370-8151

Glossary

Absolute humidity
The concentration (g m^{-3}) of water vapour in a volume of wet air. Varies with temperature and pressure for the same amount of water vapour.

Air (dry-bulb) temperature
Air temperature measured by a dry thermometer shielded from all radiation sources and sinks.

Albedo
The fraction of solar energy that is reflected by a surface. This ranges from 0 (all energy is absorbed; black body) to 1 (all energy is reflected; perfect mirror).

Conductive heat flow
Heat exchange between the body and solid surfaces or static fluids.

Convective heat flow
Heat exchange between the body and a mobile fluid (air or water). This exchange can be forced (when there is imposed movement of the fluid relative to the body, e.g. by ambient wind or by body motion), free (when fluid movement is induced by temperature differences between the fluid and the body surface) or mixed (when there is both forced and free convection).

Critical thermal maximum
The dry-bulb temperature at which an animal dies, or loses control of body movements, because of heat stress.

Energy (or heat) balance of an animal with its environment
This is defined by the equation of flow rates: metabolic heat + external work + radiation + convection + conduction + evaporation = storage (with the values for energy flows towards the animal being given a positive sign). External work is energy transferred to (positive value in the equation) or from (negative value) the body by movement against an external force or caused by an external force.

Evaporative cooling
Heat flow between the body and adjacent air that is induced by a phase change of water between liquid and gas at a body surface (including the upper respiratory tract), and accompanying movement of water vapour.

Mean radiant temperature
The temperature of an imaginary isothermal 'black' enclosure around an occupant (human or other animal) that would emit or absorb infrared radiant heat at the same rate as the radiant heat that is emitted or absorbed by the actual non-uniform environment, with sources and sinks of ultraviolet, visible and infrared radiation.

Operative temperature
The temperature of an imaginary isothermal 'black' enclosure around an occupant (human or other animal) that would exchange infrared radiant heat with the occupant at the same rate that the occupant exchanges heat with the actual environment by radiation, convection and conduction combined.

Pyranometer
A device for measuring the heating power of solar radiation, in the waveband of 0.3 to 3 μm, usually that falling downward on a horizontal surface from the hemisphere above the surface.

Pyrgeometer
A device for measuring the heating power of infrared radiation, in the waveband of 4.5 to 100 μm (so, excluding visible and ultraviolet solar radiation), usually falling downward on a horizontal surface from the hemisphere above the surface.

Radiant heat flow
Heat exchange by electromagnetic waves, e.g. visible light waves, ultraviolet waves or infrared waves. Solar radiation is radiation emanating from the sun, whereas thermal radiation is heat flow in the waveband emitted by surfaces with temperatures typical of animal surfaces.

Relative humidity
The concentration of water vapour in wet air expressed as a fraction (or percentage) of the maximum possible concentration of water vapour in air that is saturated at that temperature.

Specific humidity
The concentration (g kg^{-1}) of water vapour in a mass of wet air. Varies with pressure but not with temperature for the same amount of water vapour.

Thermal equilibrium
The state of energy balance in which the rate of storage of heat in the body is zero. In the energy (heat) balance equation, storage may be positive (body gaining heat) or negative (body losing heat) or zero.

Water vapour pressure
The partial pressure of water vapour in wet air. Proportional to absolute humidity and to specific humidity but not proportional to relative humidity except at constant air (dry-bulb) temperature.

Wet-bulb globe temperature index
An index of environmental heat stress based on wet-bulb temperature (the lowest temperature to which air can be cooled by evaporating water without transferring external heat into or out of the air) and globe temperature (see text).

convective and conductive heat flow (see Glossary). In each case, the net transfer of heat depends on the temperature difference between the animal's body surface and the environment. Depending on the direction of the difference, the microclimate directs heat towards, or accepts heat from, an animal's surface. In the case of an animal with fur, feathers or scales, that surface is not its skin, and radiation, convection and conduction may not occur at the same surface (Mitchell et al., 2018). Although conduction is important for a bear lying in a den, for example, active animals, with some exceptions (such as snakes), seldom have appreciable contact with solid surfaces, so we shall not pursue conduction. For convective heat transfer, the relevant temperature difference is that between microclimate air and the surface of the animal exposed to the air, modulated by wind speed (Mitchell, 1974). Historical accounts of animal convective heat transfer usually report microclimate air temperatures lower than the animal's surface temperature, but with global warming there are likely to be more hours of the day, in more places, when air temperature exceeds surface temperature. Convection then will load heat on the animal. In itself, an air temperature that exceeds body surface temperature may drive some terrestrial animals, especially small ones, beyond their limits of thermal tolerance. However, for exposed terrestrial animals, a greater threat to their thermal welfare will come from radiant heat load, and that threat may put animals at risk even if air temperature is well below body surface temperature (Mitchell et al., 2018).

We suggest that mean radiant temperature (MRT, see Glossary) is more important than air temperature in defining the thermal threat to

Box 1. Microclimates

The Intergovernmental Panel on Climate Change is concerned primarily with climatic variables that determine the broad nature of the habitat and distribution of biota (e.g. mean annual temperatures, mean annual rainfall, average hours of sunshine). By contrast, meteorological services are concerned with variables such as wind speed or maximum 24 h air temperature, which determine the weather from day to day and month to month. But neither the climate nor the weather directly determines the continuous exchange of thermal energy between an animal and its microclimate, which, for terrestrial animals, is made up of the solid surfaces and the air boundary layer with which they are in contact and the radiation sources and sinks within their view, some of which may be remote. The rate of heat exchange depends on two groups of variables. One group describes the microclimate itself, and includes dry-bulb temperature, mean radiant temperature (MRT), ambient wind speed and water vapour pressure. The other group relates to the animal, and includes size and shape, posture, surface characteristics, nature of evaporative cooling, and speed and type of movement. Even in the same microclimate, the different animals in the photographs below will have different rates of heat exchange.

Microclimates vary with time; for example, from day to night and across seasons. Furthermore, microclimates in an environment do not necessarily change at the same rate (Meyer et al., 2023); for example, exposed rocks stay warm in the evening long after air temperature has fallen. Many microclimate variables can be measured near instantaneously, but this speed of measurement is not yet possible for MRT, as the globe thermometers used to measure MRT in the field take many minutes to stabilise. Microclimates also vary with space. For example, an ant and an antelope standing at the same site do not experience the same microclimate (see Fig. 1), because microclimate variables change with height above the ground. Taking one step sideways will move the ground squirrel in B (below) to a completely different microclimate. Because of this heterogeneity, measurements from a single weather station at a site will not accurately represent the thermal mosaic of microclimates. Even less useful will be data obtained from meteorological services.

Ectotherms are not impacted by microclimates in the same way as the endotherms in the photographs below. Mammals and birds employ shade seeking and other microclimate selection as part of their repertoire of behavioural thermoregulation, but they can also employ autonomic thermo-effectors (e.g. skin blood flow changes, panting and sweating) to counteract the effects of unfavourable microclimates. If the giraffe in C (below) is too hot in the shade, it will sweat. Some ectotherms (e.g. some species of large lizard) also have access to autonomic thermo-effectors, but these are much less effective than they are in mammals and birds. Therefore, for most ectotherms, thermoregulation is crucially dependent on the selection of appropriate microclimates. Photo credit: (A) Ségio Fidelis; (B) Andrea Fuller; (C) James Kamerman.

an exposed animal. MRT is the mean temperature of the surrounding sources and sinks of radiation, assuming that they are perfect radiators. It is the microclimate variable that best defines the contribution of radiation to an animal's dry heat transfer. The importance of MRT over air temperature can be illustrated with an example. On 17 August 2020, a reliable air temperature of 54.4°C was recorded at Furnace Creek, CA, USA. A naked person standing outside on that day probably would have been sweating heavily, and so would have had a skin temperature of about 35–36°C (Notley et al., 2023). Assuming a wind speed of 1 m s^{-1} would give a whole-body convective heat transfer of 8.3 W m^{-2} °C^{-1} (Mitchell and Whillier, 1971) and so a heat gain from the air of about 160 W m^{-2} of skin. About half of the person's 1.8 m^2 of skin would have been exposed to direct solar radiation, some of which would be reflected from the skin, depending on skin tone (46% for pale skin and 25% for a dark skin). Thus, the direct solar heat load absorbed by the body would range between 486 W (1000 W m^{-2}×0.9 m^{-2}×0.54 for pale skin) and 675 W (1000 W m^{-2}×0.9 m^{-2}×0.75 for dark skin), more than double the convective heat load in either case. To dissipate this additional heat gained from solar radiation, the person would need to drink and evaporate additional water: three more standard glasses per hour for a pale-skinned person and 4.5 more glasses if the person were dark skinned. Those are underestimates; the total radiant heat load on the body would have been more than that imposed by direct solar radiation (see below). As Virginia Finch (1972) showed, radiation coming from the ground nearly doubles the radiant heat load on an antelope standing on the ground of high albedo (see Glossary), and the same applies to dairy cows (Da Silva et al., 2010). So, although the 54.4°C air temperature in the above example was extreme, it was not the main thermal threat to our naked person. Under global warming, MRT will remain far more important than air temperature in defining the heat load on animals. However, meteorological services do not measure MRT (and although they measure solar irradiance they usually do not report it). Nor is MRT measured by most biologists who explore the biological responses of animals to global warming.

Measurement of mean radiant temperature

The typical radiant environment for an animal outdoors extends far beyond direct solar radiation and radiation from the ground (Fig. 1). Therefore, the measurement of MRT is not straightforward (Kántor and Unger, 2011). The gold-standard method, at least for the built environment, is to position combinations of pyranometers and pyrgeometers (see Glossary) at the site of the occupant of the environment, pointing up, down and in the four horizontal directions. The measured radiant flows then are integrated with the 'view' that the occupant has of the radiant sources or sinks in every direction (e.g. Acero et al., 2023; Vanos et al., 2021). This method is impracticable for biologists working in the field, but a simpler alternative is available (Johansson et al., 2014), developed originally to measure MRT for humans indoors (Bedford and Warner, 1934; Vernon, 1932). The method involves placing a hollow sphere painted matte black (a globe or black-bulb thermometer) at the site of the occupant (or the site of an animal in the field), allowing it to reach thermal equilibrium (see Glossary), and measuring its temperature. At thermal equilibrium, convective and radiant heat transfer at the sphere balance each other out. Thus, if the rate of convective heat transfer can be calculated (from sphere

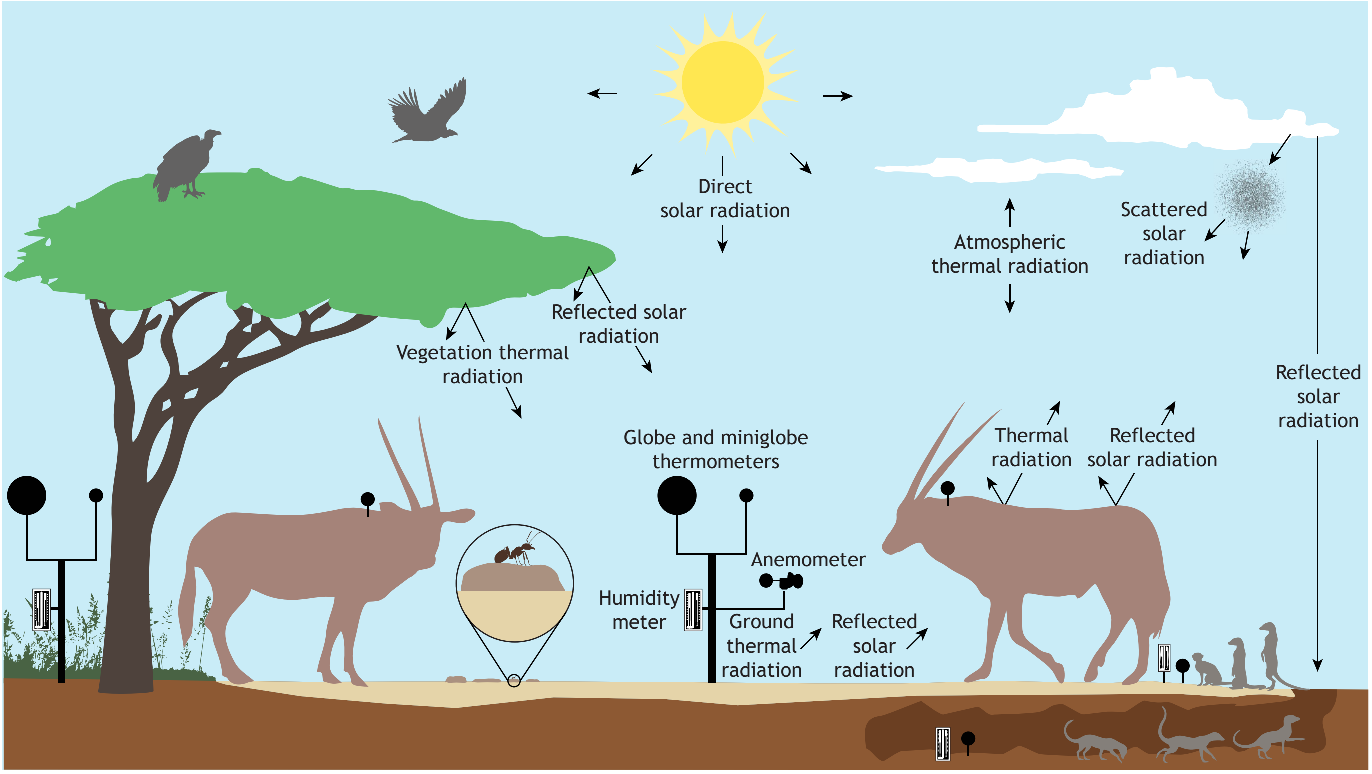

Fig. 1. Direct solar radiation is only one avenue of radiation that affects terrestrial animals. There are multiple sources and sinks of radiation, atmospheric and terrestrial. Pyranometers pointing upwards can massively overestimate the protection from radiation that results from animals (including humans) seeking cover under shade. Radiation reflected off and emitted from the ground can impose a radiant heat load on animals almost as intense as that imposed by direct solar radiation (Finch, 1972). Trees do not interfere with radiant heat exchange with external sources and sinks as completely as do burrows. Proper assessment of an animal's thermal environment requires measurements in multiple microclimates in its habitat, including in the shade.

size and temperature, wind speed, and air temperature), then the rate of radiant heat transfer at the sphere can be derived, and MRT calculated (e.g. Kuehn et al., 1970). The original sphere used in this context was ∼150 mm in diameter, a copper float from the cistern of a domestic toilet (Aitken, 1888). However, for many applications, especially in the field, that sphere is too big or responds too slowly, so other spheres of between 30 mm (Fuller et al., 1999; Hetem et al., 2007) and 100 mm (Vega et al., 2020) diameter have been used, with 'miniglobes' of 38 mm being popular (legacy table tennis balls; De Dear, 1988; Humphreys, 1977; Thorsson et al., 2007).

For nearly a century, there was confidence in the derivation of MRT from globe temperature (Bond and Kelly, 1955; Graves, 1974; Kuehn et al., 1970; Oliveira et al., 2019). That confidence has waned, mainly because of doubts about the convective heat transfer coefficient that is assigned to the globe thermometer, and especially to miniglobes (d'Ambrosio Alfano et al., 2021a,b; Teitelbaum et al., 2022). The original formula for the convective heat transfer coefficient does not apply when the globe is in still air and therefore under free or mixed convection (see Glossary entry for 'convective heat flow'; Acero et al., 2023; d'Ambrosio Alfano et al., 2021a; Teitelbaum et al., 2020). The formula breaks down when the air flow is turbulent (Acero et al., 2023), in rain (Acero et al., 2023) or if wind speed at the globe is estimated rather than measured (Guo et al., 2018). Furthermore, sometimes when the globe is used outdoors, asymmetrical surface heating can result in errors in calculated MRT of up to 20°C (Guo et al., 2020; Kántor and Unger, 2011; Vanos et al., 2021). However, these sources of error do not render the globe obsolete. The calculation of MRT is essential to evaluate the heat balance of terrestrial animals, and the globe is the only practical way of measuring MRT in the field. Making users aware of the potential errors should help them avoid or account for these errors. Below, we suggest an alternative to the calculation of MRT when heat balance measurement is not required: using globe temperature as a metric in its own right.

MRT in shade often far exceeds air temperature

Given the danger of overheating under a radiant heat load, it is not surprising that many small terrestrial animals that are diurnally active retreat periodically to refuges such as burrows, tree cavities and deep rock crevices where they can escape solar radiation (e.g. Chappell and Bartholomew, 1981; Fick et al., 2009). Even the largest of terrestrial animals, elephants, which are clearly excluded from burrows, seek shade under trees (Mole et al., 2016). The temperature of air under tree canopies tends to be a few degrees Celsius lower than that of the surrounding air, but the ground is much cooler than adjacent ground exposed to solar radiation (Lin and Lin, 2010). Shade-seeking under a tree, however, will not allow an animal to escape radiation as well as would entering a burrow, as solar radiation reflecting off the ground can contribute substantially to the radiant heat load on animals (Da Silva et al., 2010; Kelly et al., 1950; Finch, 1972), and there are several other routes by which radiation can penetrate into shade (Fig. 1).

Surprisingly few comparisons have been made of the radiant microclimate in shade and simultaneously in nearby open habitats. Table 1 gives some examples. It shows that making an incomplete measurement of the radiant heat load may lead to a false conclusion regarding the protection provided by shade. For example, pyranometers may lead to the conclusion that trees exclude almost all of the radiation. But pyranometers usually are set up to record only downcoming radiation and not radiation from the other directions illustrated in Fig. 1, much of which penetrates into and below the tree canopy (Kelly et al., 1950). When globe thermometers are used to measure radiation, they detect the complete radiant heat load in shaded microclimates, and reveal that the protection offered by trees is much less than is indicated by pyranometers (Table 1). Typically, animals under trees, or under artificial shelters (e.g. roofing or solar panels), receive 60% or more of the radiation that they would in the sun. During daylight hours, MRT in the shade of an overhead shelter can far exceed air

Table 1. Examples of reduction of radiant heat load in shade

	Cover	Measurement	Reduction in radiant heat load	Reference
Pyranometer	North European deciduous tree species	Upper-hemisphere radiation (0.4–1.1 µm)	86–92% (foliated) 41–52% (leafless)	Gardner and Sydnor, 1984
	Negev desert native trees	Direct downward radiant flux only	87%	Kotzen, 2003
	Small desert tree above kangaroo daytime resting site	Direct downward radiant flux only	80%	Dawson and Denny, 1969
	US ornamental tree species	Upper-hemisphere radiation	56–75% (foliated) 24–43% (leafless)	Konarska et al., 2014
	Galvanised steel cattle shades	Upper-hemisphere radiation	47–51%	Bond et al., 1967
Standard globe thermometer	Overhead shelter (solar panels) (see Fig. 2)	Standard globe 1 m above ground	30–40%	Fonsêca et al., 2023; Faria et al., 2023
	Brazilian silvopastoral native trees (545 trees ha^{-1})	Standard globe 1.5 m above ground	22% maximum	Pezzopane et al., 2019
	Brazilian native trees (scattered)	Standard globe 1.3 m above ground	24% (July) 16% (August) 30% (September)	Karvatte et al., 2016
	Brazilian savanna trees (4 species)	Standard globe 1 m above ground	15% (08:30–16:30 h) 20% (11:00–14:00 h)	Teixeira et al., 2022
	Eucalyptus trees on pasture (360 trees ha^{-1})	Standard globe 1.3 m above ground	17% (July) 5% (August) 8% (September)	Karvatte et al., 2016
	Eucalyptus trees on pasture (333 trees ha^{-1})	Standard globe 1.5 m above ground	12% mean	Pezzopane et al., 2019

Trees and artificial shelters block direct downward radiant flow. Consequently, pyranometers set up to measure only downward radiation indicate much greater reduction of heat load than do globe thermometers, which measure radiation coming from all directions.

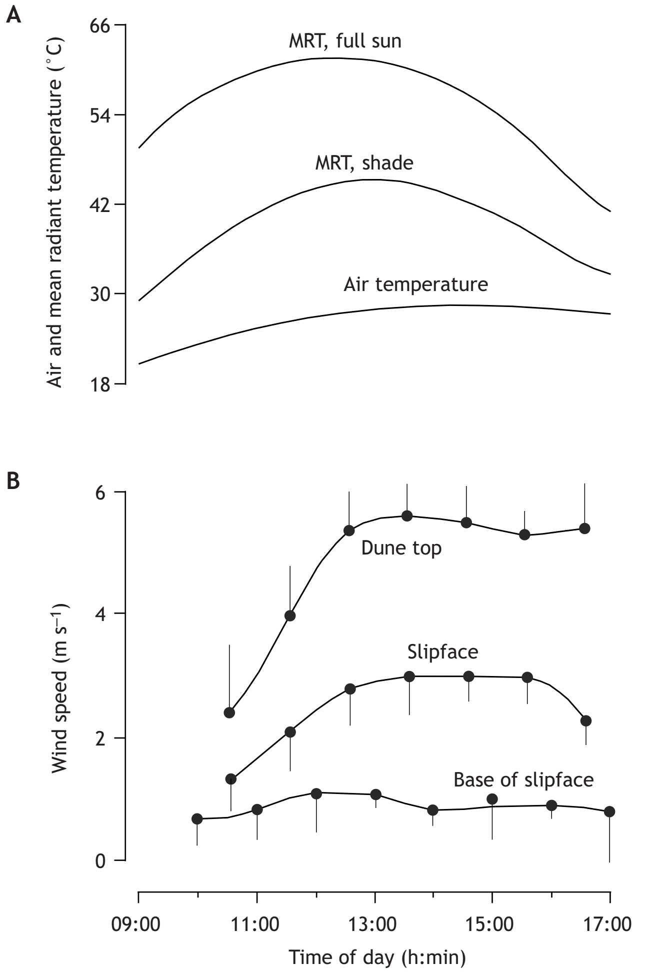

Fig. 2. Microclimate variables at two sites, as a function of time of day. (A) The first site, at Jaboticabal in Brazil, is shown in panel A of Box 1 figure. Presented here is the mean air temperature (averaged across five consecutive summer days) under the overhead shelter as well as the mean radiant temperature (MRT, calculated from measurements of globe temperature) under that shelter and in adjacent direct solar radiation (original data, V.d.F.C.F.). There is substantial penetration of radiation under the shelter. (B) The second site is from a sand dune, occupied by lizards and other surface-dwelling organisms, in the Namib Desert of Namibia. Wind speed (mean±s.d., averaged across four consecutive days) was recorded 1.5 m above the dune top, 300 mm above the sand surface on the slipface (both using cup anemometers), and 20 mm above the sand surface at the base of the dune slipface (using a hot-wire anemometer). Wind speed 300 mm above the sand surface bears no resemblance to wind speed at heights relevant to the lizards. Redrawn from Seely et al. (1990).

temperature under that shelter (Fig. 2A). Thus, although MRT may be close to air temperature in deep shade, one never should assume that MRT and air temperature are equivalent. Radiant heat has to be measured even in the shade.

Although deep shade, such as dense forest canopy or a burrow, clearly must benefit the thermoregulation of animals that can reach it, Table 1 indicates that animals in sparse shade, such as those in the Box 1 figure, may not enjoy the full benefit. Indeed, in the tropics, the mean (Gaughan et al., 2010; Gebremedhin et al., 2011) and maximum (Faria et al., 2023; Tucker et al., 2008) daily deep-body temperature does not differ significantly between cattle in the shade and those in direct solar radiation. So why do large animals, including humans, seek shade so routinely? Perhaps shade helps the animal to reduce the evaporative water loss required to maintain body temperature (e.g. Maia et al., 2023; Wolf and Walsberg, 1996). It may also help the animal to reduce body surface temperature, to escape high ground temperature or to avoid the burning short-wave radiation from the sun, especially on exposed skin.

Wind speed must be measured in the microclimate, not above it

Air movement has a large impact on both convective and evaporative heat exchange. Just as MRT has to be measured in an animal's microclimate, so too does wind speed, as the example in Fig. 2B illustrates. The figure shows wind speed measured at different times of the day and at different locations on a Namib Desert sand dune. Notably, according to the authors, 'wind speeds indicated by an anemometer in the free air stream bear no resemblance to the wind regimen experienced by lizards and other organisms living close to the slipface surface' (Seely et al., 1990). This wind profile is not peculiar to sand dunes of the Namib Desert. In any environment, the profile of wind speed must decrease progressively from the free stream to zero at the ground surface. The profile shape depends on the physical structure of the environment (Garratt and Hicks, 1973), and the wind speed that affects an animal depends on what part (or parts) of the profile the animal occupies (Meyer et al., 2023). As Fig. 2B shows, it may not be possible to predict wind speed near the ground from wind speeds measured higher, for example, by anemometers on weather stations.

Another example from the Namib Desert illustrates how narrow the microclimate might be in which wind speed would have to be measured to obtain an accurate picture of conditions experienced by an animal. *Ocymyrmex barbiger* is a 4 mg Namib ant, active in full sunlight in the middle of the day (Marsh, 1985), even when sand temperature reaches 67°C, which is well above the ant's critical thermal maximum (see Glossary). The ants avoid thermal death by engaging in short bouts of activity (5–9 s), between which they climb onto any pedestal available, typically reaching 10–20 mm above the sand surface. There, they use a few limbs to grip the refuge object and 'rapidly flail their other limbs about in the air' (Marsh, 1985). Climbing to 20 mm puts the ant in an air layer that could be 20°C below the temperature of air at the ground surface. Flailing increases convection from their narrow limbs (Mitchell, 1974; Mitchell et al., 2018). Historically, the only anemometers small enough to make valid measurements of wind speed in a 20 mm thick microclimate have been hot-wire anemometers, which use a fine heated wire to determine wind speed. However, hot-wire anemometers are not presently amenable to continuous operation with output collected by data loggers. Thus, the future of wind speed measurement for studies in thermal biology will lie in ultrasonic anemometers, which also provide measurements of wind direction, air temperature and humidity, with no moving parts (Nakayoshi et al., 2015). Palm-sized ultrasonic anemometers that connect to data loggers already are available commercially (e.g. TriSonica™ 91×91×52 mm; ULSA™ 75×75×54 mm).

For most animals, however, the most important reason to measure wind speed in the microclimate will not be to determine convection, because, as we have already established, convection will probably play a minor role in comparison to radiation as the major thermal challenge. Wind speed affects evaporation in the same way that it affects convection (Mitchell et al., 2018). Effective evaporation is driven by the difference in water vapour pressure (WVP; see Glossary) between an animal's evaporating surfaces and its immediate environment (see below), but the rate of evaporation is amplified by increased wind speed. Effective evaporative cooling will be increasingly important if animals are to avoid hyperthermia under an increasing frequency and intensity of heatwaves.

Measuring RH is routine, but inferences drawn from RH can be misleading

It is commonly known that evaporative cooling is hindered in environments with high RH and high air temperature, but it is a misconception that air saturated with water vapour – that is, with 100% RH – prevents evaporation from the skin or upper respiratory tract (e.g. Luber and McGeehin, 2008; Mora et al., 2017). Evaporation can occur into saturated air. It can do so because water vapour in air, like any other uncharged motile substance, moves down its concentration gradient, which, according to the ideal gas equation, is proportional to the WVP gradient. If the water vapour concentration is expressed as absolute humidity (g m^{-3}; see Glossary), the relationship between WVP and concentration depends on air temperature, but if it is expressed as specific humidity (g kg^{-1}; see Glossary), it does not.

So, during evaporative cooling, water vapour will move from the surface of the skin or upper respiratory tract into the microclimate, provided that the WVP in the microclimate is lower, even if its RH is 100% (Mitchell et al., 2018). If microclimate RH is 100%, for surface WVP to be higher than that of the microclimate, surface temperature has to be above microclimate air temperature. If sweat evaporates into the saturated air, the excess water vapour in the air will condense out; what happens to the water vapour after it leaves an animal has no thermal consequences for the animal.

RH, in its own right (i.e. without the context of prevailing air temperature) provides no information about an animal's ability to cool by evaporation. As an illustration of this concept, we can compare a hot, sweaty human in two different environments: Heathrow Airport and a hot dry desert (Fig. 3A). On New Year's Day 2023, the RH at Heathrow Airport reached 94%. Would that high RH have impeded evaporative cooling? The maximum air temperature at Heathrow on that day was 11°C. So, even at 94% RH, WVP at Heathrow would have been far below that on the body surface (Fig. 3A). Indeed, the WVP at Heathrow would have been similar to that of the hot dry desert at 40°C and 17% RH (Fig. 3A). So the WVP gradient (the driving force for evaporative cooling) from saturated skin at 36°C would have been the same at Heathrow as in the desert (ca. 6.0−1.2=4.8 kPa), despite the RH being 94% and 17%, respectively. In neither location would evaporative cooling be impeded. If there was a burrow in the desert with a temperature of 25°C and RH of 30% (WVP ca. 1.0 kPa), some water vapour would have flowed from the atmosphere into the burrow mouth, down the WVP gradient but against the RH gradient.

There is another way that reporting RH can be misleading. There are many diagrams in the literature similar to that shown in Fig. 3B, here depicting average air temperature and RH over 12 days in Brazil. The commentary on such diagrams may conclude that the deleterious thermoregulatory effects of the morning increase in air temperature are offset by the coincident decrease in RH, allegedly aiding evaporative cooling. But WVP hardly changes over the course of the day; RH decreases because air temperature increases, not because WVP changes (Fig. 3C). A decrease in RH, not accompanied by a decrease in WVP, does not aid evaporative cooling.

With global warming, at sites where sufficient liquid water is available (Simpson et al., 2024), the quantity of water in the Earth's atmosphere will increase, while RH will stay much the same (Trenberth, 2011; Trenberth et al., 2003). Hotter air will hold more water vapour: approximately 7% more water per degree Celsius rise in air temperature (Trenberth et al., 2003). A focus on RH may well miss the increase in atmospheric water vapour with a warming climate, leading to a failure to consider its consequences (Matthews et al., 2022). As we have emphasised, in the context of evaporative cooling, the relevant metric is WVP (or absolute or specific humidity), but not RH (Jenkins et al., 2023; Mitchell et al., 2018). As well as being important in studies on animal responses in a warming world, this notion is also relevant to work on human health, but is sometimes ignored. Of 260 publications between 2013 and 2016 related to human heat stress, 65% reported RH and only 5% reported absolute humidity (Davis et al., 2016). The manufacturers of instruments designed to measure water vapour should play a role in emphasising the importance of WVP; their instruments usually have RH as their primary output, but should instead give the calculated WVP.

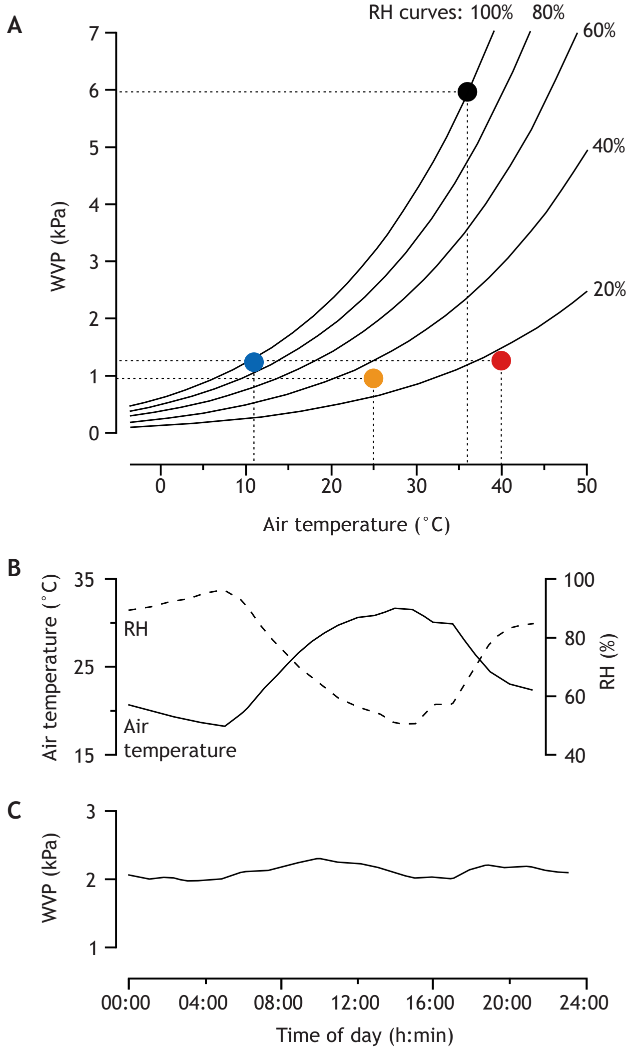

Fig. 3. How relative humidity (RH) may lead to misinterpretations about evaporative cooling. (A) Relationship between water vapour pressure (WVP) and air temperature for different RH curves. Indicated in the figure are the conditions for human skin fully wet with sweat (black circle), the air at Heathrow Airport on New Year's Day 2023 (blue circle), the air in a hot dry desert (red circle) and the air in a burrow in that desert (orange circle). The vapour pressure difference that drives evaporation is the same at Heathrow Airport (94% RH) and in the desert (17% RH), and evaporative cooling is not impeded by the 94% RH at Heathrow. (B) Air temperature and RH at Jaboticabal in December 2021, measured every 5 min and averaged over 12 days (unpublished data, V.d.F.C.F.). (C) WVP (calculated from air temperature and RH in B) remains relatively unchanged and does not facilitate accelerated evaporative cooling in the morning as one might assume from changes in RH.

Conclusions and solutions: keep measurement simple when microclimates are complex

Given the complexity of microclimates, is it possible to implement a measurement of the microclimate to which one can relate the biological responses of terrestrial animals in the field? Is there a method that measures variables that influence dry heat exchange and evaporative cooling in a microclimate? Is there a method that is straightforward, size-appropriate, widely applicable and affordable? We believe that these requirements can be met best by measuring globe temperature (the equilibrium temperature of which depends on MRT, air temperature and wind speed), calculating WVP (or absolute or specific humidity) and measuring wind speed, all within the relevant microclimate, or as close to it as possible.

The derivation of MRT from globe temperature has some issues (see above), which require attention by those calculating MRT, but the calculation of MRT will remain essential in studies aiming to analyse the full heat balance of an animal in the field. Some of the issues can be avoided by using only the original 150 mm diameter globe when MRT has to be calculated, because there is less uncertainty about how it is affected by air temperature, so the derived MRT is more accurate than that derived from smaller globes. However, in the many studies of animal responses to thermal challenge that do not require a detailed breakdown of heat balance, the errors associated with the calculation of MRT could be avoided by employing globe temperature itself – rather than MRT – as a thermal metric, a role it fulfils in the widely used wet-bulb globe temperature index (see Glossary) of human heat stress (Yaglou and Minard, 1957). More recently, globe temperature in its own right has been used occasionally, and successfully, as a metric of the microclimate in studies of the responses of free-living animals (e.g. Carroll et al., 2016; Cunningham et al., 2015; Fick et al., 2009; McFarland et al., 2020; Panagakis, 2011; Seely et al., 1990). We envisage globe temperature as a primary metric of the microclimate, not as a substitute for operative temperature (see Glossary; Bakken, 1976; Walsberg and Weathers, 1986). Operative temperature (which can be measured with taxidermic models or phantoms such as copper casts and agar models) certainly will be better than globe temperature in determining the environmental thermal stress on an animal of a specific size and shape, in a specific posture, with a specific orientation to the sun and wind, but that operative temperature will not apply to other animals in the same microclimate.

We propose that in experimental studies of the responses of animals to global warming, globe temperature should be measured routinely and biological responses should be correlated with globe temperature, not with air temperature. We propose further that globes of just two diameters should be used. For humans (e.g. Acero et al., 2023; Kuehn et al., 1970) and other large animals (e.g. Santos et al., 2017; Valtorta et al., 1997), the original 150 mm diameter globe has an established track record. For small animals and small microclimates, we propose a 40 mm diameter miniglobe; this is the diameter of current readily available and inexpensive table-tennis balls, which can be painted matte black and fitted with an internal thermometer (De Dear, 1988). These acrylic balls have low thermal inertia and so have a fast response time (Nikolopoulou et al., 1999). If wind speed is known, the equivalent temperature for the 150 mm globe can be calculated from miniglobe temperature (Hetem et al., 2007).

If animals of different sizes are under study, every weather station used in the field should have both globes installed (see Fig. 1). Miniglobes also can be attached to some study animals; for example, affixed to a stalk on a collar, so that globe temperature can be measured in the microclimate selected by the animal (Fuller et al., 1999; Hetem et al., 2007; Nakayoshi et al., 2015). The temperature of attached sensors of radiation inevitably will be influenced by the surface temperature of the animal itself, but so will the animal's microclimate; the attributes of an occupied and unoccupied microclimate, such as that of a burrow, are not the same. Where an attached miniglobe is not feasible, an array of miniglobes with a random distribution across the habitat would allow animal preferences to be assessed. Furthermore, measurements should not be confined to daylight hours, because radiation to the cold night sky, which the globe thermometer will detect, can provide substantial heat loss (Adelard et al., 1998; Swinbank, 1963).

Small data loggers (e.g. iButtons™) are widely used as measures of microclimate in studies of thermal biology (e.g. Levy et al., 2016; Sepulveda et al., 2014; Tillman et al., 2021; Van Jaarsveld et al., 2021; Vitt and Sartorius, 1999). When attached to the animal, these loggers allow detection of whether animals are in refuges (e.g. Murray and Smith, 2012). However, they will not measure air temperature reliably (their usual intended role) whenever they are not fully protected from radiation (Maclean et al., 2021). Furthermore, with their irregular shapes and age-dependent surface properties, they also will not properly integrate radiant heat load, air temperature and wind speed, as standard globe thermometers can do. The solution is to put the logger inside a table-tennis ball painted matte black.

As we have discussed above, when considering an animal's thermal environment, WVP also will be required. WVP usually will be calculated from RH and air temperature, and air temperature has to be measured with a thermometer protected from thermal radiation. Such protection is not achieved well by most naturally ventilated radiation shields (Nakamura and Mahrt, 2005), whereas fine-wire (<1 mm diameter) thermocouples painted white do surprisingly well in the measurement of air temperature even when unprotected (Christian and Tracy, 1985; Maclean et al., 2021). Furthermore, thermocouples are cheap and convenient for field work. The finer the wire, the less it is contaminated by radiation. Although wind speed often can be measured by using small cup anemometers (provided that wind speed is not too low), we expect that they will be replaced entirely by new technologies, perhaps miniaturised ultrasonic anemometers, in the suite of instruments for measurement of microclimate.

If we are to accurately assess the performance and predict the persistence or demise of terrestrial animals in a warming world, we must understand the biological responses of animals to their immediate microclimate, within which they operate and exchange thermal energy. To realise this goal will require the measurement of variables that allow us to properly understand the exchange of heat and water vapour between animals and their environment. This Commentary, we hope, will help to achieve those aims.

Competing interests

The authors declare no competing or financial interests.

References

Acero, J. A., Dissegna, A., Tan, Y. S., Tan, A. and Norford, L. K. (2023). Outdoor performance of the black globe temperature sensor on a hot and humid tropical region. *Environ. Technol.* **44**, 961-973. doi:10.1080/09593330.2021.1989057

Adelard, L., Pignolet-Tardan, F., Mara, T., Lauret, P., Garde, F. and Boyer, H. (1998). Sky temperature modelisation and applications in building simulation. *Renew. Energy* **15**, 418-430. doi:10.1016/S0960-1481(98)00198-0

Aitken, J. (1888). 13. Addition to thermometer screens. Part IV. *Proc. R. Soc. Edinb.* **14**, 428-432. doi:10.1017/S0370164600004302

Bakken, G. S. (1976). A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* **60**, 337-384. doi:10.1016/0022-5193(76)90063-1

Bedford, T. and Warner, C. G. (1934). The globe thermometer in studies of heating and ventilation. *Epidemiol. Infect* **34**, 458-473. doi:10.1017/S0022172400043242

Bond, T. E. and Kelly, C. F. (1955). The globe thermometer in agricultural research. *Agric. Eng.* **36**, 251-255.

Bond, T. E., Kelly, C. F., Morrison, S. R. and Pereira, N. (1967). Solar, atmospheric, and terrestrial radiation received by shaded and unshaded animals. *Trans. ASABE* **10**, 622-625. doi:10.13031/2013.39745

Carroll, J. M., Davis, C. A., Fuhlendorf, S. D. and Elmore, R. D. (2016). Landscape pattern is critical for the moderation of thermal extremes. *Ecosphere* **7**, e01403. doi:10.1002/ecs2.1403

Chappell, M. A. and Bartholomew, G. A. (1981). Activity and thermoregulation of the antelope ground squirrel *Ammospermophilus leucurus* in winter and summer. *Physiol. Zool.* **54**, 215-223. doi:10.1086/physzool.54.2.30155822

Christian, K. A. and Tracy, C. R. (1985). Measuring air temperature in field studies. *J. Therm. Biol.* **10**, 55-56. doi:10.1016/0306-4565(85)90012-9

Coleman, J. C. and Downs, C. T. (2010). Characterizing the thermal environment of small mammals: what should we be measuring, and how? *Open Access Anim. Physiol.* **2**, 47.

Cunningham, S. J., Martin, R. O. and Hockey, P. A. (2015). Can behaviour buffer the impacts of climate change on an arid-zone bird? *Ostrich* **86**, 119-126. doi:10.2989/00306525.2015.1016469

d'Ambrosio Alfano, F. R., Dell'isola, M., Ficco, G., Palella, B. I. and Riccio, G. (2021a). On the measurement of the mean radiant temperature by means of globes: An experimental investigation under black enclosure conditions. *Build. Environ.* **193**, 107655. doi:10.1016/j.buildenv.2021.107655

d'Ambrosio Alfano, F. R., Ficco, G., Frattolillo, A., Palella, B. I. and Riccio, G. (2021b). Mean radiant temperature measurements through small black globes under forced convection conditions. *Atmosphere* **12**, 621. doi:10.3390/atmos12050621

Da Silva, R. G., Guilhermino, M. M. and de Morais, D. A. E. F. (2010). Thermal radiation absorbed by dairy cows in pasture. *Int. J. Biometeorol.* **54**, 5-11. doi:10.1007/s00484-009-0244-1

Davis, R. E., McGregor, G. R. and Enfield, K. B. (2016). Humidity: A review and primer on atmospheric moisture and human health. *Environ. Res.* **144**, 106-116. doi:10.1016/j.envres.2015.10.014

Dawson, T. J. and Denny, M. J. S. (1969). A bioclimatological comparison of the summer day microenvironments of two species of arid–zone kangaroo. *Ecology* **50**, 328-332. doi:10.2307/1934861

de Castro Junior, S. L., Silveira, R. M. F. and da Silva, I. J. O. (2023). Psychrometry in the thermal comfort diagnosis of production animals: A combination of the systematic review and methodological proposal. *Int. J. Biometeorol.* **68**, 45-56. doi:10.1007/s00484-023-02569-2

De Dear, R. (1988). Ping-pong globe thermometers for mean radiant temperatures. *H and V Eng.* **60**, 10-11.

Domeisen, D. I., Eltahir, E. A., Fischer, E. M., Knutti, R., Perkins-Kirkpatrick, S. E., Schär, C., Seneviratne, S. I., Weisheimer, A. and Wernli, H. (2023). Prediction and projection of heatwaves. *Nat. Rev. Earth Environ.* **4**, 36-50. doi:10.1038/s43017-022-00371-z

Faria, A. F. P., Maia, A. S., Moura, G. A., Fonsêca, V. F. C., Nascimento, S. T., Milan, H. F. and Gebremedhin, K. G. (2023). Use of solar panels for shade for Holstein heifers. *Animals* **13**, 329. doi:10.3390/ani13030329

Fick, L. G., Kucio, T. A., Fuller, A., Matthee, A. and Mitchell, D. (2009). The relative roles of the parasol-like tail and burrow shuttling in thermoregulation of free-ranging Cape ground squirrels, *Xerus inauris*. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **152**, 334-340. doi:10.1016/j.cbpa.2008.11.004

Finch, V. A. (1972). Thermoregulation and heat balance of the East African eland and hartebeest. *Am. J. Physiol.* **222**, 1374-1379. doi:10.1152/ajplegacy.1972.222.6.1374

Fonsêca, V. d. F. C., de Andrade Culhari, E., Moura, G. A. B., Nascimento, S. T., Milan, H. M., Neto, M. C. and Maia, A. S. C. (2023). Shade of solar panels relieves heat load of sheep. *Appl. Anim. Behav. Sci.* **265**, 105998. doi:10.1016/j.applanim.2023.105998

Fuller, A., Moss, D. G., Skinner, J. D., Jessen, P. T., Mitchell, G. and Mitchell, D. (1999). Brain, abdominal and arterial blood temperatures of free-ranging eland in their natural habitat. *Pflügers Arch.* **438**, 671-680. doi:10.1007/s004249900105

Gardner, T. J. and Sydnor, T. D. (1984). Interception of summer and winter insolation by five shade tree species. *J. Am. Soc. Hortic. Sci.* **109**, 448-450. doi:10.21273/JASHS.109.4.448

Gardner, A. S., Maclean, I. M., Rodríguez-Muñoz, R., Hopwood, P. E., Mills, K., Wotherspoon, R. and Tregenza, T. (2024). The relationship between the body and air temperature in a terrestrial ectotherm. *Ecol. Evol.* **14**, e11019. doi:10.1002/ece3.11019

Garratt, J. R. and Hicks, B. B. (1973). Momentum, heat and water vapour transfer to and from natural and artificial surfaces. *Q. J. R. Meteorol. Soc.* **99**, 680-687. doi:10.1002/qj.49709942209

Gaughan, J. B., Bonner, S., Loxton, I., Mader, T. L., Lisle, A. and Lawrence, R. (2010). Effect of shade on body temperature and performance of feedlot steers. *J. Anim. Sci.* **88**, 4056-4067. doi:10.2527/jas.2010-2987

Gebremedhin, K. G., Lee, C. N., Hillman, P. E. and Brown-Brandl, T. M. (2011). Body temperature and behavioral activities of four breeds of heifers in shade and full sun. *Appl. Eng. Agric.* **27**, 999-1006. doi:10.13031/2013.40620

Graves, K. W. (1974). Globe thermometer evaluation. *Am. Ind. Hyg. Assoc. J.* **35**, 30-40. doi:10.1080/0002889748507003

Guo, H., Teitelbaum, E., Houchois, N., Bozlar, M. and Meggers, F. (2018). Revisiting the use of globe thermometers to estimate radiant temperature in studies of heating and ventilation. *Energy Build.* **180**, 83-94. doi:10.1016/j.enbuild.2018.08.029

Guo, H., Aviv, D., Loyola, M., Teitelbaum, E., Houchois, N. and Meggers, F. (2020). On the understanding of the mean radiant temperature within both the indoor and outdoor environment, a critical review. *Renew. Sust. Energ. Rev.* **117**, 109207. doi:10.1016/j.rser.2019.06.014

Hetem, R. S., Maloney, S. K., Fuller, A., Meyer, L. C. R. and Mitchell, D. (2007). Validation of a biotelemetric technique, using ambulatory miniature black globe thermometers, to quantify thermoregulatory behaviour in ungulates. *J. Exp. Zool. A Ecol. Genet. Physiol.* **307**, 342-356. doi:10.1002/jez.389

Humphreys, M. A. (1977). The optimum diameter for a globe thermometer for use indoors. *Ann. Occup. Hyg.* **20**, 135-140.

IPCC (2022). Climate Change 2022: Impacts, Adaptation and Vulnerability (ed. H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem and B. Rama). Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

IUPS (International Union of Physiological Sciences), Commission for Thermal Physiology (2001). Glossary of terms for thermal physiology. *Jpn. J. Physiol.* **51**, 245.

Jenkins, E. J., Campbell, H. A., Lee, J. K., Mündel, T. and Cotter, J. D. (2023). Delineating the impacts of air temperature and humidity for endurance exercise. *Exp. Physiol.* **108**, 207-220. doi:10.1113/EP090969

Johansson, E., Thorsson, S., Emmanuel, R. and Krüger, E. (2014). Instruments and methods in outdoor thermal comfort studies–The need for standardization. *Urban Clim.* **10**, 346-366. doi:10.1016/j.uclim.2013.12.002

Kántor, N. and Unger, J. (2011). The most problematic variable in the course of human-biometeorological comfort assessment – The mean radiant temperature. *Open Geosci.* **3**, 90-100. doi:10.2478/s13533-011-0010-x

Karvatte, N., Klosowski, E. S., de Almeida, R. G., Mesquita, E. E., de Oliveira, C. C. and Alves, F. V. (2016). Shading effect on microclimate and thermal comfort indexes in integrated crop-livestock-forest systems in the Brazilian Midwest. *Int. J. Biometeorol.* **60**, 1933-1941. doi:10.1007/s00484-016-1180-5

Kearney, M. R., Porter, W. P. and Huey, R. B. (2021). Modelling the joint effects of body size and microclimate on heat budgets and foraging opportunities of ectotherms. *Methods Ecol. Evol.* **12**, 458-467. doi:10.1111/2041-210X.13528

Kelly, C. F., Bond, T. E. and Ittner, N. R. (1950). Thermal design of livestock shades. *Agric. Eng.* **31**, 601-606.

Konarska, J., Lindberg, F., Larsson, A., Thorsson, S. and Holmer, B. (2014). Transmissivity of solar radiation through crowns of single urban trees—application for outdoor thermal comfort modelling. *Theor. Appl. Climatol.* **117**, 363-376. doi:10.1007/s00704-013-1000-3

Kotzen, B. (2003). An investigation of shade under six different tree species of the Negev desert towards their potential use for enhancing micro-climatic conditions in landscape architectural development. *J. Arid Environ.* **55**, 231-274. doi:10.1016/S0140-1963(03)00030-2

Kuehn, L. A., Stubbs, R. A. and Weaver, R. S. (1970). Theory of the globe thermometer. *J. Appl. Physiol.* **29**, 750-757. doi:10.1152/jappl.1970.29.5.750

Levy, O., Dayan, T., Porter, W. P. and Kronfeld-Schor, N. (2016). Foraging activity pattern is shaped by water loss rates in a diurnal desert rodent. *Am. Nat.* **188**, 205-218. doi:10.1086/687246

Lin, B. S. and Lin, Y. J. (2010). Cooling effect of shade trees with different characteristics in a subtropical urban park. *Hortscience* **45**, 83-86. doi:10.21273/HORTSCI.45.1.83

Luber, G. and McGeehin, M. (2008). Climate change and extreme heat events. *Am. J. Prev. Med.* **35**, 429-435. doi:10.1016/j.amepre.2008.08.021

Maclean, I. M., Duffy, J. P., Haesen, S., Govaert, S., De Frenne, P., Vanneste, T., Lenoir, J., Lembrechts, J. J., Rhodes, M. W. and Van Meerbeek, K. (2021). On the measurement of microclimate. *Methods Ecol. Evol.* **12**, 1397-1410. doi:10.1111/2041-210X.13627

Maia, A. S., Moura, G. A., Fonsêca, V. F. C., Gebremedhin, K. G., Milan, H. M., Chiquitelli Neto, M., Simão, B. R., Campanelli, V. P. C. and Pacheco, R. D. L. (2023). Economically sustainable shade design for feedlot cattle. *Front. Vet. Sci.* **10**, 1110671. doi:10.3389/fvets.2023.1110671

Marsh, A. C. (1985). Thermal responses and temperature tolerance in a diurnal desert ant, *Ocymyrmex barbiger*. *Physiol. Zool.* **58**, 629-636. doi:10.1086/physzool.58.6.30156067

Masson-Delmotte, V., Zhai, P., Pörtner, H. O., Roberts, D., Skea, J. and Shukla, P. R. (2022). *Global Warming of 1.5°C*. Cambridge University Press. https://doi.org/10.1017/9781009157940

Matthews, T., Byrne, M., Horton, R., Murphy, C., Pielke Sr, R., Raymond, C., Thorne, P. and Wilby, R. L. (2022). Latent heat must be visible in climate communications. *Wiley Interdiscip. Rev. Clim. Change* **13**, e779. doi:10.1002/wcc.779

McFarland, R., Barrett, L., Costello, M. A., Fuller, A., Hetem, R. S., Maloney, S. K., Mitchell, D. and Henzi, P. S. (2020). Keeping cool in the heat: Behavioral thermoregulation and body temperature patterns in wild vervet monkeys. *Am. J. Phys. Anthropol.* **171**, 407-418. doi:10.1002/ajpa.23962

Meyer, A. V., Sakairi, Y., Kearney, M. R. and Buckley, L. B. (2023). A guide and tools for selecting and accessing microclimate data for mechanistic niche modeling. *Ecosphere* **14**, e4506. doi:10.1002/ecs2.4506

Mitchell, D. (1974). Convective heat transfer from man and other animals. In *Heat Loss from Animals and Man* (ed. J. L. Monteith and L. E. Mount), pp. 59-76. London: Butterworths.

Mitchell, D. and Whillier, A. (1971). Cooling power of underground environments. *J. South. Afr. Inst. Min. Metall.* **72**, 93-99.

Mitchell, D., Snelling, E. P., Hetem, R. S., Maloney, S. K., Strauss, W. M. and Fuller, A. (2018). Revisiting concepts of thermal physiology: predicting responses of mammals to climate change. *J. Anim. Ecol.* **87**, 956-973. doi:10.1111/1365-2656.12818

Mole, M. A., Rodrigues D'Áraujo, S., Van Aarde, R. J., Mitchell, D. and Fuller, A. (2016). Coping with heat: behavioural and physiological responses of savanna elephants in their natural habitat. *Conserv. Physiol.* **4**, cow044. doi:10.1093/conphys/cow044

Mora, C., Dousset, B., Caldwell, I. R., Powell, F. E., Geronimo, R. C., Bielecki, C. R., Counsell, C. W., Dietrich, B. S., Johnston, E. T., Louis, L. V. et al. (2017). Global risk of deadly heat. *Nat. Clim. Change* **7**, 501-506.

Murray, I. W. and Smith, F. A. (2012). Estimating the influence of the thermal environment on activity patterns of the desert woodrat (*Neotoma lepida*) using temperature chronologies. *Can. J. Zool.* **90**, 1171-1180. doi:10.1139/z2012-084

Nakamura, R. and Mahrt, L. (2005). Air temperature measurement errors in naturally ventilated radiation shields. *J. Atmos. Ocean Technol.* **22**, 1046-1058. doi:10.1175/JTECH1762.1

Nakayoshi, M., Kanda, M., Shi, R. and de Dear, R. (2015). Outdoor thermal physiology along human pathways: a study using a wearable measurement system. *Int. J. Biometeorol.* **59**, 503-515. doi:10.1007/s00484-014-0864-y

Nikolopoulou, M., Baker, N. and Steemers, K. (1999). Improvements to the globe thermometer for outdoor use. *Archit. Sci. Rev.* **42**, 27-34. doi:10.1080/00038628.1999.9696845

Notley, S. R., Mitchell, D. and Taylor, N. A. S. (2023). A century of exercise physiology: concepts that ignited the study of human thermoregulation. Part 1: Foundational principles and theories of regulation. *Eur. J. Appl. Physiol.* **123**, 2379-2459. doi:10.1007/s00421-023-05272-7

Oliveira, A. V. M., Raimundo, A. M., Gaspar, A. R. and Quintela, D. A. (2019). Globe temperature and its measurement: requirements and limitations. *Ann. Work Expo. Health* **63**, 743-758. doi:10.1093/annweh/wxz042

Panagakis, P. (2011). Black-globe temperature effect on short-term heat stress of dairy ewes housed under hot weather conditions. *Small Rumin. Res.* **100**, 96-99. doi:10.1016/j.smallrumres.2011.06.006

Perkins-Kirkpatrick, S. E. and Lewis, S. C. (2020). Increasing trends in regional heatwaves. *Nat. Commun.* **11**, 3357. doi:10.1038/s41467-020-16970-7

Pezzopane, J. R. M., Nicodemo, M. L. F., Bosi, C., Garcia, A. R. and Lulu, J. (2019). Animal thermal comfort indexes in silvopastoral systems with different tree arrangements. *J. Therm. Biol.* **79**, 103-111. doi:10.1016/j.jtherbio.2018.12.015

Pincebourde, S., Murdock, C. C., Vickers, M. and Sears, M. W. (2016). Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments. *Integr. Comp. Biol.* **56**, 45-61. doi:10.1093/icb/icw016

Rahimi, J., Mutua, J. Y., Notenbaert, A. M., Marshall, K. and Butterbach-Bahl, K. (2021). Heat stress will detrimentally impact future livestock production in East Africa. *Nat. Food* **2**, 88-96. doi:10.1038/s43016-021-00226-8

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T. and Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Commun. Earth Environ.* **3**, 168. doi:10.1038/s43247-022-00498-3

Santos, S. G. C. G. D., Saraiva, E. P., Pimenta Filho, E. C., Gonzaga Neto, S., Fonsêca, V. F. C., Pinheiro, A. D. C., Almeida, M. E. V. and de Amorim, M. L. C. M. (2017). The use of simple physiological and environmental measures to estimate the latent heat transfer in crossbred Holstein cows. *Int. J. Biometeorol.* **61**, 217-225. doi:10.1007/s00484-016-1204-1

Seely, M. K., Mitchell, D. and Goelst, K. (1990). Boundary layer microclimate and *Angolosaurus skoogi* (Sauria: Cordylidae) activity on a northern Namib dune. In *Namib Ecology: 25 Years of Namib Research* (ed. M. K. Seely). Transvaal Museum Monograph No.7. pp. 155-162. Pretoria, South Africa: Transvaal Museum.

Sepulveda, M., Sabat, P., Porter, W. P. and Fariña, J. M. (2014). One solution for two challenges: The lizard *Microlophus atacamensis* avoids overheating by foraging in intertidal shores. *PLoS One* **9**, e97735. doi:10.1371/journal.pone.0097735

Simpson, I. R., McKinnon, K. A., Kennedy, D., Lawrence, D. M., Lehner, F. and Seager, R. (2024). Observed humidity trends in dry regions contradict climate models. *Proc. Natl. Acad. Sci. U.S.A* **121**, e2302480120. doi:10.1073/pnas.2302480120

Swinbank, W. C. (1963). Long–wave radiation from clear skies. *Q. J. R. Meteorol. Soc.* **89**, 339-348. doi:10.1002/qj.49708938105

Teitelbaum, E., Chen, K. W., Meggers, F., Guo, H., Houchois, N., Pantelic, J. and Rysanek, A. (2020). Globe thermometer free convection error potentials. *Sci. Rep.* **10**, 2652. doi:10.1038/s41598-020-59441-1

Teitelbaum, E., Alsaad, H., Aviv, D., Kim, A., Völker, C., Meggers, F. and Pantelic, J. (2022). Addressing a systematic error correcting for free and mixed convection when measuring mean radiant temperature with globe thermometers. *Sci. Rep.* **12**, 6473. doi:10.1038/s41598-022-10172-5

Teixeira, B. E., Nascimento, S. T., do Nascimento Mós, J. V., De Oliveira, E. M., Dos Santos, V. M., Maia, A. S. C., Fonsêca, V. d. F. C., Passos, B. M. and Murata, L. S. (2022). The potential of natural shade provided by Brazilian savanna trees for thermal comfort and carbon sink. *Sci. Total Environ.* **845**, 157324. doi:10.1016/j.scitotenv.2022.157324

Thompson, V., Mitchell, D., Hegerl, G. C., Collins, M., Leach, N. J. and Slingo, J. M. (2023). The most at-risk regions in the world for high-impact heatwaves. *Nat. Commun* **14**, 2152. doi:10.1038/s41467-023-37554-1

Thorsson, S., Lindberg, F., Eliasson, I. and Holmer, B. (2007). Different methods for estimating the mean radiant temperature in an outdoor urban setting. *Int. J. Climatol.* **27**, 1983-1993. doi:10.1002/joc.1537

Tillman, F. E., Bakken, G. S. and O'Keefe, J. M. (2021). Design modifications affect bat box temperatures and suitability as maternity habitat. *Ecol. Solut. Evid.* **2**, e12112. doi:10.1002/2688-8319.12112

Trenberth, K. E. (2011). Changes in precipitation with climate change. *Clim. Res.* **47**, 123-138. doi:10.3354/cr00953

Trenberth, K. E., Dai, A., Rasmussen, R. M. and Parsons, D. B. (2003). The changing character of precipitation. *Bull. Am. Meteorol. Soc.* **84**, 1205-1218. doi:10.1175/BAMS-84-9-1205

Tucker, C. B., Rogers, A. R. and Schütz, K. E. (2008). Effect of solar radiation on dairy cattle behaviour, use of shade and body temperature in a pasture-based system. *Appl. Anim. Behav. Sci.* **109**, 141–154. doi:10.1016/j.applanim.2007.03.015

Van Jaarsveld, B., Bennett, N. C., Czenze, Z. J., Kemp, R., Van de Ven, T. M., Cunningham, S. J. and McKechnie, A. E. (2021). How hornbills handle heat: sex-specific thermoregulation in the southern yellow-billed hornbill. *J. Exp. Biol.* **224**, jeb232777. doi:10.1242/jeb.232777

Vanos, J. K., Rykaczewski, K., Middel, A., Vecellio, D. J., Brown, R. D. and Gillespie, T. J. (2021). Improved methods for estimating mean radiant temperature in hot and sunny outdoor settings. *Int. J. Biometeorol.* **65**, 967-983. doi:10.1007/s00484-021-02131-y

Varner, J. and Dearing, M. D. (2014). The importance of biologically relevant microclimates in habitat suitability assessments. *PLoS One* **9**, e104648. doi:10.1371/journal.pone.0104648

Valtorta, S. E., Leva, P. E. and Gallardo, M. R. (1997). Evaluation of different shades to improve dairy cattle well-being in Argentina. *Int. J. Biometeorol.* **41**, 65-67. doi:10.1007/s004840050055

Vega, F. A. O., Ríos, A. P. M., Saraz, J. A. O., Quiroz, L. G. V. and Damasceno, F. A. (2020). Assessment of black globe thermometers employing various sensors and alternative materials. *Agric. For. Meteorol.* **284**, 107891. doi:10.1016/j.agrformet.2019.107891

Vernon, H. M. (1932). The globe thermometer. *Proc. Inst. Heat. Vent. Eng.* **39**, 100-104.

Vitt, L. J. and Sartorius, S. S. (1999). HOBOs, Tidbits and lizard models: the utility of electronic devices in field studies of ectotherm thermoregulation. *Funct. Ecol.* **13**, 670-674. doi:10.1046/j.1365-2435.1999.00357.x

Yaglou, C. P. and Minard, C. D. (1957). Control of heat casualties at military training. *AMA Arch. Ind. Hyg. Occup. Med.* **16**, 304-314.

Walsberg, G. E. and Weathers, W. W. (1986). A simple technique for estimating operative environmental temperature. *J. Therm. Biol.* **11**, 67-72. doi:10.1016/0306-4565(86)90020-3

Wolf, B. O. and Walsberg, G. E. (1996). Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology* **77**, 2228-2236. doi:10.2307/2265716