

Effects of different heat and light sources on the behaviour of captive reptiles

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ABSTRACT – Reptiles are sensitive to electromagnetic radiation at wavelengths between the ultra-violet and infrared bands. Husbandry practitioners designing artificial lighting arrays should aim to provide spectra that approximate those to which a given species has become adapted in nature. This would satisfy biological needs ranging from thermoregulation and vitamin D₃ photobiosynthesis to vision and communication. We evaluated the spectral outputs of two artificial lighting arrays (A & B) in their ability to provide this. Array A was designed to replicate those used as standard over the last decade in many controlled environments, while the Array B was intended to provide a more solar-like output. We measured behaviour and calculated a modified Spread of Participation Index (mSPI) for three species of reptile (turtle, lizard and snake) as the arrays were alternated in an A-B-A design (in observation periods 1, 2 and 3). Data were analysed using randomisation to deal with small sample size and repeated measures. Although in theory Array B provided a better spectrum than Array A, there were no clear patterns where behaviour and mSPI shifted going from Array A to B then reverted when going from Array B to A. However, the lizard and turtle both showed unexplained behavioural shifts, and the lizard an associated mSPI shift, when going from Array B to A. Our results demonstrate the power of combination lighting arrays to better approximate solar spectra, but also that behavioural observations may not reflect theoretical implications. We suggest reasons for this and directions for future research.

INTRODUCTION

Reptiles kept under controlled environmental conditions, such as in zoos and private collections, are typically maintained using artificial heating and lighting as they are held outside of their natural habitats but are dependent on conditions found therein (Baines et al., 2016). Being ectotherms, reptiles are particularly sensitive to the electromagnetic spectrum, and especially wavelengths from and between ultra-violet B (UVB) and infrared C, to which they are exposed. Under controlled conditions, current herpetocultural thinking holds that artificial lighting should replicate the solar spectra to which a species is exposed in the wild (Silvestre, 2014). Benefits of this may include, inter alia, the ability to reach and maintain a suitable body temperature (Tosini & Avery, 1996), to maintain metabolic processes such as vitamin D₃ photobiosynthesis (Baines et al., 2016), as well as appropriate vision and circadian rhythms. Vision is, in many species, sensitive to light outside the spectrum visible to humans (Vergneau-Grosset & Péron, 2020).

Thermo- and photo-sensitive behaviours are intrinsically coupled such that the two often occur in tandem. That is, the exposure to different intensities of light via behavioural means often dictates, to a large extent, the body temperature of an ectothermic animal. During the day, warmth and brightness are frequently correlated so that in nature direct sunlight is the primary creator of basking zones. Thermoregulation can be achieved via behavioural or physiological means (Seebacher & Franklin, 2005; Tattersall

et al., 2006). Moreover, all solar wavelengths are important for warming tissues, although some more so than others (Barolet et al., 2016). In many diurnally active reptile species this is often most clearly exhibited by basking in direct sunlight to increase body temperature or retreating to cooler or less intensely irradiated microhabitats to decrease body temperature (Carrière et al., 2008), as well as retreating to dark areas for sleep or rest.

Wavelengths of light of 780–4,000 nm are in the infrared spectrum and occur naturally in sunlight. Infrared-A (IR-A), from 780–1,400 nm, is relatively short wavelength radiation that provides a larger amount of energy when absorbed compared to longer wavelengths of infrared. Along with visible light, it is the primary source of energy for basking species. Red light and IR-A radiation are transmitted through the skin and directly into the deeper subcutaneous tissues, giving more rapid bodily warming than solarinfrared-B (IR-B) (Barolet et al., 2016). The epidermis is heated most intensely by visible light and IR-B radiation, with 60–70 % of incident sunlight being absorbed at this level, compared to 10–20 % for the underlying muscle (Porter, 1967). With these wavelengths, much of the inner heating of the deeper tissues occurs through conduction of heat from the skin. Lower energy wavelengths, in the infrared-C (IR-C) (3–1,000 µm) range, which are not components of natural sunlight, are less able to penetrate the core of objects but do constitute a relevant source of heat as they are naturally radiated from the surface of sun-warmed objects in the environment. Warmed objects may also transmit heat energy by conduction

(Thomas et al., 2019), which enables thigmothermic species to warm themselves by direct contact with objects that are warmer than themselves (Garrick, 2008).

Radiation at wavelengths of 380–780 nm are classed as human-visible light (Kasajima, 2019), however biologically relevant wavelengths of light are not confined within this range. The time a lizard spends basking has been shown to depend on the wavelengths supplied, with basking duration increasing when wavelengths <540 nm are removed (Tosini & Avery, 1996). It is possible that all wavelengths from ultraviolet to infrared may be important to any given reptile species, and specific requirements may be linked to activity patterns and microhabitat preferences.

In the case of UV radiation, terrestrial wavelengths of UVB range approximately 290–320 nm, while UVA wavelengths are somewhat longer at 320–400 nm (Baines et al., 2016). Of the terrestrial UV wavelengths, those in the shorter ranges are more closely associated with vitamin D₃ synthesis in the skin (Lindgren et al., 2008). Furthermore, important physiological feedback mechanisms require in addition short wavelength UVA ranging from 320–335 nm. A review of the relevance of UV light to reptiles is provided by Baines et al. (2016). UVA, from around 350 nm, and visible light are important for most reptile species to enable visual processing of information, vital for essential intra-specific communication and identification of food items (Govardovskii & Zueva, 1974; Honkavaara et al., 2002; Fleishman et al., 2011). In recent years an increasing number of species have been shown to utilise markings visible in the UV spectrum, with most hypotheses for function favouring selective communication (Prötzel et al., 2018; Thompson et al., 2019; Badiane & Font, 2021; Mendyk, 2021).

A wide array of potential heating and lighting technologies are available commercially and each is associated with different emission spectra, none of which in isolation resembles the spectrum of natural sunlight. Available technologies include mercury vapour (MV), fluorescent, incandescent, light-emitting diode (LED), and metal halide lamps (MH), designed specifically for reptile husbandry and/or adapted from domestic or industrial use. All these technologies have often radically different output spectra.

Self-ballasted MV lamps have traditionally been used to provide basking zones for reptiles in controlled conditions (Baines et al., 2016; Thomas et al., 2019). These lamps emit a mixture of UVA and UVB as well as visible light and IR-A and -B. Fluorescent T5 tubes are also commonly used to provide UV as well as a relatively small amount of visible light. However, most of their visible light is distributed between discontinuous peaks rather than over a continuous and broad range, as is found in unfiltered sunlight (Baines et al., 2016). Therefore, these lamps alone cannot be relied upon to provide light similar to unfiltered sunlight. Incandescent lamps, which include halogen lamps, emit predominantly short-wavelength infrared (IR-A) with a very small proportion of UVA, moderate levels of visible light (predominantly red) and some IR-B and IR-C, in a continuous spectrum (MacIsaac et al., 1999). These are therefore well-suited as basking lamps but are lacking in UV and provide only low intensity visible light. LED lamps, which are typically designed to emit

light that appears white to humans, currently provide no safe UV or infrared but can provide a broad spectrum of high illuminance in the human-visible range. Metal halide lamps (unless of the type designed for use with reptiles) produce no significant UVB but do often produce moderate UVA and visible light distributed continuously up to around 750 nm. Details of the spectra of specific lamps are often available for download from the manufacturers' websites and may be of particular interest to herpetoculturalists.

Combining different lighting technologies in composite lighting arrays is being increasingly considered best practice for reptile husbandry (Griffiths & Kane, pers. obs.). These composite arrays can provide overlapping spectra that better replicate natural sunlight. Each lighting component is chosen to complement the spectra of the others to provide wavelengths across as much of the spectrum of natural sunlight as practical, providing increased physiological and behavioural potential for reptiles. However, little peer-reviewed published evidence exists to demonstrate the efficacy of combining lighting arrays to replicate solar spectra.

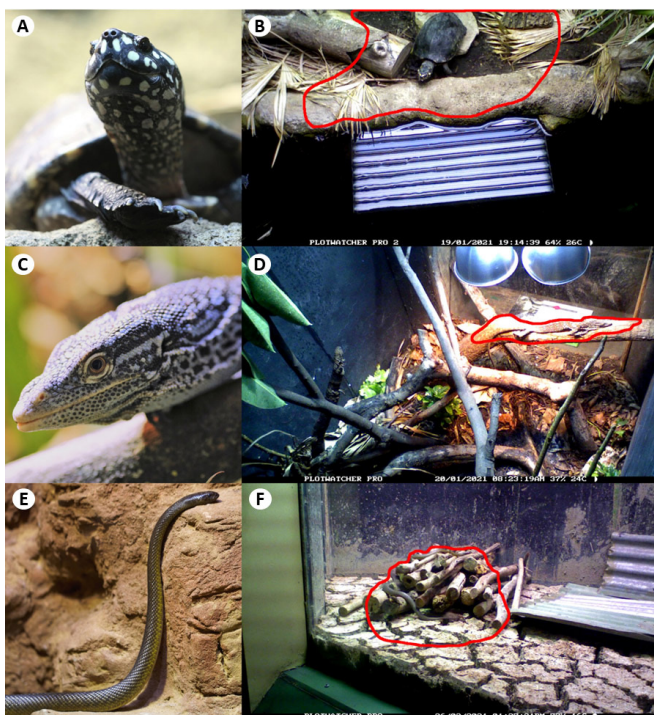
It is important to underpin husbandry practice with evidence, but there have been only a few studies looking at the impact of theoretical best practice on reptiles in captivity (Ferguson et al., 2010; Schmidt et al., 2010; Ferguson et al., 2021). Without evidence, heating and lighting strategies risk falling into the compass of 'folklore husbandry' (Arbuckle, 2013). Physiological evidence (Ferguson et al., 2010; 2021) may provide insight into the impact of lighting strategies on specific biological processes, such as vitamin D₃ production, but is not available for the majority of captive collections of reptiles, and for most taxa. Behavioural observations are readily collected and may provide a broad brush insight into the impact of lighting strategies, and therefore can be more easily applied to a range of species. In the present work we seek to assess the efficacy of two different lighting arrays at replicating a solar spectrum and to evaluate any behavioural effects these arrays may have on three phylogenetically and ecologically disparate reptile species. Our experimental hypothesis was that there would be observable changes in reptile behaviour when a heating/lighting array providing a relatively poor sunlight spectrum was switched to an array with better sunlight replication and vice versa.

MATERIALS & METHODS

Data were collected from January to April 2021 during which time London Zoo, a ZSL conservation zoo, was closed to the public due to the COVID-19 pandemic. An ethical review of the project was deemed unnecessary since it fell within the normal bounds of husbandry and the project was approved on this basis (internally registered as ZDZ149). Data were collected and recorded on an ethogram, adapted from Thomas et al. (2019) and provided in Table 1. Observations were made on three species of reptiles from three separate suborders: a spotted turtle *Geoclemys hamiltonii* (Testudines; Cryptodira), a blue tree monitor *Varanus macraei* (Squamata: Anguimorpha) and a pair of inland taipans *Oxyuranus microlepidotus* (Squamata: Serpentes) (Fig. 1A, C & E). These species were chosen as they can all be

Table 1. Ethogram of categorised behaviours and areas of the enclosures used in the present study

	Behaviour/Activity	Definition
Behavioural state	Locomotion	Animal moving anywhere within the field of view
	Basking	Animal stationary in the bask zone
	Resting	Animal stationary outside the bask zone
	Out of sight	Animal not visible in field of view
Area of enclosure	Basking site	Area of highest temperature and UVI, directly beneath bask lamps
	Elevated wall/branches	Area of enclosure above the floor, created by branches or vertical walls
	Floor	Terrestrial ground area of enclosure
	Out of sight	The area outside the field of view of the camera(s)

**Figure 1.** Portraits of the focal species and their enclosures - **A. & B.** *Geoclemys hamiltonii*, **C. & D.** *Varanus macraei*, **E. & F.** *Oxyuranus microlepidotus*. Basking zones for each enclosure are outlined in red.

generally categorised as diurnal species which, in captivity, seek out basking zones in order to thermoregulate and are known to be active throughout the year. This allowed for a representative view across phylogenetically distant taxa to investigate the effect different heating and lighting has on each species' behaviour.

We compared two primary lighting arrays (A & B) for the three species. Lighting Array A represented current standard practice in many reptile keeping institutions (e.g. Harding et al., 2017; Kane et al., 2021) while Array B represented a lighting approach aimed at better sunlight replication. The lighting arrays varied between species in the nature of the lamps used (Supplementary material Table S1) but in principle lighting Array A was self-ballasted MV lamps combined with T5-HO UVB fluorescent lamps, while Array B was incandescent lamps combined with T5-HO UVB fluorescent

lamps and metal halide lamps. Spectrographs showing the different spectral qualities of these lighting arrays are shown in Figure 2. The lighting arrays were designed, as far as possible, to maintain identical surface and air temperatures and UV index (UVI) provision as well as thermoregulatory resource areas (basking zones) across treatments (see Table S1 in Supplementary material). Basking zone surface temperatures were measured with a non-contact infrared thermometer (GM320; Zanmax, USA) and UVI was measured with a Solarmeter 6.5 (Solar Light Company, LLC., USA).

The two lighting arrays (A & B) were applied alternately in an A-B-A design, each with a 10-day observation period, termed observation period 1, 2 and 3. In almost all cases, MV lamps and incandescent lamps were exchanged within the same fittings so that the position of the devices did not change. T5-HO lighting units also remained unmoved and metal halide lamps were installed prior to the study, but not turned on until observation period 2 of the study.

Spectrograms (Fig. 2) were obtained from individual enclosures under lighting Arrays A and B for each species using an Ocean Optics USB2000 + spectral radiometer with a UVB-compatible fibre-optic probe with cosine adaptor and a FLAME UV-Vis spectral radiometer with a UVB-compatible fibre-optic probe with cosine adaptor (both Ocean Optics, Inc., Dunedin, Florida USA). Recordings of the arrays were taken in-situ with the fibre-optic probe perpendicular to the axis of the lamp at the approximate height of the different species whilst basking.

To record reptile behaviour, time-lapse video cameras (Plotwatcher Pro, Day6 Outdoors, USA) were placed in, but out of reach, or outside of each enclosure to have as full a view as was practical of the inside of each enclosure. Cameras were set to take a photograph every 30 seconds, but recording in a video format, during pre-set observation windows of 09:30–10:00 h, 13:00–13:30 h and 17:30–18:00 h. These observation windows were designed to capture diel behavioural changes, as reptiles usually display predictable changes in behaviour across the day (Tosini et al., 2001). Cameras were light activated so that when natural light penetrated the enclosures and enclosure lighting turned on, cameras automatically began recording. Natural light was always indirect and diffuse, though actual levels were not measured and likely some difference existed between

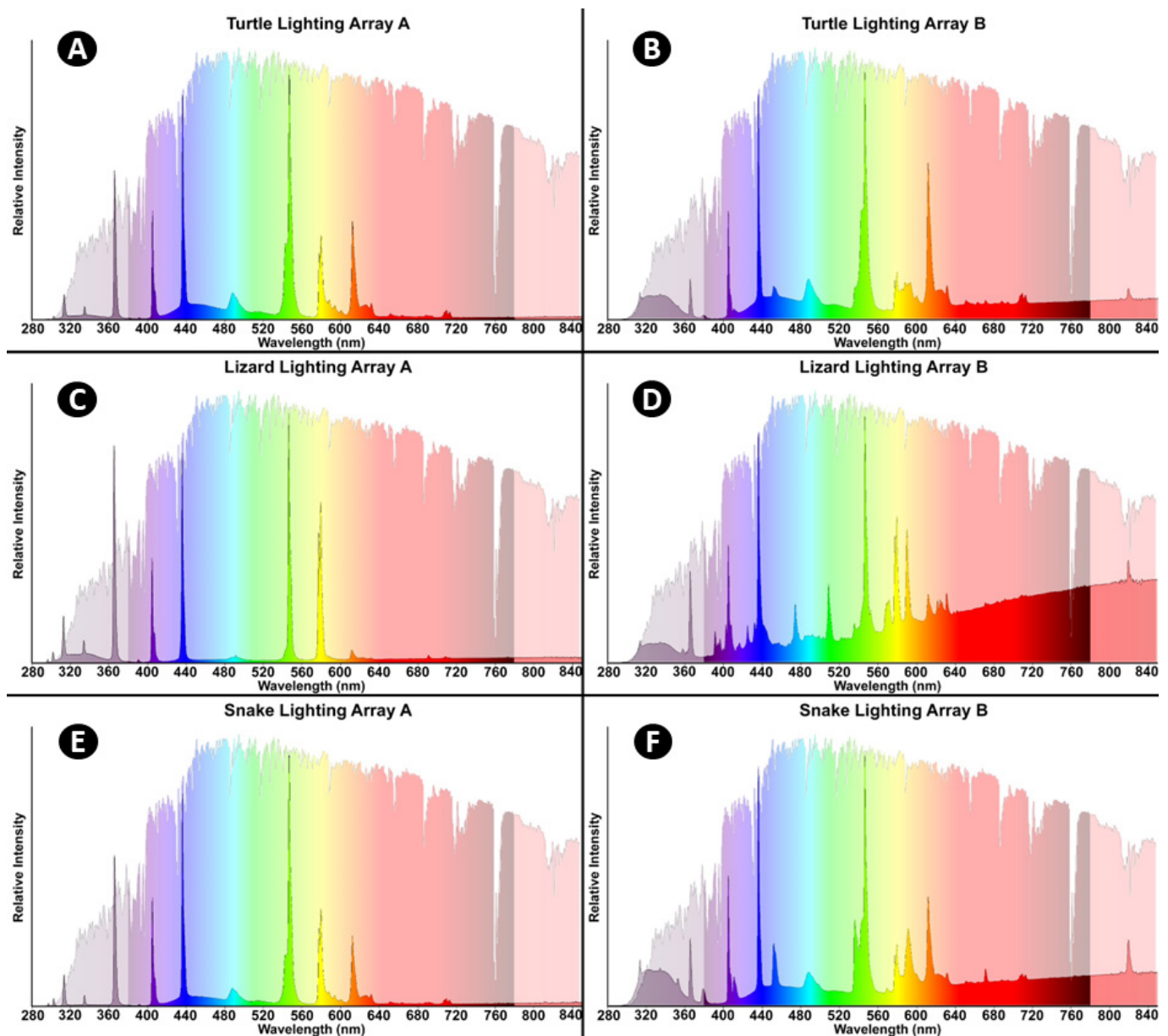


Figure 2. Spectral measurements of lighting arrays over basking areas during observation period 1 (lighting Array A) and observation period 2 (lighting Array B, intended to be a better simulation of the solar spectrum), for **A. & B.** the turtle, **C. & D.** the lizard and **E. & F.** the snakes. The solar spectrum ASTM standard provides a useful point of reference when visually evaluating the wavelengths generated by each lighting array. Relative intensity is presented with no units to aid visibility of the peak wavelengths of the corresponding lighting array used in this study, though all lamps show equal relative intensity on the scale. The spectral plot of the lighting array and the solar spectrum ASTM standard (ISO 98451) are not to scale.

enclosures. Cameras were installed one day prior to data collection to allow the reptiles to habituate to their presence, and the following ten days of footage was recorded for each of the three observation periods. Ten days was viewed as an acceptable time period to capture relevant behaviours while not extending data collection across a large amount of environmental change, which could influence results. This yielded a total of thirty days of data per species. Media files were analysed in GameFinder Module software (V.1.7.2, Day6 Outdoors, USA) as this software is able to display the file in a time-lapse video format. Each reptile enclosure was divided into functional resource areas following Thomas et al. (2019) and Plowman (2003), allowing different behaviours, such as basking and resting, to be effectively defined and

recorded (Fig. 1B; 1D; 1F). Functional resource areas for all three species included a basking zone. In addition, for the lizard, non-basking zone (arboreal) and non-basking zone (terrestrial); for the snake, non-basking zone (terrestrial); and for the turtle, non-basking zone (terrestrial) and water. Only those observation windows when the reptile(s) were within the field of view of the cameras were included in analysis; this affected only the snakes, as the turtle and lizard were always visible for at least part of each observation period.

Reptiles were recorded as occupying a given resource when the largest proportion of their body was contained within that resource. If the reptile's body appeared to be positioned equally between multiple resources, then the resource that included the reptile's head was recorded; if the

Table 2. Results of primary one-way ANOVA-like randomisation analyses. Significant results (Bonferroni-adjusted P values) are indicated in bold

Species	Analysis	Bonferroni-adjusted P value			
		mSPI	Locomotion	Basking	Resting
Turtle	Primary (one-tailed)	0.057	0.021	0.019	>0.999
	Post hoc (two-tailed)	N/A	1 vs 2: 0.391 2 vs 3: 0.001 1 vs 3: 0.001	1 vs 2: 0.958 2 vs 3: 0.006 1 vs 3: 0.248	N/A
Lizard	Primary (one-tailed)	0.016	0.038	0.028	>0.999
	Post hoc (two-tailed)	1 vs 2: >0.999 2 vs 3: 0.054 1 vs 3: 0.007	1 vs 2: >0.999 2 vs 3: 0.036 1 vs 3: 0.688	1 vs 2: >0.999 2 vs 3: 0.002 1 vs 3: 0.002	N/A
Snake	Primary (one-tailed)	>0.999	0.065	>0.999	0.076
	Post hoc (two-tailed)	N/A	N/A	N/A	N/A

reptile was in line with the boundary between two opposing resources and equally occupied both, then the resource to the right of the reptile's head, from the perspective of the animal, was chosen. In almost every instance a resource zone occupied could be confidently assigned. Data were entered into Microsoft Excel for 365 (version 2111) and 10 % of the time lapse video footage spread across all three species was re-scored, and Spearman's rank correlation coefficients were used to assess reliability of observations.

The modified Spread of Participation Index (mSPI - Plowman, 2003) is an index derived from the proportions of time an animal spends in each resource-based zone of its enclosure. The index varies between 0 (even enclosure use, all zones used equally) and 1 (completely uneven use, only one zone used). This is a simple descriptor of how evenly the available space is used by a captive animal. Even enclosure usage is often sought-after, but ultimately interpretation is dependent on the specific context, especially with regards to the intended use of resource zones, and animals' behaviour and ecology (Plowman, 2003). We analysed behavioural counts and standardised for time spent in view by dividing counts of locomotion, basking and resting behaviour by the sum of counts of those three behaviours. mSPI was calculated using only in-view observations with a reasonable assumption that out of sight (OOS) reptiles could be in any part of the resource zones not in the field of view.

Data from individuals represent repeated measures, this violates assumptions around independence of the observations so that standard parametric and non-parametric analysis techniques were not appropriate. Although Generalised Linear Mixed Models (GLMMs) could have accounted for Poisson distributed behavioural count data, they could not control for repeated measures as with only three repeated units (species) showing different overall patterns, random effects could not be reliably estimated (Oberpriller et al., 2021). The most appropriate analytical approach was to use randomisation analysis, which makes no assumptions of independence or data distribution as it relies on internally generated probability distributions (Dugard et al., 2012). Initial analyses represented randomisation

equivalents of one-way ANOVAs. Using the mosaic package (Pruim et al., 2017), experimental observation period labels (1, 2 and 3) associated with each data point were shuffled in order to randomly assign each observation to an experimental observation period. An F-statistic, which summarises the ratio of variation between and within groups, was then calculated for the shuffled data comparing the now randomised observation period labels to define groups, using the ANOVA function of the stats package (R Core Team, 2022). This was repeated for 9,999 replicates and used to create a null distribution, i.e. the distribution of F-statistics expected if the data were random rather than influenced by experimental observation period. The true observed F-statistic was then calculated from original data (making the 10,000th observation in the sample) and compared with the null distribution to calculate a p-value. (see Dugard et al. (2012) for further details). This process was conducted for each species and for each behaviour; Bonferroni corrections were applied to the resulting p values to correct for multiple comparisons. For species-behaviour combinations that yielded a significant corrected p-value, we then conducted post-hoc pair-wise randomisation comparisons with the same method, but using the difference between treatment means as the test statistic instead of an F ratio, which is appropriate when only two groups are compared (Dugard et al., 2012); these comparisons were also subject to Bonferroni corrections. All analyses were performed using R version 4.2.0 in RStudio 2022.02.02.

RESULTS

Spectrograms were taken of the basking zones in each enclosure (Fig. 1) under lighting array A. Discrete peaks of irradiance were emitted by lighting array A in all three enclosures, and are visible in the spectrographs (Figs. 2A, C & E) whereas the use of lighting array B provided more continuous spectra (Figs. 2B, D & F). The relatively high intensity of continuously distributed light shown in the lizard enclosure under lighting array B (Fig. 2D) is likely due to the physically close positioning of the two incandescent

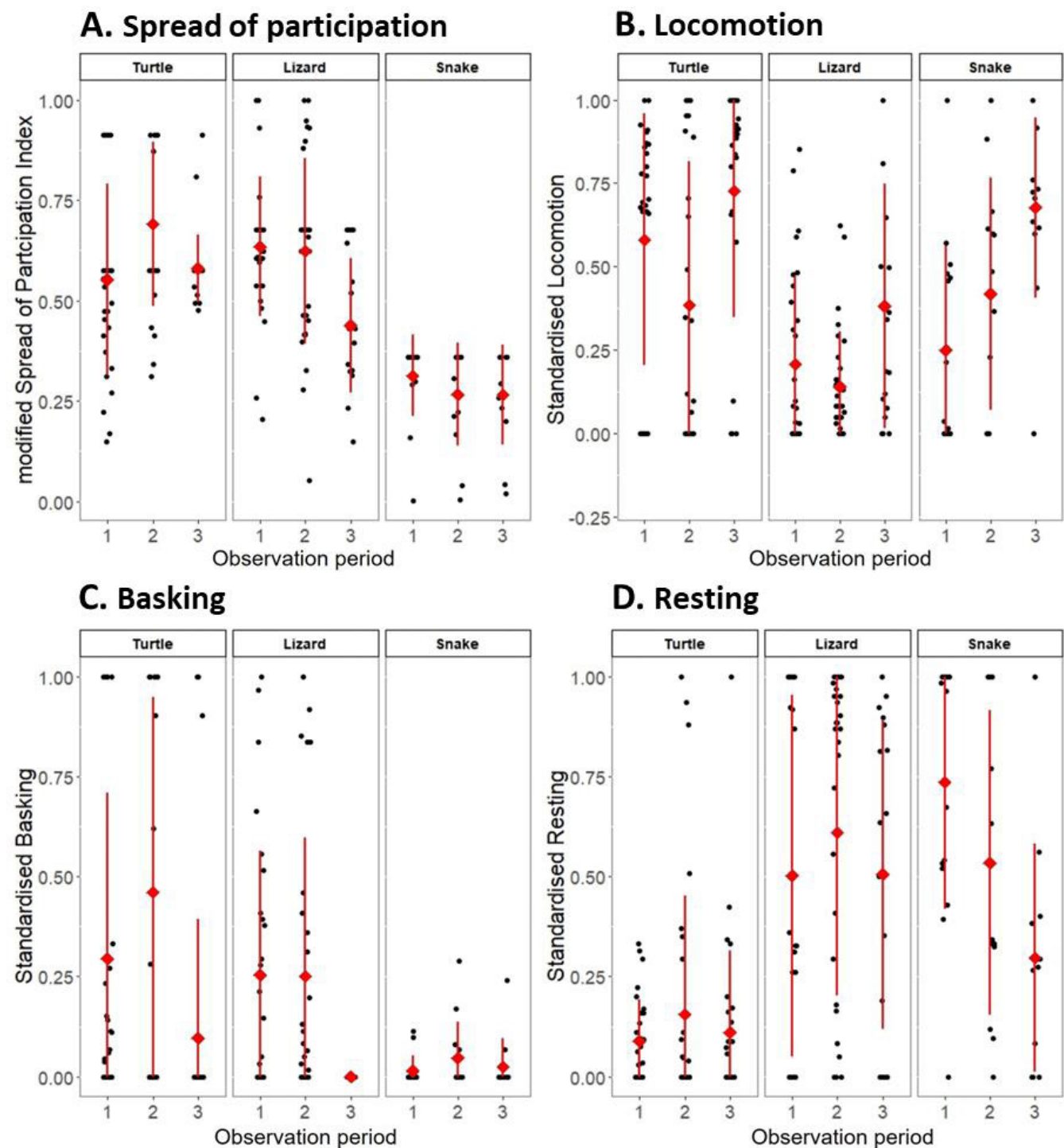


Figure 3. Behavioural responses of the three focal reptile species across three observation periods 1–3. Standardised square root counts of – **A.** modified Spread of Participation Index, **B.** Locomotion, **C.** Basking and **D.** Resting. Black points represent actual data, red diamonds indicate means and red bars show standard deviations.

lamps to the basking zone. This resulted in a relatively larger proportion of the light emitted by these lamps being recorded by the spectrometer compared to that emitted by lighting array B in the other enclosures, where they were positioned physically more distant from the basking zones. Spearman's rank correlation coefficients were greater than 0.9 for all four response variables comparing original and re-scored data, indicating good reliability in data collection.

For the turtle, analyses detected significant effects of observation period on locomotion and basking behaviour, for the lizard significant effects on mSPI, locomotion and basking behaviour, but for the snakes there were no significant effects of observation period on any of the four parameters (Table 2, Fig. 3A–D). Post-hoc pairwise tests for both the turtle and the lizard demonstrated a significant increase in the proportion of time spent in locomotion, and a

significant decrease in the proportion of time spent basking. A significant decrease in mSPI (i.e. more even enclosure usage) was observed in the lizard, during observation period 3 (Table 2). Mean and standard deviation values are presented in Supplementary material Table S2.

DISCUSSION

The enhanced lighting (Array B) achieved the aim of improving spectral coverage and intensity of represented wavelengths across more of the solar spectrum, with associated increased brightness. However, as demonstrated in Fig. 2, these wavelengths were not fully representative of those found in unfiltered sunlight expected in the natural range of the focal reptile species. Array B did provide a measured improvement over Array A, but there is a need for more technological development if relative amounts of the wavelengths found in natural, unfiltered, sunlight are to be better replicated. The addition of full spectrum LED lights could help achieve this, as well as raise the overall brightness of enclosures. We encourage future work to incorporate this principle, as well as encourage more field study of the light environment in the natural habitat of these three species and other captive species of interest. While no two solar spectra will be identical, in general, far more continuous provision of light when compared to artificial lighting arrays is expected. Due to equipment shortage there was an unavoidable decrease in measured basking zone UVB under the lizard Array B lighting (Supplementary material Table S1) however the overall spectrum still showed fuller coverage of key wavelengths compared to Array A (Fig. 2C & D).

Our results show that the turtle and the lizard spent a greater proportion of visible time in locomotion during the third observation period at the expense of basking behaviour (Fig. 3B & C). For the lizard this was associated with more even use of the enclosures (Fig. 3A).

Our experimental hypothesis was that a change in behaviour may be induced by the more complete solar-like spectrum of lighting Array B compared with Array A. The interpretation of behavioural changes in response to lighting changes is challenging, due to the complex interactions of physiology, physics, social and species-specific behaviour, as well as external factors. At least theoretically, each species should be able to reach an optimal core body temperature more quickly when exposed to lighting Array B. This is due to the shorter wavelengths of light more effectively heating the reptiles' core, thus increasing time available for non-basking behaviours. Alternatively, attraction to basking sites with richer spectra might cause an increase in basking behaviour. In previous work, reduced spectra in a basking zone, containing only wavelengths > 480 nm, was shown to increase basking duration and lower heating rate of lizards (Tosini & Avery, 1996). Additionally, research on captive *V. macraei*, including the individual in the present work, showed that lighting arrays with a greater reliance on infrared B radiation also affected the durations of basking and other behaviours (Thomas et al., 2019). In the present study, our results were unexpected; with no changes in mSPI when going from array A to array B for all three species.

However, changes were noticed when going from array B to array A for the turtle and lizard, with no changes at all for the snakes. This is hard to interpret and highlights the difficulty of using behaviour to evaluate artificial lighting arrays for reptiles.

The snakes present the simplest data for interpretation as no behavioural effects were detected across the experiment. Correcting for the higher proportion of observations that were spent out of sight, the overall proportion of visible time spent basking showed that the snakes spent less of their visible time basking than did the other two species. Being observed to be more cryptic than the other two species, for thermoregulation the snakes may have relied more on conducted rather than on radiated heat, or had preferred body temperatures closer to the ambient temperature than did the turtle or the lizard and so were less sensitive to the quality of the basking lamps. Additionally, the snakes were housed together whereas the turtle and lizard were housed individually, so it is possible that social interactions may have influenced the observed behaviours.

For both the turtle and the lizard, reductions of time spent engaged in basking behaviour were detected on return to Array A with corresponding increases in locomotion. This pattern does not fit that expected under either our null (no difference) or alternative hypothesis (B is better than A) and is difficult to explain. Also, we are unable to determine whether changes in locomotion are a result of changes in basking behaviour, or vice versa. The reduction in basking and increase in locomotion is particularly striking for the lizard and is suggestive of an unidentified process also influencing behaviour. By collecting data from the same three time periods and restricting data collection to one season, the timing and experimental design controlled for, as far as was feasible, external disturbance (as in Carter et al., 2021), and seasonal and diel changes in thermobiology (Secor & Nagy, 1994; Díaz & Cabezas-Díaz, 2004; Arribas, 2010; Millar et al., 2012; Zamora-Camacho et al., 2013; Amadi et al., 2020) but other potential uncontrollable changes intrinsic or extrinsic to individual reptiles are diverse. For example, social behavioural effects were not controlled for and there is no literature available assessing the relative impact of social compared to solitary behaviour for the focal reptile species. Therefore, given that we do not understand the drivers behind the pattern of behavioural changes observed, it is difficult, too, to interpret the change in mSPI seen in the lizard. Although usually used to imply better welfare (Michaels et al., 2020), in this case mSPI changes were likely driven by the same forces that drove increased locomotion and should probably not be used to infer better welfare.

The phylogenetic and ecological differences between our chosen study species, along with the desire to collect data that were comparable between species, meant that the ethogram used to record data may not have been fine scale enough to capture all behaviours relevant to each species. For example, the blue tree monitor spent much time climbing whereas the turtle did not. However, the turtle did spend much time swimming whereas the snakes spent much time beneath cover. It may also be expected

that, for example, reptiles which spend much time in trees would have a higher daily exposure to light than would a reptile which spends much time below ground. Intrinsic behavioural differences such as these may present an unavoidable bias during data collection. This is because the amount of time spent in each resource zone, due to factors not experimentally manipulated, may differ due to certain life history traits. By generalising, for example, any movement as 'activity' we were not able to differentiate between locomotory behaviours as different as climbing, swimming, mating or feeding. Future more focused data collection with a greater sample size containing more closely related species would likely reveal any such more subtle effects. Additionally, there was a potential bias towards the basking zones as the cameras were set up so that 100 % of this zone was in view, at the expense of other zones. In reality, this bias existed across all treatments so should not be a dramatically limiting factor, though there may have been a slight, unavoidable, inflation of the proportion of time spent basking. This is because the data analysed was the proportion of visible time spent performing the behaviours, and as all of the bask zone for each species was in the field of view, this behaviour could not have occurred out of view, whereas other behaviours could have.

Overall, our data demonstrate that incorporation of a wider range of different light sources in lighting arrays allows an improvement in the ability to replicate expected solar spectra under artificial conditions and highlights the importance of multi-parameter assessment of lighting arrays, and of viewing heating and lighting as two intertwined parts of one aspect of captive care. However, our behavioural data showed that animal responses to theoretically improved conditions may not be as predicted, and that substantially more research is required to better link theoretical ideas underpinning modern herpetoculture. It is essential to understand the differing methods, context and requirements for artificial provision of heat and light for reptiles. However, we suggest that an important starting point in this endeavour is the ecologically appropriate provision of heat and light. As with any change in methodology, it is important to continually monitor physiological and behavioural measures of health of reptiles maintained under novel conditions to assess any change. Reporting results such as these is important to avoid positive publication bias which may go on to influence further study. However, despite the absence of fully interpretable data, we suggest that reptile keepers should aim to create lighting conditions that are as close as possible to natural sunlight.

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REFERENCES

- Amadi, N., Belema, R., Obodo Chukwu, H., Dendi, D., Chidinma, A., Meek, R. & Luiselli, L. (2020). Life in the suburbs: artificial heat source selection for nocturnal thermoregulation in a diurnally active tropical lizard. *Web Ecology* 20: 161–172.
- Arbuckle, K.E. (2013). Folklore husbandry and a philosophical model for the design of captive management regimes. *Herpetological Review* 44: 448–452.
- Arribas, O.J. (2010). Activity, microhabitat selection and thermal behavior of the Pyrenean rock lizards *Iberolacerta aranica* (Arribas, 1993), *I. aurelioi* (Arribas, 1994) and *I. bonnali* (Lantz, 1927). *Herpetozoa* 23: 3–23.
- Badiane, A. & Font, E. (2021). Information content of ultraviolet-reflecting colour patches and visual perception of body coloration in the Tyrrhenian wall lizard *Podarcis tiliguerta*. *Behavioral Ecology and Sociobiology* 75: 1–14.
- Baines, F.M., Chattell, J., Dale, J., Garrick, D., Gill, I., Goetz, M., ... & Swatman, M. (2016). How much UVB does my reptile need? The UV-tool, a guide to the selection of UV lighting for reptiles and amphibians in captivity. *Journal of Zoo and Aquarium Research* 4: 42–63.
- Barolet, D., Christiaens, F. & Hamblin, M.R. (2016). Infrared and skin: friend or foe. *Journal of Photochemistry and Photobiology B: Biology* 155: 78–85.
- Carrière, M.A., Rollinson, N., Suley, A.N. & Brooks, R.J. (2008). Thermoregulation when the growing season is short: sex-biased basking patterns in a northern population of painted turtles (*Chrysemys picta*). *Journal of Herpetology* 42: 206–209.
- Carter, K.C., Keane, I.A., Clifford, L.M., Rowden, L.J., Fieschi-Méric, L. & Michaels, C.J. (2021). The effect of visitors on zoo reptile behaviour during the COVID-19 pandemic. *Journal of Zoological and Botanical Gardens* 2: 664–676.
- Díaz, J.A. & Cabezas-Díaz, S. (2004). Seasonal variation in the contribution of different behavioural mechanisms to lizard thermoregulation. *Functional Ecology* 18: 867–875.
- Dugard, P., File, P. & Todman, J. (2012). *Single-case and Small-n Experimental Designs: A Practical Guide to Randomization Tests* (2nd Edition). Abingdon: Routledge. 304 pp.
- Ferguson, G.W., Brinker, A.M., Gehrmann, W.H., Bucklin, S.E., Baines, F.M. & Mackin, S.J. (2010). Voluntary exposure of some western-hemisphere snake and lizard species to ultraviolet-B radiation in the field: how much ultraviolet-B should a lizard or snake receive in captivity? *Zoo Biology* 29: 317–334.
- Ferguson, G.W., Gehrmann, W.H., Vaughan, M.S., Kroh, G.C., Chase, D., Slaets, K. & Holick, M.F. (2021). Is the natural UV zone important for successful captive propagation of the panther chameleon (*Furcifer pardalis*); are different UVB irradiance exposures that generate a similar dose equally successful? *Zoo Biology* 40: 150–159.
- Fleishman, L.J., Loew, E.R. & Whiting, M.J. (2011). High sensitivity to short wavelengths in a lizard and implications for understanding the evolution of visual systems in lizards. *Proceedings of the Royal Society B: Biological Sciences* 278: 2891–2899.

- Garrick, D. (2008). Body surface temperature and length in relation to the thermal biology of lizards. *Bioscience Horizons* 1: 136–142.
- Govardovskii, V.I. & Zueva, L.V. (1974). Spectral sensitivity of the frog eye in the ultraviolet and visible region. *Vision Research* 14: 1317–1321.
- Harding, L., Tapley, B., Gill, I., Kane, D., Servini, F., Januszczak, I., Capon-Doyle, J. & Michaels, C.J. (2017). Captive husbandry and breeding of the tree-runner lizard (*Plica plica*) at ZSL London Zoo. *The Herpetological Bulletin* 138: 1–5.
- Honkavaara, J., Koivula, M., Korpimäki, E., Siitari, H. & Viitala, J. (2002). Ultraviolet vision and foraging in terrestrial vertebrates. *Oikos* 98: 505–511.
- Kane, D., Tapley, B., Servini, C., Aevansson, U. & Michaels, C.J. (2021). Reproduction of *Lachesis stenophrys* (Central American Bushmaster) at ZSL London Zoo. *Herpetological Review* 52: 564–566.
- Kasajima, I. (2019). Measuring plant colors. *Plant Biotechnology* 36: 63–75.
- Lindgren, J., Gehrmann, W.H., Ferguson, G.W. & Pinder, J.E. (2008). Measuring effective vitamin D₃-producing ultraviolet B radiation using Solartech's Solarmeter 6.4 handheld, UVB radiometer. *Bulletin of the Chicago Herpetological Society* 43: 57–62.
- MacIsaac, D., Kanner, G. & Anderson, G. (1999). Basic Physics of the Incandescent Lamp (Lightbulb). *The Physics Teacher* 37: 520–525.
- Mendyk, R.W. (2021). Cranial biofluorescence in the cuban false chameleon *Anolis barbatus* (Squamata: Dactyloidae): A further character shared with true chameleons (Chamaeleonidae). *Herpetology Notes* 14: 1315–1317.
- Michaels, C.J., Gini, B.F. & Clifford, L. (2020). A persistent abnormal repetitive behaviour in a false water cobra (*Hydrodynastes gigas*). *Animal Welfare* 29: 371–378.
- Millar, C.S., Graham, J.P. & Blouin-Demers, G. (2012). The effects of sex and season on patterns of thermoregulation in Blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada. *Chelonian Conservation and Biology* 11: 24–32.
- Oberpriller, J., de Souza Leite, M. & Pichler, M. (2022). Fixed or Random? On the Reliability of Mixed-effects Models for a Small Number of Levels in Grouping Variables. *Ecology and Evolution* 12: e9062.
- Plowman, A.B. (2003). A note on a modification of the spread of participation index allowing for unequal zones. *Applied Animal Behaviour Science* 83: 331–336.
- Porter, W.P. (1967). Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. *Ecological Monographs* 37: 273–296.
- Prötzel, D., Heß, M., Scherz, M.D., Schwager, M., Padje, A.V.T. & Glaw, F. (2018). Widespread bone-based fluorescence in chameleons. *Scientific Reports* 8: 1–9.
- Pruim, R., Kaplan, D.T. & Horton, N.J. (2017). The mosaic package: Helping students to 'think with data' using R. *The R Journal* 9: 77–102.
- R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online: <https://www.R-project.org/>.
- Schmidt, D.A., Mulkerin, D., Boehm, D.R., Ellersieck, M.R., Lu, Z., Campbell, M., ... & Holick, M.F. (2010). Quantifying the vitamin D₃ synthesizing potential of UVB lamps at specific distances over time. *Zoo Biology* 29: 741–752.
- Secor, S.M. & Nagy, K.A. (1994). Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* 75: 1600–1614.
- Seebacher, F. & Franklin, C.E. (2005). Physiological mechanisms of thermoregulation in reptiles: a review. *Journal of Comparative Physiology B* 175: 533–541.
- Silvestre, A.M. (2014). How to assess stress in reptiles. *Journal of Exotic Pet Medicine* 23: 240–243.
- Tattersall, G.J., Cadena, V. & Skinner, M.C. (2006). respiratory cooling and thermoregulatory coupling in reptiles. *Respiratory Physiology & Neurobiology* 154: 302–318.
- Thomas, O., Kane, D. & Michaels, C.J. (2019). Effects of different heat sources on the behaviour of blue tree monitors (*Varanus macraei*) in captivity. *The Herpetological Bulletin* 149: 41–43.
- Thompson, M.E., Saporito, R.A., Ruiz-Valderrama, H.D., Medina-Rangel, G.F. & Donnelly, M.A. (2019). A field-based survey of fluorescence in tropical tree frogs using an LED UV-B flashlight. *Herpetology Notes* 12: 987–990.
- Tosini, G. & Avery, R. (1996). Spectral composition of light influences thermoregulatory behaviour in a lacertid lizard (*Podarcis muralis*). *Journal of Thermal Biology* 21: 191–195.
- Tosini, G., Bertolucci, C. & Foà, A. (2001). The circadian system of reptiles: a multioscillatory and multiphotoreceptive system. *Physiology & Behavior* 72: 461–471.
- Vergneau-Grosset, C. & Péron, F. (2020). Effect of ultraviolet radiation on vertebrate animals: update from ethological and medical perspectives. *Photochemical & Photobiological Sciences* 19: 752–762.
- Zamora-Camacho, F.J., Reguera, S., Moreno-Rueda, G. & Pleguezuelos, J.M. (2013). Patterns of seasonal activity in a Mediterranean lizard along a 2200 m altitudinal gradient. *Journal of Thermal Biology* 38: 64–69.

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