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RESEARCH ARTICLE

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?

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Studies of voluntary exposure to ultraviolet-B (UVB) radiation from the sun in the field were conducted in the southern US and Jamaica for 15 species of lizards and snakes occupying various habitats. Species were sorted into four zones of UVB exposure ranging from a median UV index of 0.35 for zone 1 to 3.1 for zone 4. Guidelines for UVB exposure in captivity of these and species occupying similar light environments are presented. Data for most species were collected during mid-day during the spring breeding season, which appeared to be the time of maximum exposure. For two species of *Sceloporus* studied more intensively there was significant variation of exposure among times of the day and among seasons. So, all-day studies over the entire active season are necessary to fully understand the pattern of natural exposure for a particular diurnal species. Environmental and body temperature and thermoregulation as well as UVB/vitamin D photoregulation influences exposure to UVB. Regressions allowing the inter-conversion of readings among some meters with different detector sensitivities are presented. Readings of natural sunlight predict the same photobiosynthetic potential for vitamin D as the same reading from artificial

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sources whose wavelength distribution within the UVB band of the source is comparable to that of sunlight. Research approaches to further increase our understanding of vitamin D and UVB use and requirements for squamate reptiles in captivity are outlined. Zoo Biol 29:317–334, 2010.

Keywords: ultraviolet; field exposure; captive requirements; UV-index

INTRODUCTION

Basking reptiles are exposed to ultraviolet-B (UVB) radiation (290–320 nm) in nature and many species have morphological adaptations to protect themselves from UVB damage to vital organs including darkly pigmented UVB-absorptive layers in the skin and peritoneal linings of the coelom and viscera [Porter, 1967]. Exposure to excess UVB can cause eye and skin damage, skin cancer and poor reproduction in reptiles and amphibians [Hays et al., 1995; Blaustein et al., 1998; Ferguson et al., 2002; Gehrmann, 2006; Baines, 2007].

In contrast to tissue and DNA damage, exposure of many vertebrate species, including reptiles, to UVB radiation results in positive consequences, including the endogenous production of vitamin D_3 [MacLaughlin et al., 1982; Chen et al., 1993; Holick et al., 1995; Tian et al., 1996; Laing and Fraser, 1999; Carman et al., 2000; Laing et al., 2001; Aucone et al., 2003; Ferguson et al., 2003, 2005, Acierno et al., 2006, 2008].Vitamin D_3 is the precursor of a vital hormone (1,25 dihydroxy-vitamin D_3 or calcitriol) that regulates calcium–phosphorus balance and immune responses [Holick, 1999; Brames, 2007].

Vitamin D_3 can also be obtained from dietary sources [Holick, 1989a; Allen et al., 1999].Vitamin D deficiency in vertebrates, including reptiles, results in poor health and reproduction [Narbaitz and Tsang, 1989; Ferguson et al., 1996; Packard and Clark, 1996]. However, excess dietary vitamin D can result in toxic effects and death [Ferguson et al., 1996 Wallach, 1996]. On the contrary, high doses of UVB, given a light source with similar spectral power distribution (SPD) to sunlight, do not cause excess vitamin D_3 and the associated toxic effects, because biologically inert photoproducts are produced in the skin with higher UVB exposures [Webb et al., 1989; Holick, 2004]. Optimum levels of UVB or Vitamin D are largely unknown for most species [but see Ferguson et al., 2002].

In addition to the beneficial role of UV in vitamin D production, there is also evidence that lizards can see UV light [Loew et al., 2002; Bowmaker et al., 2005], adjust their exposure to UV for vitamin D photoregulation [Ferguson et al., 2003; Karsten et al., 2009], as well as use reflected UV light from the skin of a social partner for communication [Fleishman et al., 1993; Whiting et al., 2006].

Armed with this knowledge, the availability of artificial UVB-producing lamps and the availability of inexpensive UVB meters, the question remains: What is the optimum UVB exposure to which a captive reptile should be subjected?

To help answer the question we need to know the natural irradiance levels of UVB to which an animal voluntarily exposes itself in the wild. In this report we provide information on the natural exposure for 15 species of lizards and snakes gathered from the wild. We provide tentative estimates of the UVB zones occupied by species as reference guidelines for levels to provide for animals in captivity. We also discuss and review procedures pioneered to more fully understand the UVB and vitamin D requirements of lizard and snake species and how knowledge gained from each of these can be applied to determine the proper UVB environment and dietary vitamin D intake for captive species.

METHODS

From 2002 to 2008 studies were conducted along the north coast of Jamaica and at several locations in the southern and western U.S. to measure the UVB exposure of lizards and snakes encountered in the field. The general procedure involved searching habitat, encountering a specimen, and recording the UVB irradiance with a broadband UVB meter and time of day at the location where the animal was first seen. Air and substrate temperatures were also recorded. Sun exposure of each specimen encountered was subjectively judged as "sun," "partial," or "shade" and in most cases measured with a visible-spectrum (400–700 nm) General Electric type 214 light meter (Cleveland, OH). Maximum possible UVB exposure within the cruising distance of the animal was also noted. Orientation of the detector surface of the meters was perpendicular to the substrate and the animal's body and/or pointed into the sun. Where both orientations were employed, the higher reading was analyzed for this report.

Three types of broadband UVB meters were employed in successive studies during the study period including Gigahertz Optik UVB meter (Gigahertz-Optik, Inc., Newburyport, MA), Solarmeter 6.2, and Solarmeter 6.4 (Solartech, Inc., Harrison Township, MI). Recent studies have shown the readings from different meters to result in different output when exposed to the same levels of sunlight [Gehrmann et al., 2004a,b]. This is partly due to differences in the detector sensitivity among meters to various wavelengths in the UVB-band of the spectrum. However, the relationships between meter readings in natural sunlight are robustly predictable and readings from different meters can be inter-converted (Figs. 1 and 2). The detectors of the S6.4 meter and another Solartech meter (S6.5) (not used in this study) are identically sensitive only to the shorter wavelengths of UVB that have been shown to most closely correlate with conversion of pro-vitamin D_3 to previtamin D_3 in vitro [Lindgren et al., 2008]. The Gigahertz Optik and S6.2 meters have a broader sensitivity within the UVB range. Readings from the S6.4 meter (IU/min) can be directly converted to those of the 6.5 m (UV index [UVI]) by dividing by 7.14. Using this quantitative relationship, or the regression in Figure 1, we converted values measured with S6.2 or 6.4 meters to UVI, because of its more general acceptance for measuring UVB irradiance. Some readings obtained only with the Gigahertz Optik meter were first converted to S6.2 readings using the regression in Figure 2.

We tested the ability of the Solartech 6.4 meter to predict photoproduct conversion of provitamin D when exposed to either natural or artificial UVB light sources to determine whether field values can be compared directly to those of indoor captive environments from the point-of-view of vitamin D production. In vitro models [ampules containing an alcohol solution of provitamin D; Lu et al., 1992; Chen et al., 1993] were exposed either to the sun or to a 20 Watt Reptisun 10.0 fluorescent tube (Zoo Med Inc., San Luis Obispo, CA), which has a UVB SPD similar to that of the sun and is widely used in herpetoculture. Exposure was for 12, 24, 40, or 56 min. Irradiance of the two sources was matched at an average of 43 IU/

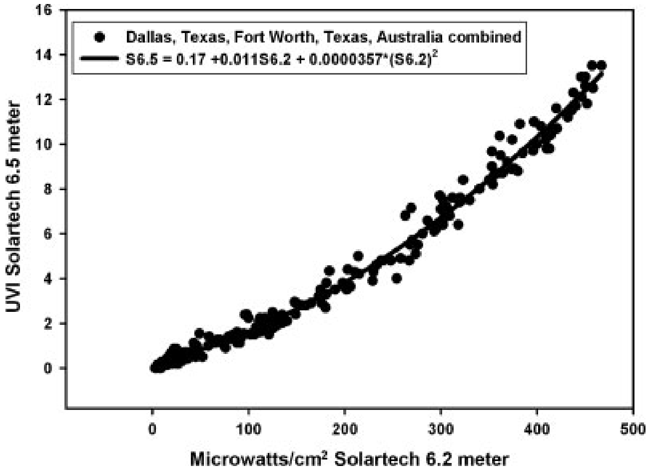

Fig. 1. Regression of simultaneous readings from the Solartech 6.2 m and the Solartech 6.5 m from sun exposure in northern Australia and the Dallas-Fort Worth metroplex in North-Texas.

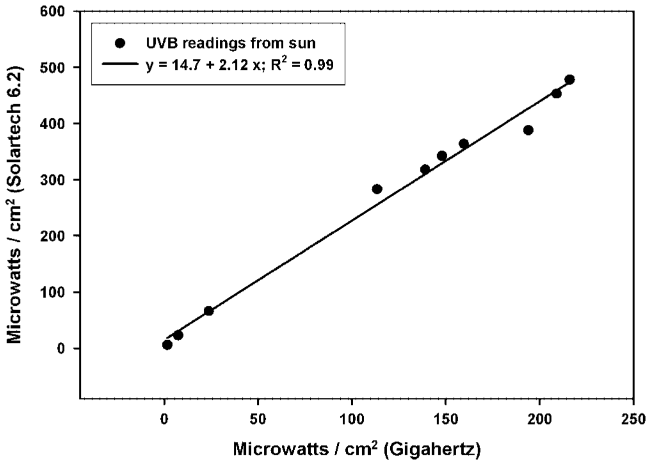

Fig. 2. Regression of simultaneous readings from the Gigahertz Optik and Solartech 6.2 m exposed to sunlight in Monahans Sandhills State Park, Texas.

min measured with a Solartech 6.4 meter. Regressions of percent photoproduct vs. exposure time were compared between sources.

Studies in Jamaica on the lizards *Anolis lineotopus*, *Anolis grahami*, and *Anolis sagrei* were conducted at the Hofstra University Marine Lab in Priory, St. Ann's Parish in March 2004. Studies in the US were conducted at several locations: (1) from April–September, 2005 at Old Sabine Wildlife Management Area on the snakes *Agkistrodon piscivorous*, *Elaphe obsoleta*, *Thamnophis proximus*, *Nerodia fasciata*, and *Nerodia erythrogaster*; (2) in May and June, 2005 at Monahans State Park, Ward Co., Texas on the lizard *Uta stansburiana stejnegeri*; (3) at Kisatchee National Forest, Natchitoches Par., Louisiana on the lizards *Sceloporus undulatus hyacinthinus* and *Anolis carolinensis*; (4) at Rita Blanca National Grassland, Dallam Co., Texas on the lizards *Holbrookia maculata* and *Sceloporus undulatus garmani*; (5) in May 2007 on *Sceloporus graciosus* at various localities in California and Colorado; (6) from April–October 2007 on the lizard *Sceloporus olivaceous* in Tarrant Co. Texas; (7) in July 2008 on the lizard *Sceloporus graciosus* in Lassen National Volcanic Park, California.

For comparison (Table 1), values from the spring and early summer corresponding to the active breeding season were used. Data were accumulated throughout the day and were mostly confined to the period of peak activity and sun exposure between 0800 and 1500 hr. All data were analyzed using Sigmastat 3.5 (Jandel Corporation) or SYSTAT version 10.2 (SYSTAT Software Inc.).

RESULTS

There was considerable variation among taxa and habitats in mean UVB exposure (Table 1). It was convenient to divide the species into four UVB-zones, which corresponded roughly to their ecological contexts and which were labeled in accord with light availability (Table 1) For localities where multiple species occurred, differences clearly reflected differences in habitat preference, which included variations in substrate, temperature, and light throughout the entire spectrum as well as UVB. The exposure of most species was not monitored throughout their entire activity season and can vary significantly with both season (Fig. 3) and the time of day [Fig. 4; Ferguson et al., 2005]. Therefore, the comparisons here may or may not use complete species- or population-typical values, which can only be determined by all-day, season-long studies. For that reason in our comparison we did not test for statistical significance of our differences among species, although standard deviations of our data are presented.

Day-long or season-long studies of two species of *Sceloporus* revealed significant variance of exposure among months of the activity season for the Texas spiny lizard *Sceloporus olivaceous* (Fig. 3) and among times of the day for the sagebrush lizard *Sceloporus graciosus* (Fig. 4). The exposure variance among months was significant for the Texas spiny lizards with exposure during July (month 4) and August (month 5) being significantly lower than exposure in April (month 1), May (month 2), and October (month 7) (Kruskal–Wallace one-way ANOVA on ranks and Dunn's multiple comparison method; $P < 0.05$). In this study UVB exposure of controls (exposed sites) was significantly higher than that of the lizards (Kruskal–Wallace one way ANOVA on ranks; $P < 0.05$).

The exposure variance among time categories was significant for the sagebrush lizards with exposure during 1100–1300 hr being significantly higher than exposure during 1500–1800 hr (Kruskal–Wallace one-way ANOVA on ranks and Dunn's multiple comparison method; $P < 0.05$). For the controls exposure during 0900–1100 hr and 1500–1800 hr was significantly lower than exposure during the 1100–1300 hr time-period. In this study also exposure of controls was significantly higher than that of the lizards (Kruskal–Wallace one way ANOVA on ranks; $P < 0.01$). In both studies lizards avoided the maximum exposure available to them most of the time (Figs. 3 and 4).

The thermal environment strongly influenced the UVB exposure of the lizards. For three lizard species (*Sceloporus undulatus hyacinthinus*, *Anolis carolinensis*, and *Holbrookia maculata*, data pooled) UVB exposure was strongly correlated with

TABLE 1. UVB zone reference guidelines determined from average irradiance of randomly encountered individuals in the field

Species (number of individuals) Common name	Average UVI ± SD (range)	UVB ZONE	UVB Zone range (median)	Zone description
Agkistrodon piscivorus (11) **Cottonmouth Water Moccasin**	0.2 ± 0.18 (0–0.6)	1	0–0.7 (0.35)	Zone 1 crepuscular or shade; thermal conformer
Elaphe obsoleta (6) **Texas Rat Snake**	0.4 ± 0.27 (0–0.8)			
Anolis lineotopus (17) **Jamaican Brown Anole**	0.6 ± 0.36 (0.2–1.4)			
Nerodia fasciata (4) **Broad-banded Water Snake**	0.7 ± 0.42 (0.2–1.1)	–	–	–
Thamnophis proximus (18) **Western Ribbon Snake**	0.8 ± 0.77 (0.2–1.1)	2	0.7–1.0 (0.9)	Zone 2 partial sun or occasional full-sun basker; thermoregulator
Anolis grahami (12) **Jamaican Blue-pants Anole**	0.8 ± 0.33 (0.3–1.1)			
Anolis carolinensis (19) **Green Anole**	0.9 ± 0.68 (0.2–3.0)			
Nerodia erythrogaster (10) **Yellow-bellied Water Snake**	0.9 ± 0.99 (0.1–2.7)	–	–	–
Uta stansburiana stejnegeri (13) **Desert Side-blotched Lizard**	1.3 ± 0.65 (0.4–2.9)	3	1.0–2.6 (1.8)	Zone 3 full-sun or partial sun; thermoregulator
Sceloporus undulatus hyacinthinus (18) **Eastern Fence Lizard**	1.7 ± 1.62 (0.3–4.9)			
Anolis sagrei (13) **Cuban brown Anole**	1.8 ± 1.13 (0.6–4.1)			
Sceloporus olivaceous (30 in May) **Texas Spiny Lizard**	2.6 ± 1.89 (0.1–7.4)	–	–	–
Holbrookia maculata (25) **Lesser Earless Lizard**	2.9 ± 0.98 (1.5–4.5)	4	2.6–3.5 or > (3.1)	Zone 4 mid day baskers; thermoregulator
Sceloporus graciosus (10) **Sagebrush Lizard**	3.1 ± 3.22 (0.4–9.5)			

Sceloporus undulatus garmani (3) **Northern Prairie Lizard**	3.2 ± 1.51 (2.2–4.9)	–	–	–

	Average IU/min ± SD (range)	ZONE	Zone range (median)	Zone description
Agkistrodon piscivorus (11) **Cottonmouth Water Moccasin**	2 ± 1.3 (0–4)	1	0–5 (2.5)	Zone 1 crepuscular or shade; thermal conformer
Elaphe obsoleta (6) **Texas Rat Snake**	3 ± 1.9 (0–6)			
Anolis lineotopus (17) **Jamaican Brown Anole**	4 ± 2.6 (1–10)			
Nerodia fasciata (4) **Broad-banded Water Snake**	5 ± 3.0 (1–8)	–	–	–
Thamnophis proximus (18) **Western Ribbon Snake**	5 ± 5.5 (1–23)	2	5–7 (6)	Zone 2 partial sun or occasional full-sun basker; thermoregulator
Anolis grahami (12) **Jamaican Blue-pants Anole**	6 ± 2.3 (2–8)			
Anolis carolinensis (19) **Green Anole**	6 ± 4.8 (1–21)			
Nerodia erythrogaster (10) **Yellow-bellied Water Snake**	7 ± 7.0 (1–19)	–	–	–
Uta stansburiana stejnegeri (13) **Desert Side-blotched Lizard**	9 ± 4.6 (3–21)	3	7–18 (13)	Zone 3 full-sun or partial sun; thermoregulator
Sceloporus undulatus hyacinthinus (18) **Eastern Fence Lizard**	12 ± 11.6 (2–34)			
Anolis sagrei (13) **Cuban Brown Anole**	13 ± 8.0 (4–29)			
Sceloporus olivaceous(30 in May) **Texas Spiny Lizard**	18 ± 13.5 (1–53)	–	–	–

TABLE 1. Continued

	Average IU/min ± SD (range)	ZONE	Zone range (median)	Zone description
Holbrookia maculata (25) **Lesser Earless Lizard**	21 ± 7.0 (10–32)	4	18–25 or > (22)	Zone 4 mid day baskers; thermoregulator
Sceloporus graciosus (10) **Sagebrush Lizard**	22 ± 23.0 (3–68)			
Sceloporus undulatus garmani (3) **Northern Prairie Lizard**	23 ± 10.8 (16–35)	–	–	–

UVB-irradiance Zone reference guidelines are based on the natural exposure levels of lizards and snakes spot-checked in the field during their activity period in the spring–early summer breeding season. The average number of sightings per species was 14 (range 3–30). Species are grouped into four light-exposure habitat zones with increasing average exposure levels from 1 to 4. Two reference guidelines are presented: one for UVI and one for IU/min.

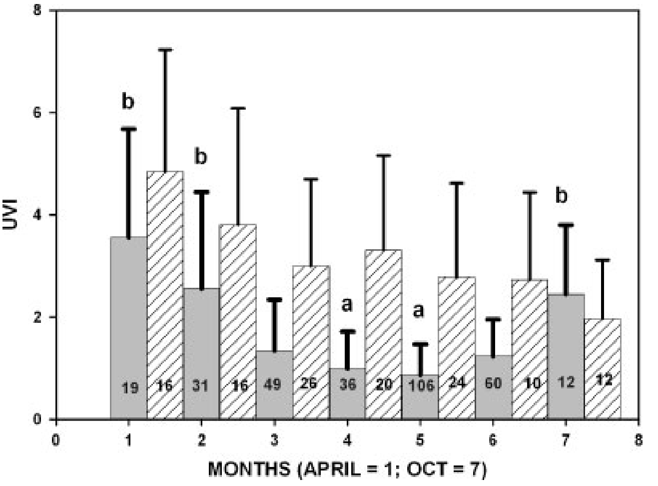

Fig. 3. Mean mid-day exposure of ultraviolet light (UVI) at the locations of randomly encountered, free-living Texas Spiny lizards *Sceloporus olivaceous* (gray bars) and nearby sun-exposed control sites (hatched bars) in Fort Worth, Texas from April through October 2007. Observations were from 1000 to1400 hr on 51 different days. Capped bars are one standard deviation. Numbers in bars are sample sizes. Comparing months, different letters above lizard bars (**a** vs. **b**) indicate significant differences of exposure. Exposure differences between lizards and controls were also significant (see text).

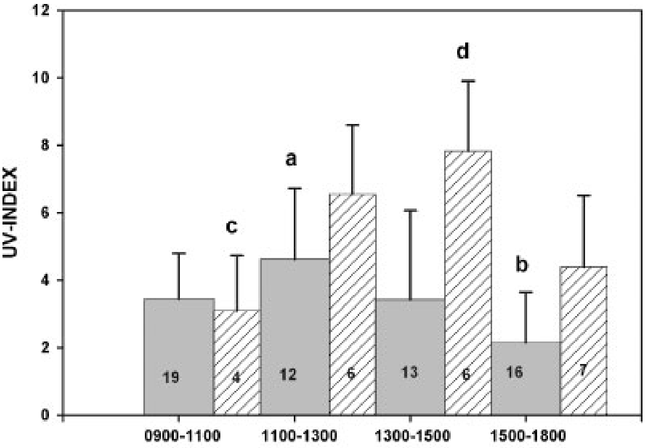

Fig. 4. Mean ultraviolet exposure (UVI) of locations of randomly encountered, free-living Sagebrush lizards *Sceloporus graciosus* (gray bars) and nearby sun-exposed control sites (hatched bars) in Lassen National Park, California from 0900 to 1800 hr monitored over a two-day observation period in July 2008. Numbers in bars are sample sizes. Comparing time periods, different letters above lizard bars (**a** vs. **b**) and above control site bars (**c** vs. **d**) indicate significant differences of exposure among time periods for lizards and control sites, respectively. Exposure differences between lizards and control sites were also significant (see text).

cloacal temperature (Fig. 5). For Texas spiny lizards (*Sceloporus olivaceous*) the seasonal variation was associated with a noticeable temperature threshold (Fig. 6). When air temperatures approached or exceeded 32°C, the animal sought shade, resulting in a lower exposure to UVB than at cooler temperatures. At high ambient temperatures the animals have considerably lower exposure than is available if fully exposed. The "preferred" temperature of this species, which is considered to be an active thermoregulator, is 32–36°C, varying somewhat with the seasons [Blair, 1960].

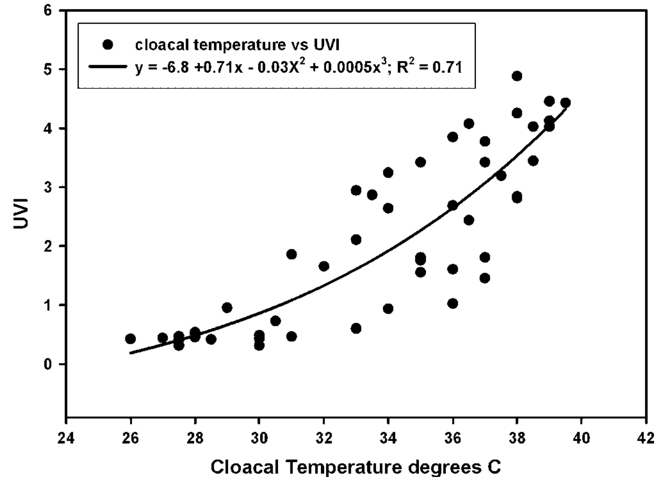

Fig. 5. UVB exposure as a function of cloacal temperature for three species of lizards (*Sceloporus undulatus hyacinthinus*, *Anolis carolinensis*, and *Holbrookia maculata*, data pooled). UVB was measured at the site where the lizard was first seen. Cloacal temperatures were recorded within 30 sec of capture and usually within 2-min of initial sighting. Data from lizards that required ≥5 min of pursuit before capture are not included.

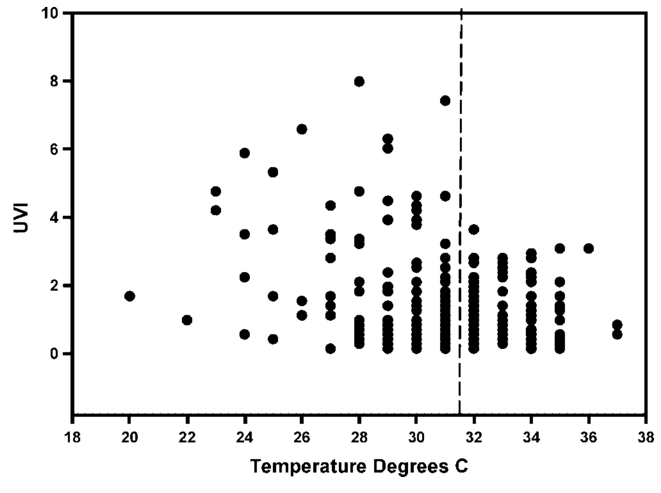

Fig. 6. UVB exposure as a function of air temperature (T_a) for Texas spiny lizards (*Sceloporus olivaceous*). Dashed line emphasizes a temperature threshold effect. At temperatures above 32°C mean and variance of UVI were noticeably reduced. Both UVB and T_a were taken at the lizard's location. Data points are individual sightings.

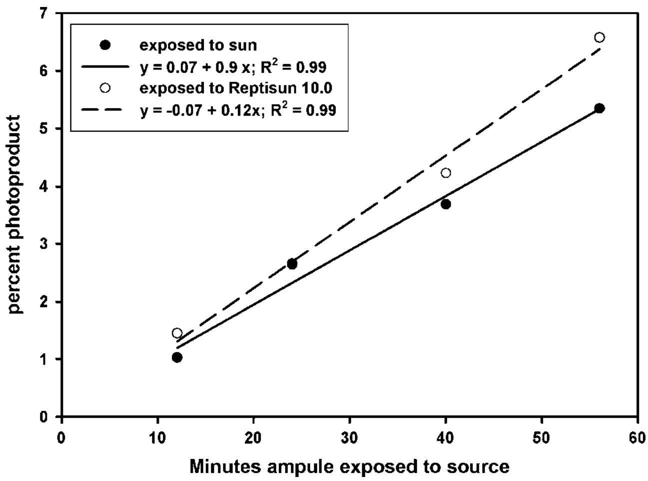

Fig. 7. Percent photoproduct in ampules vs. time exposed to sunlight or an artificial UVB source (20 Watt ZooMed Reptisun 10.0 fluorescent tube). Each ampule was exposed to the same average irradiance (43 IU/min) measured with the Solartech 6.4 m. There were no significant differences in slope or intercept of the regressions for the sun vs. the Reptisun tube (see text).

The UVI at the exposed control sites in the Texas spiny lizard study was lower than the exposed, sunny, clear, mid-day readings reported for the Dallas/Fort Worth area for the past several years (maximum 10–11) (http://www.cpc.ncep.noaa.gov/products/stratosphere/uv_index/uv_annual.shtml). Also, the seasonal variation was not as expected (highest in spring vs. mid-summer). This may have been due to the greater than average cloud-cover for the summer of 2007 and/or that the sites were not in fully open exposed areas. Also, any effects of nearby trees would be greater in mid-summer when leaf cover is increased.

Comparison of photoproduct conversion from in vitro models vs. duration of exposure with irradiance levels controlled revealed no significant difference between the slopes or intercepts of the regressions for the sun and the ZooMed Reptisun 10.0 fluorescent tube (ANOVA Source by exposure time interaction and source effect, $P > 0.05$; Fig. 7). Therefore, the same average irradiance reading from either source predicted the same potential vitamin D production.

DISCUSSION

To our knowledge this is among the first reports quantitatively estimating natural UVB-exposure of lizards and snakes [see also Carman et al., 2000; Ferguson et al., 2005]. Based on the natural UVB exposure levels of 15 species of snakes and lizards from the southern and western U.S. and Jamaica, general recommendations of average and range of levels of exposure (irradiance) are presented for species occupying certain types of light environments (Table 1). Keepers of these species in captivity can reasonably expect to subject an animal to these levels with no danger caused by overexposure (but see Baines [2007] for cautions associated with certain types of artificial light sources). If animals are kept in an enclosure large enough to produce a suitable UVB gradient and which provides a UVB refuge (we recommend this) so that they can photo-regulate their UVB exposure based on their vitamin D-condition, the maximum values in the zone range column of Table 1 are recommended for the closest accessible point to the UVB source. If animals are kept in small enclosures where a UVB irradiance gradient is difficult to attain and there is no UVB refuge (we do not recommend this), the median values in the zone range column of Table 1 are probably more appropriate. Data on UVB dose (irradiance × time) for free-living natural species require monitoring individuals throughout their activity cycle and are just now becoming available for a handful of species [Carman et al., 2000; Ferguson et al., 2005]. For captive species of special concern, field data on dose will provide information on what voluntary exposure durations might be expected in captivity and provide information on the UVB requirements of the species. The general application of these guidelines may be limited to Western-Hemisphere-dwelling small lizards and snakes. More field data on turtles, crocodilians, and large-sized squamates from more regions of the world are needed to update and increase the general value of these guidelines.

At least four cautions need to be emphasized in applying these guidelines to captivity. First, because the exact UVB irradiance tolerances and requirements for a given species other than those in this study are unknown and may vary with age, reproduction, and health of a specimen, it is important to provide a captive animal with a refuge from any UVB source, i.e., to provide a large UVB gradient accessible by the animal. There is evidence that lizards can use a gradient to self-regulate their exposure (see below).

Second, an animal should be closely watched after a new UVB source is established in an enclosure and adjustments made depending on the captive's behavior. Studies have shown that some lizards are capable of precisely regulating their exposure to UVB [Ferguson et al., 2003; Karsten et al., 2009]. Ferguson et al. [2003] showed that panther chameleons exposed to UVB gradients, that were not linked to thermal gradients and were generated using artificial fluorescent lamps in the laboratory, can regulate UVB exposure independently from temperature regulation. Nevertheless, lizards in the field readily seek refuge from the sun, which is a strong UVB and heat source, when their thermal requirements are satisfied (Figs. 3, 4, and 6) and thermal preferences can influence and constrain UVB exposure and vitamin D/UVB photoregulation. If the captive animal avoids a UVB source, the UVB may be too strong, or the temperature at that location may be too hot or too cold, or the visible light may be inappropriate; the source should be evaluated. It is important to make sure that the ambient cage temperature is not too hot or cool and that unnaturally high levels of UVB are not accessible to a basking species at the thermal basking site.

Third, when setting up a UVB source it is important to consider not the total UVB output of the lamp but the actual irradiance at the basking site and the UVB gradient produced by the lamp, in other words, its UVB "footprint" in the vivarium. This depends upon the distance of the basking site from the light source, the shape of the beam (which is determined by the type of the lamp and any reflectors in use), and also the UV absorption properties of any barrier between the lamp and the reptile, such as mesh, plastic, or glass. Such barriers may attenuate or even completely block out the UVB irradiance [Burger et al., 2007].

A fourth caution for applying these guidelines is that, despite the results presented here, a reading from these meters from the field may or may not be directly comparable to the same reading from some artificial light sources regarding vitamin

D production potential. MacLaughlin et al. [1982] showed that UVB from some artificial sources can result in a substantially higher rate of photoproduct production than natural sunlight. The SPD of the Zoo Med Reptisun fluorescent tube, as well as most artificial light sources manufactured for use in reptile herpetoculture, is broadly similar to that of the sun in the UVB range. The Solartech 6.4 and 6.5 meters will predict vitamin D synthesis equally well from either the sun or the artificial sources of this type (*Note*: some models of the Solartech 6.4 and 6.5 meters manufactured after August 2008 may be suitable for outdoor use only; ours were manufactured before this date).

However, some artificial lamps, including the FS sunlamps intended for use in research, produce significant amounts of low-wavelength irradiance (short wavelength UVB 280–290 nm and, rarely, UVC), which, although it will enhance vitamin D production, can also cause serious damage to eyes and skin, and even cause death [Hibma, 2004; Baines, 2007]. Because of the differences in the SPD of these sources with that of the sun, these sources produce more vitamin D than predicted by the meters along with deleterious effects due to short wavelength ultraviolet radiation. We strongly discourage the use of artificial light sources that have not been manufactured and tested for specific use in herpetoculture (see Baines [2007] and Lindgren et al. [2008] for comparison of various artificial UVB sources manufactured for herpetoculture).

Our knowledge of natural intake of vitamin D_3 from the diet is meager and the few data for insectivorous species suggest that it is low (maximum daily intake of 37 ng or 1.5 IU/g of food based on stomach content analysis of animals collected in the field during a day and the assumption that they fill their stomachs once a day) [Carman et al., 2000; Ferguson et al., 2005]. While some herpetoculturists have avoided the use of UVB and report successful propagation from the use of dietary sources alone [see Ferguson et al., 1996], to our knowledge there are no quantitative studies determining optimal doses of dietary vitamin D_3 for any reptile species maintained without access to UVB. Nor are there any data indicating an ability of lizards or snakes to regulate their dietary vitamin D intake via behavioral selection of food sources rich or poor in vitamin D content. There are data that some lizards can selectively choose dietary alternatives presumably to balance nutrient intake [Auffenberg, 1988; Eason, 1990], so behavioral regulation of dietary vitamin D is theoretically possible, but current knowledge makes it difficult to recommend an appropriate level of dietary supplementation. We recommend that lizard and snake keepers rely primarily on UVB exposure for provisioning of vitamin D. Since small amounts of vitamin D_3 have been found in gut contents of diurnal insectivorous lizards, a combination of suitable UVB lighting and very low levels of vitamin D_3 supplementation may be appropriate for most diurnal lizards and snakes.

Once the natural UVB exposure levels are determined for a species, several other questions must be answered through field and laboratory study to more fully understand the UVB and vitamin D requirements of a species.

(1) *How long does an animal expose itself to its preferred levels in nature?* This determines the UVB dosage (irradiance $\times$ time) that an animal normally receives and the UVB requirements of a species. Such data can be obtained during noninvasive field studies by monitoring single animals for the duration of an activity cycle. In recent research, animals have been followed throughout an activity cycle and time spent at specific locations monitored (focal-day). On a subsequent day of similar

solar conditions, animal locations were revisited and UVB exposure determined by placing in vitro models at the previous-day locations and for the same time (retrace-day). The models were exposed for 3 hr time periods during which they were repeatedly relocated to follow the lizard's previous day pathway. Using a regression equation relating UVB dose (*Y*) to percent photoproduct produced from the original provitamin D content of the models (*X*), UVB exposure dose of the lizard can be estimated for that time period [Ferguson et al., 2005]. Instead of retracing the lizard's path with ampules, retrace can involve measuring UVB irradiance at short intervals with a meter. From these data the average irradiance per unit time and dose can be calculated.

Other useful information, which is much more difficult to obtain and requires invasive and expensive analytical procedures, is as follows.

(2) *What is the natural dietary intake levels of vitamin D_3?* The higher the dietary intake, the less UVB exposure may be required to maintain vitamin D condition. Stomach contents of wild, free-living animals need to be obtained and analyzed by HPLC techniques [Carman et al., 2000; Ferguson et al., 2005]. Small animals may need to be sacrificed to obtain complete stomach contents, although stomach-flushing techniques and behavioral observation may be feasible for some species [Legler and Sullivan, 1979; Watters, 2008]. If the diet is specialized and well-known, preingested samples can be collected in the field and analyzed [Watters, 2008].

(3) *What are the circulating calcidiol and vitamin D_3 levels of animals in nature and in captivity?* Calcidiol (25-hydroxy vitamin D_3) is the immediate precursor to calcitriol and is considered the primary storage form of vitamin D_3 [Haddad, 1999; Laing and Fraser, 1999]. Calcidiol is considered to be the best indicator of the vitamin D status of an animal. Levels in nature provide a benchmark for the suitability of the UVB environment and dietary vitamin D levels in captivity [Gillespie et al., 2000; Laing et al., 2001; Aucone et al., 2003; Ramer et al., 2005]. Animals need to be bled and the serum analyzed [Chen et al., 1990]. In captivity, low levels of calcidiol are indicative of vitamin D deficiency. Circulating levels of calcidiol that are too high can result in toxicity. This is unlikely to occur in wild reptiles, since excess vitamin D_3 is never produced by sunlit skin, and natural reptile diets contain very little vitamin D_3. In captivity over-supplementation with dietary vitamin D_3 is the most likely cause.

(4) *What is the degree to which a species can regulate its exposure to UVB depending on its vitamin D-condition?* While one species, the panther chameleon, has been shown to do this with great precision [Jones et al., 1996; Ferguson et al., 2003; Karsten et al., 2009] and other species may have this ability [Bernard et al., 1991; Aucone et al., 2003], careful laboratory and field research is required to document this ability in other species. If a species can self-regulate its UVB exposure to maintain optimal vitamin D_3 status, then providing a suitable species-specific UVB gradient in the vivarium may be all that is necessary for this to occur. However, the thermal influence on the expression of UVB/vitamin D photoregulation is of particular importance. Further study is essential to evaluate the way in which the location of heat and visible light sources in the vivarium affect photoregulatory behavior. The natural co-existence of heat and UV found under sunlight is not guaranteed under artificial lighting and thermoregulation may take precedence if this co-existence is not provided [Dickinson and Fa, 1997].

(5) *How sensitive is the skin to UVB regarding the production of vitamin D_3?* Skin sensitivity to UVB with regard to conversion of provitamin D to vitamin D and other photoproducts has been documented in all vertebrates from fish to primates [Holick, 1989b; Holick et al., 1995]. By exposing patches of skin to artificial UVB lights, lizard species have been shown to vary in skin sensitivity inversely to the average UVB-irradiance to which the species is exposed in the field [Carman et al., 2000; Ferguson et al., 2005]. Animals from high UVB zones may require high levels in captivity to avoid vitamin D deficiency. Study of more species is warranted to test the generality of this relationship.

(6) *What are the optimum levels of vitamin D condition for proper health and reproduction of the animal?* In a study of panther chameleons [Ferguson et al., 2002], neonate females were raised through maturity and reproduction under different enforced daily UVB levels. Their reproductive success was measured in terms of the number of second-generation hatchlings produced. An optimum dose with maximum success was determined above or below which reproductive success was lower. In the absence of these labor-intensive studies, matching the captive levels of circulating vitamin D and calcidiol to those in wild breeding animals can be an estimate of optimum levels. This, of course, assumes that field levels are always optimal.

CONCLUSIONS

1. North American and Jamaican squamate reptiles occupied habitats consisting of four zones of voluntary UVB exposure, ranging from a median UV exposure index of 0.35–3.1.
2. Exposure levels vary significantly throughout the day and across seasons, so future studies should encompass the entire day and all seasons to gain a more complete understanding of typical exposure for a target species.
3. Environmental and body temperatures influence exposure to the sun and exposure to UVB. Thermoregulation may constrain exposure to the sun and UVB when environmental temperatures exceed optimal temperature.
4. From these data zoo keepers and herpetoculturists can estimate optimum median and maximum exposure levels for enclosures of captive species whose natural light habitat is known or can be surmised. When Solartech 6.4 or 6.5 UVB meters are used, identical readings from the sun and an artificial UVB source, whose SPD is similar to that of the sun in the UVB range, at a given distance indicate that a similar rate of photobiosynthesis of Vitamin D_3 may be expected from the sunlight and from that lamp at that particular distance.
5. Because animals may be able to regulate their exposure to UVB, we recommend that keepers maintain animals with a UVB gradient from the maximum levels ascertained in this study to a zero UVB-refuge and watch their animals to determine how they use the gradient. If they expose themselves continuously, the maximum level might be adjusted upward gradually by moving the source closer or using a stronger UVB source, but care should be taken to not set maximum levels unnaturally high. If the animals avoid the UVB source or continuously use the refuge, the maximum available level of UVB should be lowered or the source

turned off temporarily to see whether the animal starts leaving the refuge in response to lower UVB. Visible light levels and temperatures near the source should also be evaluated.
6. Optimal dietary vitamin D_3 levels are unknown for any lizard or snake species. If supplemental dietary vitamin D_3 is offered when adequate UVB lighting is used, levels of vitamin D should not exceed those currently reported from the intestinal contents of wild diurnal insectivorous lizards (about 1–2 IU/g of food/day).
7. Several experimental approaches to better understand UVB and vitamin D requirements of lizards and snakes are suggested when time, space, money, animal care regulations, and manpower permit.

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