

Ultraviolet Light Exposure and Response to Dietary Vitamin D₃ in Two Jamaican Anoles

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ABSTRACT.— In Jamaica, free-living male and female-sized *Anolis sagrei* are exposed to more natural ultraviolet-B (UVB) from sunlight than male and female-sized *Anolis lineatopus*. In the laboratory, we tested predictions derived from the hypothesis that *Anolis* possess a mechanism for behaviorally photo-regulating their exposure to UVB depending on their dietary intake of vitamin D₃. *Anolis sagrei* voluntarily exposed themselves more frequently to visible and UVB light and received higher doses of UVB in an artificial light gradient when fed a low vitamin D₃ diet for 6 weeks than when subsequently fed a high dietary vitamin D₃ diet for 6 weeks. When we returned the anole's diet to the low vitamin D₃ regimen for a third 6-week period, UVB exposure remained lower than in the first 6-week period. This suggests an initial UV photo-regulatory adjustment to high dietary vitamin-D₃ but a slow return to greater reliance on UVB-induced endogenous vitamin D₃ production. Conversely, while exposing themselves to UVB with similar frequency and doses as *A. sagrei* over the course of the 18-week experiment, *A. lineatopus* did not show the same decreased attraction to visible and UVB light in response to increased dietary vitamin D₃. The response of *A. sagrei* in the laboratory to visible light without UVB was similar to their response to visible light with UVB. Therefore, the anoles appeared to be responding primarily to visible light. *Anolis lineatopus* may be unable to use dietary vitamin D₃ to restore low vitamin D status.

It is well established that active basking by many heliophilic lizards is a critical mechanism for thermoregulation (Cowles and Bogert, 1944; Pough et al., 2005). Some lizard species attain preferred body temperatures quickly by basking early in the day. This high preferred temperature may be maintained throughout their activity periods within narrow limits and may not match the temperature of their immediate surroundings. In contrast, other lizard species are thermal conformers and bask less frequently. When active, they maintain a variable body temperature that conforms to the range of their environment (Huey, 1982). In Jamaica, *Anolis sagrei* is a precise thermoregulator, whereas *Anolis lineatopus* is a thermal conformer (Lister, 1976).

However, the sun is not only a source of heat but also ultraviolet radiation. In many vertebrates, the exposure of skin to ultraviolet-B radiation (UVB; 290–315 nm) causes photolysis of provitamin D₃ (7-dehydrocholesterol) to previtamin D₃ followed by thermal isomerization to vitamin D₃, which then enters the circulation. Subsequent hydroxylations in the liver and kidneys produce the biologically active form of vitamin D₃, 1,25-dihydroxyvitamin D₃, a hormone critical to calcium and phosphorus metabolism (Holick, 1996, 1999, 2004). Vitamin D₃ can also enter the circulation by ingestion of food containing vitamin D₃.

Although the literature often implies that basking serves solely as a means of behavioral thermoregulation, studies increasingly report that basking is sometimes unaccompanied by thermal adjustment (Manning and Grigg, 1997; Plummer et al., 2005) and may serve other important physiological functions, such as UVB photo-regulation of vitamin D₃ status. Panther Chameleons, for example, adjust their UVB exposure in response to changes in dietary vitamin D₃ intake in the absence of precise photo-thermoregulation (Ferguson et al., 2003; Karsten et al., 2009). They are the first vertebrate and so far the only lizard species shown to possess the ability to photo-regulate their vitamin D₃ status by adjusting their exposure to UVB.

We report new data on the natural UVB exposure for two species of Jamaican *Anolis* lizards (*A. lineatopus* and *A. sagrei*). This report extends previous field reports (Ferguson et al., 2005, 2010) with larger sample sizes and includes information on both adult male and female-sized individuals. Also, with a laboratory experiment, we tested the hypothesis that *Anolis*, similar to Panther Chameleons, have a mechanism of behavioral UVB photo-regulation of vitamin D₃ status. With *A. sagrei*, a heliophilic thermoregulator, and *A. lineatopus*, a shade-dwelling thermal conformer (Lister, 1976), we tested the predictions from this hypothesis that both anole species fed a diet low in vitamin D₃ will expose themselves to high UVB light zones more times and receive higher UVB doses than when fed a diet higher in vitamin D₃.

MATERIALS AND METHODS

Field Study.—We located free-living adult specimens of *A. sagrei* and *A. lineatopus* on and around the campus of Hofstra University Marine Laboratory (HUML) in Priors, St. Ann's Parish, Jamaica from 14–17 March 2004 and again on 11 and 12 March 2006. The lizards were surveyed between 0830 and 1330 h under partly overcast to sunny skies. When a lizard was located, we determined the species and size of the lizard visually and noted the precise location and time of day. Lizards were disturbed as little as possible and were not captured. Large individuals were easily recognized as adult males; smaller individuals were either subadult males or adult females and were difficult to sex without capturing. Therefore, we combined them into a single sex-size category (female-sized). At the location where a lizard was initially discovered, we recorded the irradiances of UVA, UVB, and visible light using three external sensors sequentially attached to a Gigahertz-Optik (P9710) broad-band light meter. For each of the three sensors, the flat window was oriented so that it was horizontal to the ground, approximately 1–3 cm from the location of the lizard.

Collection for Laboratory Experiment.—In March 2004, we collected four adult males and four adult females each of *A. sagrei* and *A. lineatopus* from the HUML campus and brought them back to our laboratory at Texas Christian University.

Terrarium Design and Placement.—Each lizard was housed in isolation in a terrarium illuminated from above with a single-bulb fluorescent luminaire containing a 100-cm Philips cool-

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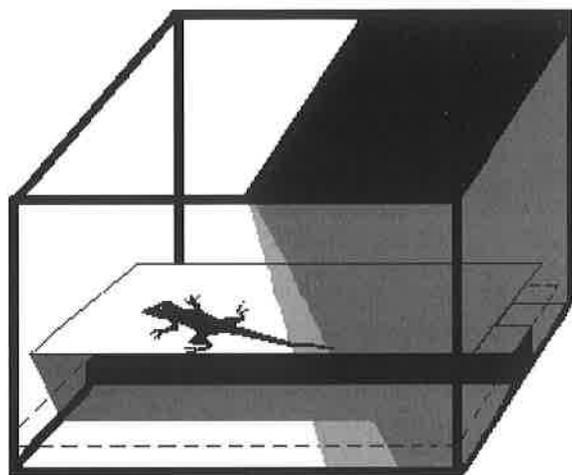


FIG. 1. Schematic diagram of laboratory enclosure showing UVB exposure zones during UV-light treatments of captive *Anolis* lizards. The unshaded zone indicates high UVB exposure; the light gray zone, medium UVB exposure; the dark gray zone, low UVB exposure. See text for details. The dashed line illustrates a thermal gradient zone. From the cage floor to the line, ambient temperature ranged from about 40–25°C throughout the cage. Above the line, temperature was uniform laboratory temperature and ranged from 23–25°C.

white light tube (Philips Co., Somerset, NJ). Terraria were 11-L plastic enclosures with a hardware cloth (0.6-cm mesh) tight-fitting lid. The sides and back of each terrarium were covered with black construction paper to prevent visual contact between adjacent subjects. Wooden platforms were placed in the cage on the bottom and at midheight to allow the lizard to easily perch above the heated floor of the cage (Fig. 1).

Lizards were provided supplementary heat with strips of heat tape (30 cm wide) placed under the enclosure floor. One strip extended under each array of eight enclosures. This established a vertical thermal gradient from the floor of each cage (Fig. 1). Cool white fluorescent light and heat supplements were set on 12 h on-off daily cycles using automatic timers. Light and heat sources were on from 0700 to 1900 h daily.

Terraria were placed adjacent to each other in a row along a laboratory bench top and separated from each other by about 10 cm. Two arrays of eight terraria each were used. Two 100-cm fluorescent luminaires spanned each array.

The Experimental Setup.—Beginning 11 May 2004, we conducted an experiment to test the effect of manipulation of dietary vitamin D₃ on voluntary exposure to UVB light. Illumination from the cool white fluorescent tubes emit no measurable UVB; hence, we used an additional single fluorescent luminaire containing a UVB-emitting fluorescent tube (FS-40 Philips sunlamp, Philips Co., Somerset, NJ) located adjacent and parallel to the luminaire containing the cool white tube. The sunlamp was illuminated manually for 1 h twice a week. With the sunlamp turned on, we established a horizontal UVB gradient by placing boards on top of the cages 10 min before illumination (Fig. 1). Prior to and after the 18-week experiment, a Gigahertz-Optik P 9719 broadband radiometer was used to measure the UVA, UVB, and visible light irradiances at various points within the enclosures. Enclosures were subsequently divided into three zones based on UVB intensity. For the sunlamp, UVB in the high UV zone averaged 42.2 $\mu\text{W}/\text{cm}^2$; medium zone, 2.5 $\mu\text{W}/\text{cm}^2$; low zone 0 $\mu\text{W}/\text{cm}^2$ (Table 1; Fig. 1). UVB irradiance during the 1-h UV treatment sessions was slightly lower than the average measured in the field for *A.*

TABLE 1. Light properties measured for anoles in the field in Jamaica and the laboratory. Irradiance values are mean $\mu\text{W}/\text{cm}^2$.

Light category	<i>Anolis sagrei</i> in field	<i>Anolis lineatopus</i> in field	Both in lab sunlamp
UVB irradiance	65.7	16.7	42.4
UVA irradiance	1,939.5	630.5	37.1
Visible irradiance	24,396.9	6,969.6	116.3

sagrei and slightly higher than field values for *A. lineatopus* (Table 1). UVA (315–400 nm) and visible (400–700 nm) irradiances were considerably lower during the UVB-treatment sessions in the laboratory than in the field.

Experimental Design.—Predictions from the hypothesis required the quantification of UVB exposure and dose and the manipulation of dietary vitamin D₃. To quantify UVB exposure during the UV treatment sessions, we noted the number of times a lizard sought out and was exposed to the medium or high UVB zones at the beginning of each 10-min segment of each hour-long treatment session. The tallies for each hour were summed for each individual for each of three, 6-week dietary vitamin D₃ manipulation periods. Period (A) included no supplementation of Vitamin D₃; period (B), supplementation of dietary vitamin D₃; period (C), no supplementation of dietary vitamin D₃. This was a repeated-measures ABA design in which each individual served as its own control before and after receiving the high vitamin D₃ diet.

In addition to the number of exposures, we also estimated the UVB dose (exposure \times time) that each individual received in periods (A), (B), and (C) as follows. When UVB lights were illuminated, individuals located in one of two light zones (medium or high UVB, Fig. 1) at the beginning of a 10-min survey of all cages were assumed to remain in that zone for the entire survey. The irradiance of that zone ($\mu\text{W}/\text{cm}^2$) was multiplied by 600 sec (10 min) to estimate the UVB dose in microjoules per square centimeter. For clarity of presentation, microjoules were converted to millijoules (microjoules / 1,000). Ten-minute doses for each lizard were summed for each 1-h observation session and for each of the three dietary manipulation periods (A), (B), (C).

Response to Visible Light.—Two additional non-UV treatment sessions per week were included to compare the responses of anoles to UVB and visible light. Observation and data-collection procedures were the same as described above except only the cool white fluorescent tubes were turned on while the sunlamps remained off. During the day, both before and after the hour-long sessions (UVB-on or UVB-off), the boards were removed, and the lizards were exposed to illumination from the cool white fluorescent tubes with no measurable UV emitted for the remaining time between 0700 and 1900 h.

Dietary Treatments.—Throughout the 6-week period before the experiment began and the remaining 18 weeks of the experiment, we fed the lizards small- to medium-sized crickets twice weekly. The crickets were fed an experimental diet from Zeigler Bros., Inc. (Gardners, PA) containing no vitamin D₃ additive. This resulted in a baseline of about one IU per dry gram of cricket and is considered to be a low vitamin D₃ diet (see Ferguson et al., 1996). Water was provided daily by spraying the walls of each cage with a hand mister.

Throughout period (A), we fed each lizard one extra cricket each week in addition to their normal semiweekly feeding of noninjected crickets. This cricket was injected with corn oil

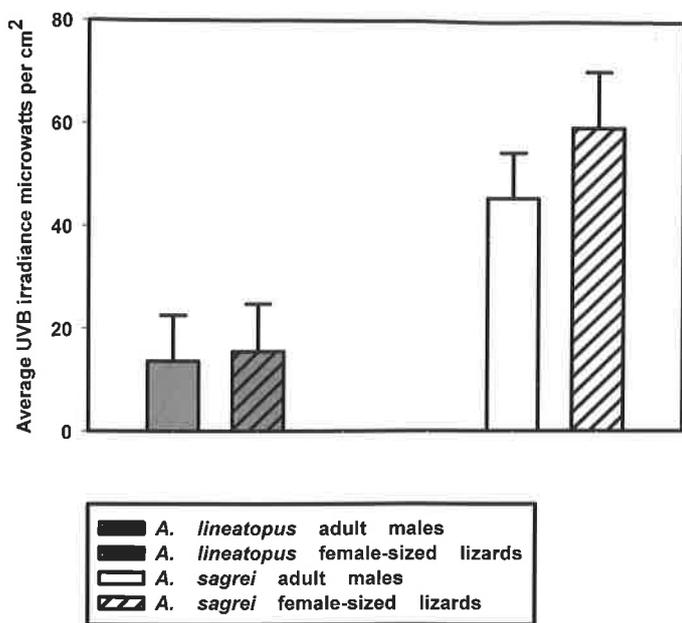


FIG. 2. UVB exposure of free-living Jamaican *Anolis* at the Hofstra University Marine Laboratory, St. Anns Parish, Jamaica in March 2004. There was a species effect but no sex-size category effect (see text).

containing no vitamin D₃. During period (B), we supplemented vitamin D₃ using a single cricket injected with corn oil containing vitamin D₃. This resulted in an additional one to two IU/g of vitamin D₃ each week. The vitamin D₃-containing cricket had about 4 (*A. sagrei*) or 30 (*A. lineatopus*) times the natural weekly dietary dose as estimated from stomach contents collected from the field in Jamaica (Ferguson et al., 2005). For period (C), we returned the supplementary diet to crickets injected with corn oil containing no vitamin D₃.

Biosynthetic Potential of UV Sources.—To compare the relative vitamin D₃ photo-biosynthetic potential of natural sunlight and the fluorescent sunlamp, we measured the production of photoproduct of in vitro models when exposed to one UV source or the other. In-vitro models are ampules containing an ethanol solution of provitamin D₃ (Lu et al., 1992; Chen et al., 1993). They were exposed either to the sun or to a 20-Watt Westinghouse FS-20 sunlamp. Exposure was for 12, 24, 40, or 56 min. Irradiance of the two sources was matched at an average UV-index of 5.8 measured with a Solartech 6.5 broadband UVB meter. The percent photoproduct was determined by HPLC procedures (for a description of the procedures, see Gehrman et al., 2004).

Data Processing.—Data were compiled using EXCEL (versions 2000 and 2003). Data were graphed and analyzed using SIGMASTAT version 3.0, SIGMA PLOT version 2001 and SYSTAT version 10.0. Data were transformed when necessary to alleviate violations of normality and homogeneity of variance when using parametric tests.

RESULTS

In the field, *A. sagrei* were exposed to more UVB than were *A. lineatopus* (Fig. 2). Two-way ANOVA showed a species effect ($F_{(1,41)} = 19.2$; $P < 0.001$; all data were ln-transformed) but no sex-size effect ($P = 0.71$).

In the laboratory experiment, the pattern of voluntary exposure to medium or high light zones by the lizards was variable. Although most individuals of both species showed a

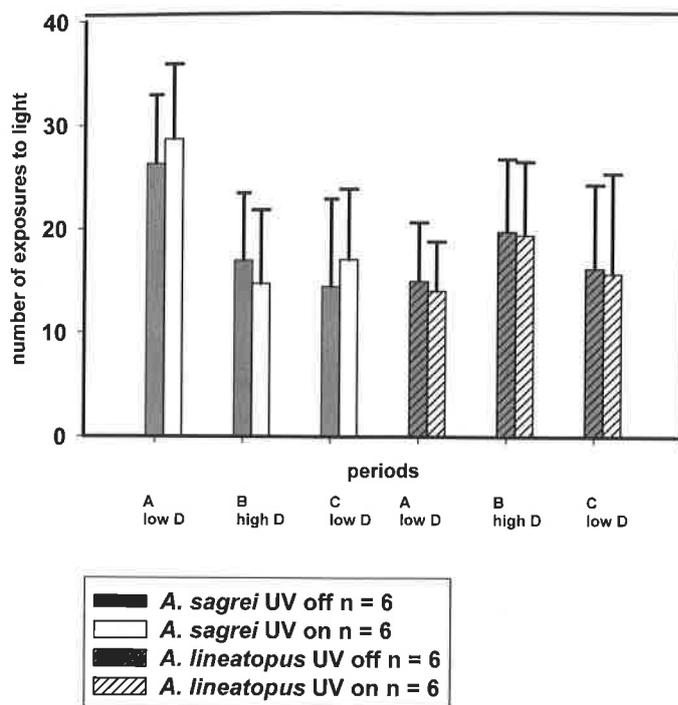


FIG. 3. Mean number of voluntary exposures of six *Anolis sagrei* and six *Anolis lineatopus* to a light source (UVB on or off) during each of three sequential 6-week periods (A), (B), (C) during which dietary vitamin D₃ was changed from low to high and back to low. Capped vertical lines above the bars are one standard error. There were 72 possible exposures for each of the three periods with the UVB source on or off. There was significant variation among the periods only for *A. sagrei* (see text).

similar species-specific response to the experimental treatments, a few of each species showed atypical responses. A single individual female of each species behaved differently from the others by basking little during the initial periods but increasing basking time to almost constant exposure during the final two experimental periods. Two additional females, one of each species, exposed themselves to the medium or high light zones rarely during the 18-week experiment. Therefore, to explore possible underlying trends and species differences, the two female outliers of each species were deleted from the analyses resulting in a sample size of six for each species (four males and two females). Because UVB exposure in the field was not different between adult males and female-sized anoles (see Results), sexes were pooled for analysis in the laboratory experiment.

***Anolis sagrei*: Effect of Dietary D₃ on Number of Voluntary Exposures to UVB.**—In the laboratory, the *A. sagrei* exposed themselves to the medium or high UVB light zone more frequently (mean = $28.7 \pm \text{SE } 7.2$ exposures) during the sunlamp treatment period (A) when fed a low vitamin D₃ diet than when fed a high vitamin D₃ diet in period (B) (mean = $14.7 \pm \text{SE } 7.1$ exposures; Fig. 3). After the resumption of low dietary D₃ in period (C), there was a tendency for a return to higher exposure (mean = $17.0 \pm \text{SE } 6.8$ exposures). There was an overall diet effect (RMANOVA: $F_{(2,17)} = 9.5$; $P = 0.005$). Post hoc testing showed that the number of exposures during period (A) was greater than those of both periods (B) and (C) (Holm-Sidak method: $P < 0.05$). Periods (B) and (C) were not different.

During the visible light treatments, when the light gradient was in place and the UVB source off, there was a diet effect for *A. sagrei* with decreasing voluntary exposure. (RMANOVA: F

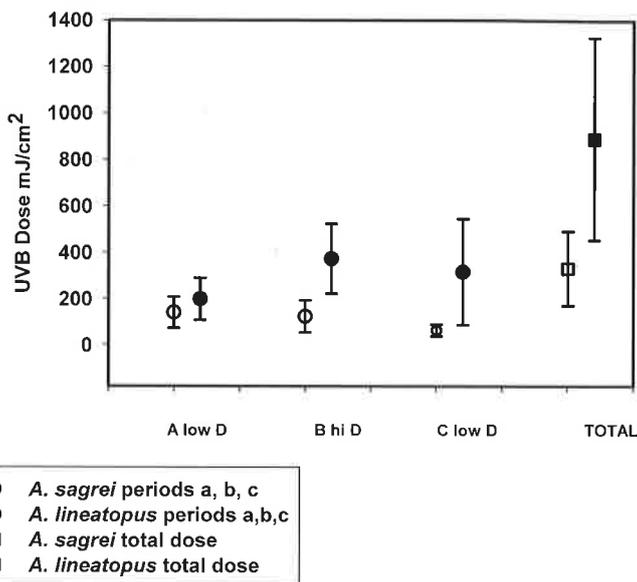


FIG. 4. Mean UVB dose for six *Anolis sagrei* and six *Anolis lineatopus* received when they voluntarily exposed themselves to medium or high exposure from the UVB source during each of three sequential 6-week periods (A), (B), (C) and also during the total 18-week experiment. There was significant variation among the periods only for *A. sagrei* (see text).

(2,17) = 5.0; $P = 0.032$; Fig. 3). Exposures were highest in period (A) (mean = $26.3 \pm SE 6.6$), lower in period (B) (mean = $16.9 \pm SE 6.5$), lowest in period (C) (mean = $14.4 \pm SE 8.4$) Post hoc testing showed that the number of exposures during period (A) was greater than that of period (C) (Holm-Sidak method: $P < 0.05$). There was no difference in the number of exposures when the sunlamps were on versus off (paired t -test; $df = 5$; $t = 1.22$, $P = 0.28$).

Anolis sagrei: Effect of Dietary Vitamin D₃ on UVB Dose.—Voluntary UVB exposure dose selected by the lizard during the sunlamp treatments decreased throughout the experiment (Fig. 4). Mean UVB dose dropped from $142.3 \pm SE 67.3$ mJ per cm² during period (A) to $125.2 \pm SE 69.8$ in period (B) to $65.2 \pm SE 25.5$ in period (C) (Friedman RMANOVA on ranks: $\chi^2 = 7.0$, $df = 2$; $P = 0.029$). Dose in period (A) was greater than that in period (C) (Tukey test: $P < 0.05$).

Anolis lineatopus: Effect of dietary Vitamin D₃ on Number of Voluntary Exposures to UVB and Dose.—In the laboratory, *A. lineatopus* (a shade dweller and thermal conformer) did not show the same dietary vitamin D₃ response as *A. sagrei* during the sunlamp treatments. They tended to increase their number of exposures from $14.9 \pm SE 5.6$ in period (A) to $19.7 \pm SE 7.0$ in period (B) and then reduce their exposure to $19.2 \pm SE 8.0$ during the second period of low dietary vitamin D₃ in period (C) (Fig. 3). However, number of exposures among the periods was not different (RMANOVA: $F_{(2,17)} = 0.50$; $P = 0.62$; Fig. 3). The number of exposures during visible light treatments with

the UVB source off closely paralleled that with the UVB on (Fig. 3). Mean UVB doses were $199.6 \pm SE 91.3$ mJ per cm² during period (A), $374.4 \pm SE 150.6$ in period (B), and $317.3 \pm SE 229.1$ in period (C). There were no differences in UVB dose among periods (A), (B), or (C) (Fig. 4; RMANOVA: $F_{(2,17)} = 0.79$; $P = 0.48$).

Species Comparison.—Total number of voluntary exposures to UVB and total UVB dose for the 18-week study did not differ between the two species (Table 2). However, although the number of exposures to UVB was slightly greater in *A. sagrei* than in *A. lineatopus*, the total UVB dose was slightly lower in *A. sagrei*. This is because the two species differed in the relative proportion of high and medium UVB exposures with *A. sagrei* exposing themselves less and *A. lineatopus* exposing themselves more to high UVB locations (Table 2).

Photoproduct Production of Sunlight and Sunlamps.—When the UVB irradiance of natural sunlight and the sunlamps registered the same reading on a UVB meter, the percent photoproduct produced by in vitro models was greater for the sunlamp than that produced upon exposure of models to sunlight (Fig. 5). When the regression lines of photoproduct produced as a function of time for each of the UVB sources were compared, there was an interaction between time and percent photoproduct for the lines from each source. The slopes of the two lines were different (ANOVA: [exposure time \times UV-source], $F_{(1,5)} = 19.8$; $P < 0.01$).

DISCUSSION

In the field, individuals of *A. sagrei* (a sun-dwelling thermoregulating species) exposed themselves to higher UVB than did individuals of *A. lineatopus* (a shade-dwelling thermal conforming species). There was no sex-size effect. This extends previous findings for adult male *A. sagrei* and *A. lineatopus* in which individuals were followed and their UVB exposure quantified for an entire day (Ferguson et al., 2005). Because there was no sex-size effect on UVB exposure in the field, the pooling of data from males and females in the laboratory experiment was justified.

In the laboratory, we obtained support for the hypothesis that *A. sagrei* shows a behavioral regulatory light response to increases in dietary vitamin D₃, namely lizards expose themselves to less UVB. *Anolis sagrei* is the second lizard species shown to possess this ability. Such a mechanism was first documented for lizards in studies of the Panther Chameleon (*Furcifer pardalis*) (Ferguson et al., 2003; Karsten et al., 2009).

After the dietary vitamin D₃ supplementation was discontinued in period (C), the slow return to higher voluntary UVB exposure was unexpected. We assumed that vitamin D₃ half-life is relatively short (i.e., less than 6 weeks). However, this assumption is not consistent with findings from a recent study of monitor lizards (Ferguson et al., 2009). The study of monitor lizards, conducted after the experiment in this report, generated

TABLE 2. Comparison of voluntary UVB exposure of *Anolis sagrei* and *Anolis lineatopus* during 36 1-h observation periods with sunlamps turned on over an 18-week period. Dose is mJ cm⁻². Species differences were tested using a Mann-Whitney rank sum tests or t -tests.

	Number exposures to UVB (mn \pm SE) N = 6		Percent UVB exposures in the high vs. medium UVB zone (mn \pm SE, N = 6)		Total UVB dose (mn \pm SE) N = 6	
<i>Anolis sagrei</i>	60.3 \pm 20.2	U = 14.5 P > 0.59	12.6 \pm 3.9	t = 2.6 P < 0.03	332.7 \pm 160.7	U = 23.0 P > 0.49
<i>Anolis lineatopus</i>	49.0 \pm 20.1		49.8 \pm 14.6		891.3 \pm 435.8	

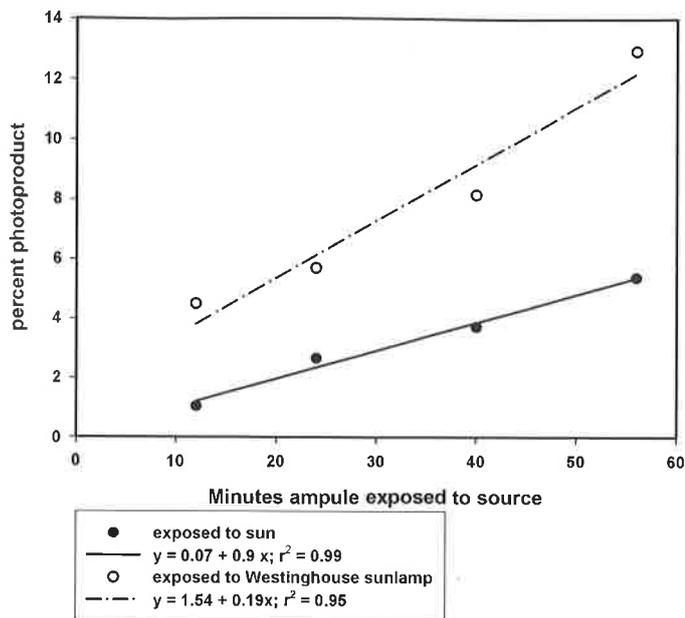


FIG. 5. Percent photoproduct production within in vitro models exposed to two UVB sources with the same average irradiance. The irradiance was measured with a Solartech 6.5 broadband UVI meter for both the sun and for a Westinghouse FS-20 sunlamp. The regressions are different (see text).

the first information on half-life of 25-OH vitamin D₃ for a lizard. In monitors, substantial 25-OH vitamin D₃ levels persist in the circulation with a half-life of 120–139 days when deprived of all sources of dietary vitamin D₃ and UVB. Although the half-life of circulating 25-OH vitamin D₃ is unknown for *Anolis*, it is probably longer than the 6 weeks of deprivation of dietary vitamin D₃ administered in period (C). The ability to store vitamin D₃ for extended periods during deprivation in lizards appears to be longer than we anticipated in our experimental design. In retrospect, to see a return to higher UV exposure attributable to a decline in stored vitamin D₃, period (C) should have been extended for more than 6 weeks.

In contrast to *A. sagrei*, the data for *A. lineatopus* failed to support the hypothesis. They showed no decrease in number of voluntary exposures to UVB in response to enhanced dietary vitamin D₃ in the laboratory during period (B) or (C) of the experiment. The reason for the difference in response to UVB between the two anole species is unclear. The stomach contents of field-collected specimens had lower vitamin D₃ than those of *A. sagrei* (Ferguson et al., 2005). Because of less availability of dietary vitamin D₃, there may be less reliance on dietary sources. Natural selection for the evolution or maintenance of an ability to use dietary vitamin D₃ or a link between dietary D₃ and behavioral response to a UVB light source in *A. lineatopus* may be absent. In addition, *A. lineatopus* has a higher sensitivity of the skin regarding production of vitamin D₃ upon exposure to UVB (Ferguson et al., 2005). If they also possess an enhanced ability to store vitamin D₃ metabolites, which also could be favored by natural selection for a species in poor UVB and vitamin D₃ environments, the *A. lineatopus* in our study may have been less vitamin D₃-deficient during our 18-week experiment than the *A. sagrei*. A similar lack of significant response to light was shown in another shade dwelling, thermal conforming species *A. gundlachi* from Puerto Rico when studied in the context of thermoregulation (Hertz et al., 1994). These lizards did not seek light because, as thermal conformers, they

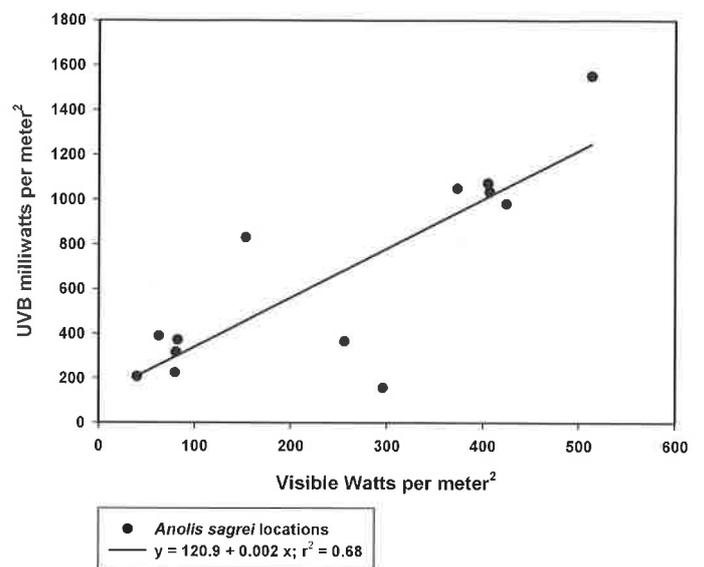


Fig. 6. Irradiance of UVB as a function of irradiance of visible sunlight at locations where *Anolis sagrei* were discovered in the field at Jamaica in March 2004. The regression is significant ($P < 0.001$).

were not heat deficient in the shade of their laboratory environment (Hertz et al., 1994).

Anoles have UV-sensitive vision (Fleishman et al., 1997; Loew et al., 2002). Some species rely on UVA vision during social communication. However, in the sunlamp experiment, neither species responded differently when the sunlamps were on versus when they were off. Apparently, lamp UVB had little if any direct effect on the dietary response of *A. sagrei*. Any UVB the lizards received was probably cued indirectly by visible light. Although the mechanism is unknown, the greater exposure to UVB when deprived of dietary vitamin D₃ during the treatments for *A. sagrei* was possibly a response to visible light upon perception of an overall beneficial physiological effect. UVB is strongly correlated with visible light in the field for *A. sagrei* (Fig. 6). Thus, UVB exposure is greater for *A. sagrei* when exposing itself to higher visible sunlight. Similarly, Hertz et al. (1994) showed that the Puerto Rican species *A. cristatellus*, a thermoregulator, responded to visible light when seeking heat and concluded that this was because the two are correlated in its natural environment.

The light environment of our laboratory differs from that in the field in Jamaica. Although the UVB irradiance was close to that measured in the field (a little lower than the average field value for *A. sagrei*, a little higher than average for *A. lineatopus*), the levels of both UVA and visible light were several orders of magnitude lower in the laboratory compared to the field for both species (Table 1). Given the importance of light spectrum components and their impact on the phototactic response of the anoles, differences between laboratory and field may have compromised our results. Furthermore, the physiological effectiveness regarding vitamin D₃ synthesis differs between a similar UVB dose generated by sunlight as compared to the same dose generated by a fluorescent FS sunlamp (Fig. 5). This is because UVB irradiance from the sun contains proportionally more long-wavelength UVB (>300 nm) and that from the lamp contains proportionally more short-wavelength UVB (<300 nm). Short wave UVB is more effective for vitamin D synthesis (MacLaughlin et al., 1982). A more efficient UVB physiological effect in the laboratory environment may cause more rapid

replenishment of vitamin D₃ and a more sporadic phototactic response.

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LITERATURE CITED

- CHEN, T. C., Z. LU, A. PEREZ, AND M. F. HOLICK. 1993. Cutaneous synthesis of vitamin D₃ in response to sun-tanning bed irradiation. *In* E. G. Jung and M. F. Holick (eds.), *Biologic Effects of Light 1993*, pp. 28–33. Walter de Gruyter, Berlin, Germany.
- COWLES, R. M., AND C. M. BOGERT. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bulletin American Museum Natural History* 83:261–296.
- FERGUSON, G. W., J. R. JONES, W. H. GEHRMANN, S. H. HAMMACK, L. G. TALENT, R. D. HUDSON, E. S. DIERENFELD, M. P. FITZPATRICK, F. L. FRYE, M. F. HOLICK ET AL. 1996. Indoor husbandry of the panther chameleon *Chamaeleo [Furcifer] pardalis*: effects of dietary vitamins A and D and ultraviolet irradiation on pathology and life-history traits. *Zoo Biology* 15:279–299.
- FERGUSON, G. W., W. H. GEHRMANN, K. B. KARSTEN, S. H. HAMMACK, M. MCRAE, T. C. CHEN, N. P. LUNG, AND M. F. HOLICK. 2003. Do panther chameleons bask to regulate endogenous vitamin D₃ production? *Physiological and Biochemical Zoology* 76:52–59.
- FERGUSON, G. W., W. H. GEHRMANN, K. B. KARSTEN, A. J. LANDWER, E. N. CARMAN, T. C. CHEN, AND M. F. HOLICK. 2005. Ultraviolet exposure and vitamin D synthesis in a sun-dwelling and a shade-dwelling species of *Anolis*: are there adaptations for lower UVB and dietary vitamin D₃ availability in the shade? *Physiological and Biochemical Zoology* 78:193–200.
- FERGUSON, G. W., W. H. GEHRMANN, B. PEAVY, C. PAINTER, R. HARTDEGEN, T. C. CHEN, M. F. HOLICK, AND J. E. PINDER III. 2009. Restoring vitamin D in monitor lizards: exploring the efficacy of dietary and UVB sources. *Journal of Herpetological Medicine and Surgery* 19:81–88.
- FERGUSON, G. W., A. M. BRINKER, W. H. GEHRMANN, S. E. BUCKLIN, F. M. BAINES, AND S. J. MACKIN. 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.
- FLEISHMAN, L. J., M. BOWMAN, D. SAUNDERS, W. E. MILLER, M. J. RURY, AND E. R. LOEW. 1997. The visual ecology of Puerto Rican anoline lizards: habitat light and spectral sensitivity. *Journal of Comparative Physiology A* 181:446–460.
- GEHRMANN, W. H., J. D. HORNER, G. W. FERGUSON, T. C. CHEN, AND M. F. HOLICK. 2004. A comparison of responses by three broadband radiometers to different ultraviolet-B sources. *Zoo Biology* 23:355–363.
- HERTZ, P. E., L. J. FLEISHMAN, AND, C. ARMSBY. 1994. The influence of light intensity and temperature on microhabitat selection in two *Anolis* lizards. *Functional Ecology* 8:720–729.
- HOLICK, M. F. 1996. The role of sunlight in providing vitamin D for bone health. *In* M. F. Holick and E. G. Jung (eds.), *Biologic Effects of Light 1995*, pp. 3–12. Walter de Gruyter, Berlin, Germany.
- . 1999. *Vitamin D: Physiology, Molecular Biology, and Clinical Application*. Humana, New York.
- . 2004. Vitamin D: importance in prevention of cancers, type 1 diabetes, heart disease, and osteoporosis. *American Journal of Clinical Nutrition* 79:362–371.
- HUEY, R. B. 1982. Temperature, physiology and the ecology of reptiles. *In* C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*. Vol. 12, pp. 25–91. Academic Press, New York.
- KARSTEN, K. B., G. W. FERGUSON, T. C. CHEN, AND M. F. HOLICK. 2009. Panther chameleons, *Furcifer pardalis*, behaviorally regulate optimal exposure to UV depending on dietary vitamin D₃ status. *Physiological and Biochemical Zoology* 82:218–225.
- LISTER, B. 1976. The nature of niche expansion in West Indian *Anolis* lizards I: ecological consequences of reduced competition. *Evolution* 30:659–676.
- LOEW, E. R., L. J. FLEISHMAN, R. G. FOSTER, AND I. PROVENCIO. 2002. Visual Pigments and oil droplets in diurnal lizards: a comparative study of Caribbean anoles. *Journal of Experimental Biology* 205:927–938.
- LU, Z., T. C. CHEN, L. KLINE, T. MARKESTAD, J. PETTIFOR, M. LADIZESKY, C. MAUTALIN, AND M. F. HOLICK. 1992. Photosynthesis of previtamin D₃ in cities around the world. *In* M. F. Holick and A. M. Kligman (eds.), *Biologic Effects of Light*, pp. 48–52. Walter de Gruyter, Berlin, Germany.
- MACLAUGHLIN, J. A., R. R. ANDERSON, AND M. F. HOLICK. 1982. Spectral character of sunlight modulates photosynthesis of previtamin D₃ and its photoisomers in human skin. *Science* 216:1001–1003.
- MANNING, B., AND G. C. GRIGG. 1997. Basking is not of thermoregulatory significance in the “basking” freshwater turtle *Emydera signata*. *Copeia* 1997:579–584.
- PLUMMER, M. V., T. L. CRABILL, N. E. MILLS, AND S. L. ALLEN. 2005. Body temperature of free-ranging softshell turtles (*Apalone spinifer*) in a small stream. *Herpetological Review* 36:371–375.
- POUGH, F. H., C. M. JANIS, AND J. B. HEISER. 2005. *Vertebrate Life*. 7th ed. Pearson, Upper Saddle River, NJ.

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