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Effects of Artificial Ultraviolet Light Exposure on Reproductive Success of the Female Panther Chameleon (*Furcifer pardalis*) in Captivity

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Having previously documented experimentally the need for ultraviolet B (UVB) irradiation (290–315 nm) in the light environment of captive female panther chameleons (*Furcifer pardalis*) to ensure hatching success of their eggs, we investigated optimal UVB irradiation levels. From 1996–1998 28 hatchling female panther chameleons were raised to maturity and bred (using vitamin and mineral-fortified insect diets low in vitamin D) in nine different artificial UVB light environments. Seven of the environments included long (12 hr/day) low irradiation exposures ranging from 1.7 to 22 $\mu W/cm^2$ UVB, with a corresponding conversion of provitamin D_3 to photoproducts in in vitro models of 0.18 to 1.52% in 2 hr. Two environments included short (0.5 and 1.0 hr/day), high irradiation exposures of 55 and 49 $\mu W/cm^2$ UVB, respectively, with a corresponding conversion of provitamin D_3 to photoproducts in in vitro models of 8.3% to 14.6% in the respective 0.5- and 1.0-hr time periods. Females raised with the mid-level long/low exposures (5–15 $\mu W/cm^2$ UVB; 0.52–1.32% conversion to photoproducts in in vitro models) produced viable eggs with a significantly higher percentage of hatching compared to those with the extreme (highest or lowest) long/low exposures. Those raised with the short-/high-exposure environments produced viable eggs with a generally high percentage of hatching, but success was variable. The results and techniques for light quality assessment are interpreted, with recommendations for practical application by the

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herpetoculturist desiring to successfully breed panther chameleons in captivity. Zoo Biol 21:525–537, 2002.

Key words: UVB; reproduction; chameleon

INTRODUCTION

The panther chameleon (*Furcifer pardalis*) is a large, colorful species of chameleon from northern Madagascar. This and about a dozen other chameleon species have been imported in large numbers by the pet trade since the 1980's [Brady and Griffiths, 1999]. A recent restriction on chameleon importation from Madagascar has left this and three other non-threatened species as the only chameleons legal for importation from Madagascar (except for the dwarf chameleons of the genus *Brookesia*). Development of a sustaining captive population of the panther chameleon will help to further relieve the collection pressure on natural populations of all Old World chameleons. While young, wild-caught, and first-generation captive-raised specimens make hardy captives, breeding success has been sporadic until recently [Ferguson, 1991, 1994; Ferguson et al., 1996].

A fundamental problem for lizards in captivity is the failure of captive-produced eggs to hatch at term [Zwart et al., 1992; Ferguson et al., 1996]. Viable eggs produced by apparently healthy captive-raised adults incubate full term but then fail to hatch. The fully developed, dead embryos appear normal but have poorly-mineralized skeletons. A similar problem occurs in chickens and has been verified experimentally to be a deficiency of vitamin D in the egg yolk caused by hypovitaminosis D in the mother [Narbaitz and Tsang, 1989; Packard and Clark, 1996]. The problem can be corrected in the panther chameleon by providing sufficient ultraviolet B (UVB) irradiation (290–315 nm) to the adult female prior to oviposition [Ferguson et al., 1996].

In many vertebrates UVB radiation causes provitamin D (7-dehydrocholesterol) in the skin to form previtamin D_3, which thermally isomerizes to vitamin D_3 [Holick et al., 1995]. After hydroxylation in the liver the biologically inert vitamin becomes 25-hydroxyvitamin D_3 [Holick and Clark, 1978]. Then it is carried by the blood to the kidney, where it is converted to its hormonally active form 1,25 dihydroxyvitamin D or calcitriol [Holick et al., 1971]. This hormone's main function is to facilitate uptake of calcium from the gut of juveniles or adults, or from yolk and shell in developing embryos. Deficiency causes bone disease and hatching failure [Packard and Clark, 1996; Holick, 1999].

UVB irradiation can be provided with exposure to natural unfiltered sunlight or with artificial UVB-producing lamps [Gehrmann, 1987, 1994, 1998; Chen et al., 1994]. This research was conducted to clarify the most effective artificial UVB exposure necessary for successful hatching by providing environments with different UVB irradiances for different exposure times throughout the growth, maturation, and reproduction periods of female panther chameleons. Dietary vitamin D was purposely low. This report includes data from a preliminary study conducted in 1996 [Ferguson et al., 1999] combined with data on additional females collected in 1997. Based on the combined data set we provide advice for the most effective lighting set-up for successful reproduction in this chameleon species.

METHODS

Twenty-eight hatchling female panther chameleons were obtained using the techniques described in Ferguson [1994] and set up to be raised from hatching to maturity in 11.4-l terraria (see Ferguson et al. [1996] for details of terrarium set-up and thermal environment). Two experiments were conducted: one in 1996–1997 [Ferguson et al. 1999] and one in 1997–1998. Nine light-exposure treatments were provided (Tables 1 and 2).

In the first experiment there were 13 hatchlings; in the second experiment there were 15. Chameleons were fed domestic crickets (*Achaeta domestica*) three times per week. Crickets were fed commercially prepared (True Chameleons, Fort Worth, TX) grain-based diets enriched with vitamins and minerals but with no vitamin D added (Table 3). Visible and UV light was provided using various UV-emitting fluorescent tubes (20 or 40 W) suspended at various distances above the mesh-covered tops of the terraria (Table 1). The Vita-Lites were from Duro-Test Corporation (Bergen, NJ). Ultraviolet Resources (Cleveland, OH) provided experimental lamps and UVB-emitting sunlamps (Philips Co., Somerset, NJ). Zoo Med (San Luis Obispo, CA) provided Reptisun 5.0 and 3.0 lamps. UV irradiances were measured with Spectronics UVA and UVB radiometers (Spectroline DM-365N and Spectroline DM-300N; Spectronics Corp., Westbury, NY), and visible light illuminance was measured with a General Electric type 214 light meter (GE, Cleveland, OH). Vitamin D production potential was assessed using in vitro models [Lu et al., 1992], which are

TABLE 1. Description of light treatments

Treatment	Light source	Hours per day	Year
1	Reptisun 5.0; two 20W tubes in double-lamp nonreflector luminaire 6–25 cm from animal	12	1996–1997
2	Ultraviolet resources; experimental single 40W tube in nonreflector luminaire 8–26 cm from animal	12	1996
3	Reptisun 3.0; two 20W tubes in double-lamp nonreflector luminaire 14–26 cm from animal	12	1997
4	Ultraviolet resources; experimental single 40W tube in nonreflector luminaire 8–26 cm from animal	12	1996
5	Ultraviolet resources; experimental single 40W tube in nonreflector luminaire 11–26 cm from animal	12	1997
6	Reptisun 3.0; two 20 W tubes in double-lamp nonreflector luminaire 20–38 cm from animal	12	1996
7	Vita-Lites; two 20 W tubes in double-lamp nonreflector luminaire 8–24 cm from animal		1996–1997
8[a]	Philips FS40 sunlamp; single tube in nonreflector luminaire 35–50 cm from animal	0.5	1997
9[a]	Philips FS40 sunlamp; single tube in nonreflector luminaire 28–45 cm from animal	1	1996–1997

[a]For treatments 8 and 9, a cool white F40 tube and a 40 watt Vita-Lite tube, respectively, were positioned alongside the sunlamp. These ancillary light sources illuminated terraria for 12 hr and contributed to the light environment during the illumination periods (0.5 or 1 hr) of the sunlamps. Also, unlike treatments 1–7, a shade retreat was provided in treatments 8 and 9.

TABLE 2. Light exposure of treatments

Treatment	H/DA	UVA $\mu W/cm^2$	UVB $\mu W/cm^2$	Percent photo-products	Illuminance (lux)
1	12	60–65	22–18	1.52–0.78	915–1076
2	12	15	15	1.34	1700
3	12	44	7	0.64	1014
4	12	11	12	1.11	1814
5	12	10	8	0.52	2027
6	12	31	6	0.82	800
7	12	15–9	2.3–1.7	0.26–0.18	1076–968
8	0.5	7	55	8.28	848
9	1	12	49	14.59	960

Irradiation ($\mu W/cm^2$), illuminance (lux), and in vitro model percent conversion of provitamin D values are from midway between the top and bottom of the terraria where chameleons usually perched. Ranges show the values in successive years when the treatment was replicated. For treatments 1–7, in vitro models were exposed for 2 hr. For treatments 8 and 9, in vitro models were exposed for 0.5 and 1.0 hr, respectively.

TABLE 3. Vitamin and mineral content of crickets fed to panther chameleons

Vitamin E IU/kg	Vitamin A IU/g	Vitamin D IU/g	Calcium ppm	Phosphorus ppm	Ca/P ratio
211 ± 50	3.3 ± 2.2	0.22 ± 0.10	7472 ± 1936	9900 ± 237	0.72 ± 0.17

Samples ($n = 9$) were drawn at monthly or bimonthly intervals throughout the experiment in 1997–1998. Values are mean $\pm$ se.

quartz ampules containing the vitamin D_3 precursor (provitamin D_3) in ethanol solution. Upon exposure to UVB light the provitamin D_3 is photolyzed to previtamin D_3 and other photoproducts. The amount of photoproducts, including vitamin D_3, that is produced in this model is proportional to the UVB irradiance (Fig. 1). Upon maturity, each female was bred to a captive-raised male by placing the female in a male's cage for periods of less than 1 hr. All UV lights were extinguished or covered in the male's cage during breeding.

RESULTS

Most chameleons survived to maturity and reproduced successfully (Tables 4 and 5). Among those receiving long/low exposure treatments (1–7), those that received the extreme lowest (<5 $\mu W/cm^2$) or highest (>15 $\mu W/cm^2$) UVB irradiation within that range (corresponding provitamin D conversions of <0.5 or $>1.3\%$; Tables 2, 4, and 5; treatments 1 and 7; Figs. 2–5) reproduced but suffered significantly lower hatching success (8.7%) than those receiving mid-levels of UVB exposure within the long/low treatments, i.e., 5–15 $\mu W/cm^2$ (corresponding provitamin D conversions ranging from 0.5% to 1.3%; Tables 2, 4, and 5; treatments 2–6; Figs. 2–5; $P < 0.01$, $t = 3.7$, $n = 9$; Table 5). Those receiving mid levels of UVB had a hatching success of viable (surviving to term) eggs of 68%. Those receiving the short/high treatments (Tables 2, 4, and 5; treatments 8 and 9) had excellent hatching success overall (79%), but there were several clutch failures (Table 5).

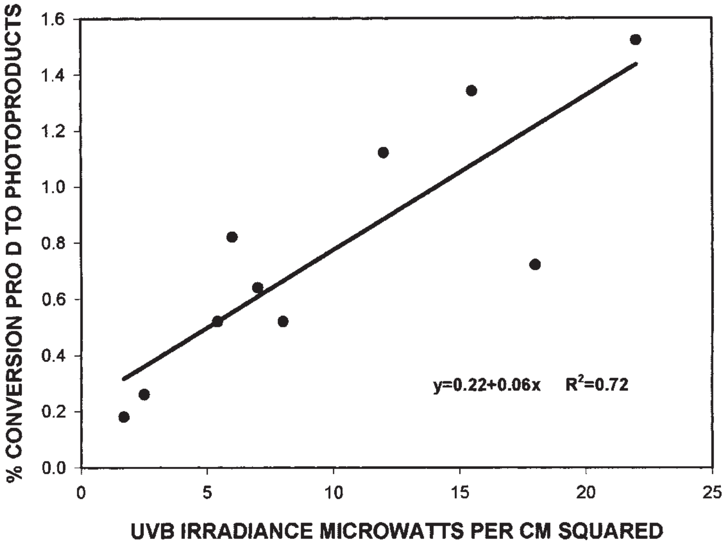

Fig. 1. Percent conversion of provitamin D in relation to UVB irradiance for low intensity UVB tubes (treatments 1–7). In vitro models containing provitamin D were placed at the terrarium perch closest to the light source for 2 hr. Irradiance was measured from the same location.

TABLE 4. Reproductive success of surviving females exposed to various light treatments

Treatment (UVB irradiance μW/cm^2)	No. of neonate females reaching adult size (adult/neonate)	No. of robust hatchlings per viable eggs for each adult female	Percent hatching of viable eggs for each female (% for treatment pooled)
1 (22-18LL)	3/3	0/10, 2/5, 0/0	0, 40 (13)
2 (15LL)	2/2	18/37, 6/12	48, 50 (49)
3 (7LL)	2/2	18/19, 0/0	95 (95)
4 (12LL)	2/2	26/40, 0/0	65 (65)
5 (8LL)	2/2	13/13, 0/0	100 (100)
6 (6LL)	2/2	39/55, 0/0	71 (71)
7 (2.3-1.7LL)		0/8	0 (0)
8 (55SH)	4/5	12/13, 14/14, 16/17, 0/0	92, 100, 94 (95)
9 (49SH)	7/8	52/53, 13/13, 21/34, 20/33, 0/10, 0/0, 0/0	98, 100, 62, 61, 0 (64)

Robust hatchlings are those surviving long enough to begin feeding and growing (about 3 weeks). Viable eggs are those surviving to term but not necessarily hatching.
LL, long/low; SH, short/high.

DISCUSSION

Female panther chameleons maintained indoors on low vitamin D diets require moderate amounts of UVB exposure to reproduce successfully. If used properly, some of the currently available low UVB-emitting fluorescent bulbs, such as those

TABLE 5. Comparative survival and reproduction statistics for female panther chameleons

Exposure (treatment no.)	Initial no. of neonates	No. surviving to maturity (%)	No. reproducing (%)	No. laying viable eggs (%)	Hatchlings per female	Percent viable, eggs hatching (hatching/viable females pooled)
Mid-level Long/low (2–6)	10	10 (100)	7 (70)	6 (60)	12	68 (120/176)
Extreme Long/low (1 and 7)	5	4 (80)	4 (100)	3 (75)	0.5	8.7 (2/23)
Short/high (8 and 9)	13	11 (85)	9 (82)	8 (73)	13.5	79 (148/187)

Long/low UVB treatments were grouped according to subjectively perceived patterns of hatching success. Percent hatching was significantly different for mid-level and extreme long/low treatments (see text).

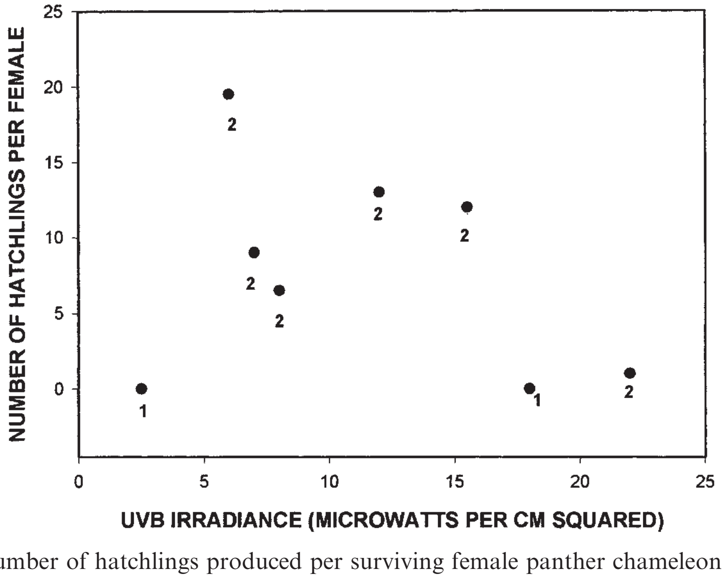

Fig. 2. Number of hatchlings produced per surviving female panther chameleon exposed to long/low treatments (1–7) in relation to UVB irradiance. Numbers next to symbols are number of females surviving to maturity (not necessarily producing viable eggs) used to calculate symbol value.

used in this study, can provide sufficient UVB. If small enclosures are used, the keeper can use the information provided in this report to position and time the light source to ensure the optimum exposure. While short exposure to high UVB-emitting sunlamps also promotes successful reproduction, extended use shortens the reproductive longevity of the adult chameleon, can promote skin tumors and shorten the life span of the chameleon (personal observation), and is potentially dangerous to the keeper. Therefore, we do not recommend sunlamps for general use.

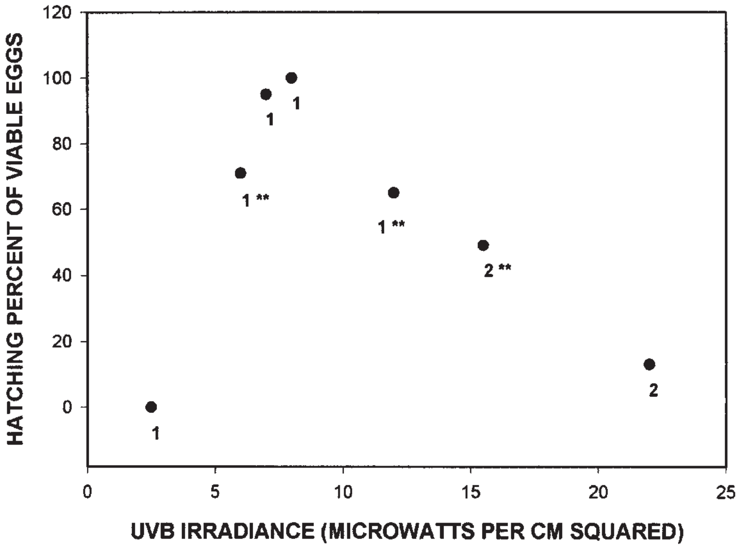

Fig. 3. Hatching percent of viable eggs produced by female panther chameleons exposed to long/low treatments (1–7) in relation to UVB irradiance. Viable eggs survived to term (but did not necessarily hatch). Numbers next to symbols are numbers of surviving females producing at least one viable egg (viable eggs pooled if 2). ** Indicates that one or both of the females indicated by the number produced more than one clutch containing at least one viable egg.

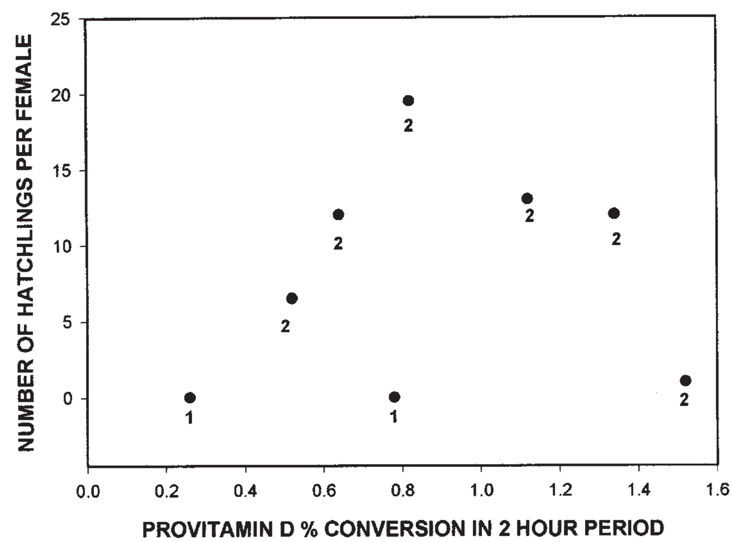

Fig. 4. Number of hatchlings per surviving female panther chameleons exposed to long/low treatments (1–7) in relation to percent provitamin D converted to photoproducts in 2 hr. Numbers are number of females surviving to maturity (not necessarily producing viable eggs) used to calculate symbol value.

Animals maintained in a larger enclosure with a significant UVB gradient may pose a special problem. If the animal is maintained in a large enclosure with a light gradient containing a high component of UVB, the animal will adjust its exposure

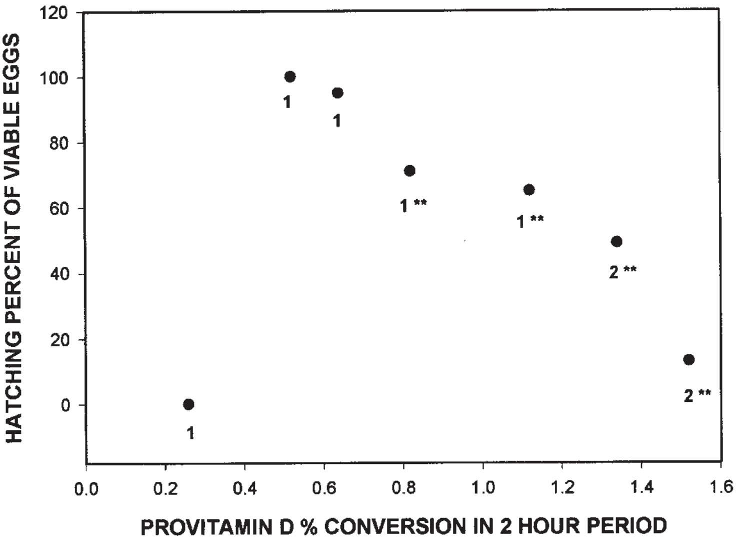

Fig. 5. Hatching percent of viable eggs produced by female panther chameleons exposed to long/low treatments (1–7) in relation to percent provitamin D converted to photoproducts in 2 hr. Numbers next to symbols are numbers of females surviving to maturity and producing at least one viable egg (viable eggs pooled if 2). ** Indicates that one or both of the females indicated by the number produced more than one clutch containing at least one viable egg.

voluntarily depending on its dietary intake of vitamin D_3 [Jones et al., 1996; Ferguson et al., 2002]. However, whether or not a chameleon can voluntarily adjust its exposure to optimize its internal levels of vitamin D_3 by behavior alone requires further study. The three females in treatment 1 (highest long/low irradiation of UVA and UVB) reproduced but eggs had a low hatch success (Tables 2, 4, and 5; Figs. 2–5). This suggests some kind of UV overdose malady when a female is forced to endure this artificial light environment for long periods. However, at the Dallas Zoo when a female was exposed to an exposure regime similar to that of treatment 1, but in a larger cage where regulation was possible [Ferguson et al., 1999], the female showed the same reproductive pattern, i.e., reproduction but hatching failure. Thus, with a large UV gradient and numerous escape possibilities, the female did not seem able to behaviorally regulate to a more optimal UVB exposure. If the maximum possible exposure that a female can receive in a large cage is the optimum level, the female may be attracted to that light environment, undergo proper vitamin D photobiosynthesis, and successfully reproduce. However, the appropriate set-up and UVA/UVB balance in artificially illuminated large enclosures with light gradients requires more study.

The number of females used in this study to support the above opinions was small, and only a few animals were reported for the extreme long/low UVB treatments (treatments 1 and 7). While only one animal was reported for treatment 7 (Vita-Lite), we are confident that this light exposure environment provides too little UVB to females to predict a high hatching success. More than 40 female panther chameleons have been raised and bred in our lab using long daily exposure to Vita-Lites [Ferguson, 1994; Ferguson et al., 1996] and very few hatchlings have been produced. Conversely, the three females reported in treatment 1 are the first that we have exposed to the high UV exposure environment of a double Reptisun 5.0. The detrimental effect of this light treatment requires further verification.

The case of one female in treatment 1 requires special mention. While a double Reptisun 5.0 produced the expected high UVB and UVA radiometer readings (Tables 1 and 2), the percent photoproduct conversion of 0.78% at her light station was unusually low, producing wild points in Figs. 1 and 4. This female produced two clutches of eggs, but despite many male introductions she never allowed copulation, so the eggs were not viable.

The anomalously low photoproduct conversion may be attributed to low energy in the optimum photobiosynthetically effective range (296 ± 3 nm [MacLaughlin et al., 1982]). Had the female not been so aggressive toward males, she might have reproduced more successfully than the other two females in this treatment group, who shared another light station with a higher (possibly too high) photobiosynthetic potential.

While commercially available UVB radiometers have been extensively used to evaluate a light environment's potential for photobiosynthesis of vitamin D, their use can be misleading. While different brands may read the same UVB range (290–315 nm), the spectral sensitivity of their detectors may differ, and may not closely match the narrow most-effective range for generating vitamin D_3 (296 ± 3 nm [MacLaughlin et al. 1982]) or have the resolution necessary to measure the low irradiances that may be sufficient. Different brand-name meters with subtly different spectral sensitivity curves give different readings from the same light source (Gehrmann, unpublished results). Thus, a reading of 9 $\mu W/cm^2$ from the Spectronics UVB meter (Spectroline DM-300N) used in this study may register 0 using the Spectronics UVB meter (DM300x), which registers in 10 $\mu W/cm^2$ increments instead of the 1 μW increments of the DM-300N units, which are currently unavailable from the company. The same UV source may read 20 or higher using a different brand of meter with a different curve of UVB spectral sensitivity. The in vitro models, which measure the potential of a light environment to cause photolysis of provitamin D_3, should be more reliable tools for the herpetoculturist. These are currently being developed as commercially available products. The models can also be used to generate standard curves that relate irradiance readings from a particular radiometer to photobiosynthetically effective UVB from a particular type of lamp (e.g., a sunlamp). Using such a curve one could estimate photobiosynthetic potential from the irradiance values alone.

Controversy remains regarding the relative efficiency of providing vitamin D to lizards through diet as compared to endogenously with UVB treatment. Studies on iguanas (*Iguana iguana*) [Allen et al., 1999] suggest that high doses of dietary vitamin D can elevate circulating 25 hydroxy-vitamin D levels. Montanucci [1997] effectively raised and bred chuckwallas (*Sauromalus obesus*) using only dietary vitamin D. Gehrmann [1998] has done the same with eyed skinks (*Chalcides ocellatus*). Larry Talent accomplished the same with oral doses of vitamin D_3 suspended in corn oil administered to adult panther chameleons [Ferguson et al., 1996]. European chameleon breeders have reported that appropriate vitamin D levels can be provided through diet alone [Schmidt et al., 1994]. In contrast, gut-loading crickets with high vitamin D failed to resolve the egg term-death problem in panther chameleons, whereas UVB exposure did [Ferguson et al., 1996]. For iguanas, UV light exposure sustained circulating vitamin D levels without possible deleterious long-term effects of high dietary vitamin D [Allen et al., 1999]. In humans a larger proportion of endogenously produced vitamin D_3 from the skin unites with vitamin D binding protein in the blood compared to that obtained in the gut [Holick, 1999]. Protein-bound vitamin D remains in the circulation longer and is thought to be more likely to be used by the liver to produce 25-hydroxyvitamin D_3, which is then converted in the kidney to the hormonally active 1,25-dihydroxyvitamin D_3 [Haddad, 1999]. Reports of both success and failure with dietary supplementation of vitamin D to lizards, combined with reports that lizards may be able to behaviorally regulate their internal vitamin D levels in a UV gradient [Jones et al., 1996; Ferguson et al., 2002] suggest that UVB irradiation may be the best way to supply appropriate vitamin D levels to lizards. However, our recommendations for appropriate light environment depend on a low vitamin D diet. The recommendations may prove to be different with higher dietary vitamin D levels. The effective balance between UVB irradiance and dietary vitamin D intake remains poorly understood for any lizard species.

Exposure to natural sunlight may be the best way to provide UVB in such a way that the lizards are able to properly regulate vitamin D. This can be accomplished by housing the animals outdoors (climate permitting) or exposing them indoors using UV-transparent glass, plastic windows, or skylights. However, photobiosynthetic potential should be monitored even if natural sunlight is used, because that potential may not exist at extreme latitudes (e.g., that of Boston, MA) in the winter [Webb et al., 1989].

Our research has focused on the female panther chameleon. Because noticeable UV/vitamin D deficiency problems have been associated primarily with the adult reproductive phase of the life cycle, we conclude that UV/vitamin D requirements are less for the pre-reproductive phases of the life cycle. Also, in rats vitamin D activity is enhanced by the female hormone estrogen [Abu-Amer and Bar-Shavit, 1994; Ishibe et al., 1995; Chen et al., 1997], suggesting greater requirements by mature females. In contrast to females, male panther chameleons have been raised to maturity in our laboratory and have been successfully bred using Vita-Lites (treatment 7) [Ferguson et al., 1996]. Thus, requirements appear to be less for adult males than for females.

Other species of chameleons adapted to sun-exposed environments may have similar requirements. However, two relatives of the panther chameleon, the Malagasy carpet chameleon (*Furcifer lateralis*) and Oustalet's chameleon (*Furcifer oustaleti*) appear to be exceptions. Based on limited study, it is our opinion that the carpet chameleon (a smaller species) has lower UVB requirements, and the Oustalet's chameleon (a larger species) has higher requirements. Application of our findings to other species adapted to similar light environments does not seem justified without further study.

Our experience with forest species of chameleons adapted to low-light environments is very limited. We have maintained Malagasy Parson's chameleons (*Calumma parsoni*) and Cameroon mountain chameleons (*Chamaeleo montium*) indoors for years with low UV light exposure. In a recent study we contrasted UV/vitamin D physiology of the nocturnal/crepuscular house gecko (*Hemidactylus turcicus*) with that of the diurnal arboreal Texas spiny lizard (*Sceloporus olivaceous*) [Carman et al., 2000]. While geckos had much more limited exposure to UV in the field than the spiny lizards (measured by retracing the time and locations of free-living individuals with in vitro models), they had much greater capacity for vitamin D production upon exposure of their skins to UVB in the lab. It is tempting to speculate that shade-dwelling chameleons are much more efficient than sun-dwelling species at manufacturing vitamin D when exposed to weak UVB sources. In any event it is unlikely that the shade-dwelling species require anything but weak UVB irradiation.

CONCLUSIONS

1. Female panther chameleons require moderate amounts of UVB irradiation to reproduce successfully when fed a diet low in vitamin D.

2. Some commercially available, low-intensity, UV-generating fluorescent tubes can provide adequate amounts of UVB in indoor artificial-light set-ups if used properly. Some may also provide too much UV if irradiation is provided for too long a period.

3. The use of commercially available UVB radiometers to evaluate a light environment's potential for photobiosynthesis of vitamin D can be misleading. Differences in spectral sensitivity of different radiometer models can generate different values from the same light source. In vitro models that measure actual photolysis of provitamin D_3 to photoproducts provide a more direct assessment of effective UVB in a light environment. The models can also be used to construct a standard curve that enables photobiosynthetically effective UVB from a particular type of lamp (e.g., a sunlamp) to be estimated using a particular meter. Inexpensive in vitro model kits should be commercially available in the near future.

4. If a UVB-containing light environment converts from 0.5% to 1.3% of provitamin D to previtamin D_3 in an in vitro model exposed for 2 hr, then female panther chameleons exposed to that environment for 12 hr/day should successfully reproduce. A stronger UVB exposure environment that converts 8% provitamin D in a model in 0.5 hr, or 14.6% in 1.0 hr is also effective for a female exposing herself for 0.5 or 1.0 hr, respectively, per day. However, the use of high UVB-generating fluorescent tubes can be harmful to the lizards and the keeper and as such are not recommended.

5. Our recommendations for an appropriate light environment depend on a low vitamin D diet. The recommendations may prove to be different with higher dietary vitamin D levels.

6. UVB requirements for juvenile and adult male panther chameleons are lower than those for adult females. Requirements for species of chameleons and lizards other than the panther chameleon probably are different.

7. Female panther chameleons are attracted to UV light, and if they are provided with a light gradient containing a substantial component of UVB they appear to be able to adjust their exposure based on dietary vitamin D intake. However, they may not be able to photoregulate effectively in an artificial UV gradient that provides too strong a UVB irradiance.

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