Do Panther Chameleons Bask to Regulate Endogenous Vitamin D_3 Production?

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ABSTRACT

Basking by ectothermic vertebrates is thought to have evolved for thermoregulation. However, another beneficial effect of sunlight exposure, specifically the ultraviolet B (UV-B) component, includes endogenous production of vitamin D_3. In the laboratory, panther chameleons exhibited a positive phototaxis to greater visible, ultraviolet A (UV-A) and UV-B light. However, with equivalent high irradiances of UV-A or UV-B, their response to UV-B was significantly greater than it was to UV-A. Exposure of in vitro skin patches of panther chameleons to high UV-B (90 μW/cm^2) for 1 h significantly enhanced vitamin D_3 concentration. Voluntary exposure to higher UV-B irradiance (70 vs. 1 μW/cm^2) resulted in greater circulating 25-hydroxyvitamin D_3 in female panther chameleons (604 vs. 92 ng/mL). Depending on dietary intake of vitamin D_3, chameleons adjusted their exposure time to UV-B irradiation as if regulating their endogenous production of this vital hormone. When dietary intake was low (1–3 IU/g), they exposed themselves to significantly more UV-producing light; when intake was high (9–129 IU/g), they exposed themselves to less. Vitamin D_3 photoregulation seems to be an important additional component of the function of basking.

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Introduction and Background

Many reptiles use sunlight for thermoregulation. The literature on reptilian basking behavior and thermoregulation is extensive (e.g., Cowles and Bogert 1944; Huey and Slatkin 1976; Huey 1982; Hutchinson 1989; Angilletta 2001; Blouin-Demers and Weatherhead 2001). A range of thermoregulatory precision exists. Classic thermoregulators shuttle between sun and shade to maintain a relatively constant body temperature above or below that of their immediate environment. Passive thermal conformers maintain a body temperature conforming closely to that of their immediate environment. Facultative thermoregulators (Kingsbury 1994) thermoregulate but with less precision or continuity than do classic thermoregulators. Although some chameleon species seem to tolerate more variable body temperatures than do many lizards (Burrage 1973; Hebrard et al. 1982), they definitely thermoregulate at temperature extremes (Burrage 1973; K. B. Karsten, unpublished data).

Understanding of thermoregulation has substantially increased over the years. Studies have defined in considerable detail many of the physical, physiological, and behavioral factors contributing to the balance of heat loss and heat gain (Huey 1982; Bauwens et al. 1996; Diaz 1997; Downes and Shine 1998; Pough et al. 1999 [see pp. 129–134]; Du et al. 2000; Angilletta et al. 2002). Various procedures and technologies, including the concept of the null model, have been used to quantify the precision of thermoregulatory behavior (Hertz 1992*b*; Hertz et al. 1993; Blouin-Demers and Weatherhead 2001). Despite the plethora of studies on thermoregulatory behavior, there have been only a few suggestions of potential functions of basking other than thermoregulation and no experiments focusing on nonthermoregulatory aspects of basking. Additional benefits of basking have often been considered to be incidental with little importance attached to their role in the evolution of basking behavior, at least until recently (Manning and Grigg 1997).

Potential benefits of basking other than thermoregulation for normal physiological maintenance include the following. Fever response to infection (Vaughn et al. 1974; Burns et al. 1996), an extended function of nonpathological thermoregulatory behavior, has been documented. Aquatic vertebrates such as turtles leave the water, dry their surface, and may benefit by removing external parasites and commensuals (Pritchard and Greenhood 1968; Hutchinson 1989). Basking turtles expose the

Table 1: Voluntary exposure of juvenile female panther chameleons fed high and low vitamin D_3 diets to available light during UV treatments in four light environments (1–4)

Light Environment during UV Treatments	Maximum UV-A Irradiance ($\mu W/cm^2$)	Maximum UV-B Irradiance ($\mu W/cm^2$)	Maximum Visible Light (lux)	No. of Lizards (Low D : High D Diets)	% Full Exposure with Low Vitamin D Diet	% Full Exposure with High Vitamin D Diet
1	150	2.1	1,184	3 : 4	76 ± 3.3	70 ± 3.1
2	12	89	1,184	3 : 4	70 ± 4.0	63 ± 3.1
3	9	70	538	4 : 3	55 ± 4.7	46 ± 3.5
4	4.4	1	507	3 : 2	47 ± 2.3	34 ± 5.0

Note. Percent full exposure values are mean ± 1 SE and represent the mean percent of the observations during a UV treatment period that a lizard located itself in the full exposure region of the light gradient (see Fig. 1). Low vitamin D_3 diets included crickets containing 1 IU/g of vitamin D_3; high vitamin D_3 diets included crickets containing 9 IU/g of vitamin D_3 (Jones et al. 1996).

skin of their extremities to ultravoilet (UV) light, which may stimulate vitamin D_3 synthesis (Pritchard and Greenhood 1968).

The panther chameleon, *Furcifer pardalis*, an arboreal lizard from Madagascar, requires ultraviolet B (UV-B) irradiation in captivity for proper health and reproduction (Ferguson et al. 1996, 2002*a*). In the course of our studies documenting the UV-B requirement, we discovered that panther chameleons are attracted to light with a strong UV-B component and voluntarily increase their exposure when deprived of dietary vitamin D_3 (Jones et al. 1996; Ferguson et al. 2002*b*). Here we present evidence that UV-B enhances vitamin D_3 condition in the panther chameleon, and we compile new and previous experimental evidence that behavioral vitamin D_3 photoregulation may exist for this species. An indoor experiment tested the behavioral response of juvenile panther chameleons fed either high or low vitamin D_3 diets to four different artificial UV-producing light environments set up as gradients (Table 1; Fig. 1). An additional indoor experiment compared the responses of chameleons fed a low dietary vitamin D_3 to ultraviolet A (UV-A) and UV-B light. An outdoor experiment tested the response of chameleons fed different vitamin D_3 diets to vitamin D_3–generating natural sunlight in arboreal sun/shade mosaic environments.

Material and Methods

In one indoor study, 26 juvenile female panther chameleons, hatched in our laboratory at Texas Christian University (TCU), were maintained in isolation in terraria in the laboratory and exposed to manipulations of dietary vitamin D_3, visible light, and UV radiation (Jones et al. 1996; Ferguson et al. 2002*b*). Light was provided using various combinations of GE cool white, Vita-Lite (Duro-Test), blacklight (GE BL-40), and sunlamp (Philips FS-40) fluorescent tubes (Table 1). UV-A and UV-B irradiances were monitored using Spectronics UV meters (models DM-365N and DM-300N, respectively), and visible illuminance was monitored with a GE light meter (model 214). The daily photophase was provided by 12 h illumination of either Vita-Lites (environments 1 and 2; Table 1) or cool white tubes (environments 3 and 4; Table 1). During UV treatments, a full-exposure/full-shade gradient was established by placing a board on top of the terrarium, which was illuminated from above (Fig. 1). UV treatments were 1 h/d 5 d/wk for light environments 1 and 2 (Table 1) and 3 d/wk for light environments 3 and 4. All UV treatments and observations occurred at midday, approximately 4 h into the photophase. The four light environments during the UV treatments were as follows: environment 1: higher UV-A, lower UV-B, higher visible; environment 2: lower UV-A, higher UV-B, higher visible; environment 3: lower UV-A, higher UV-B, lower visible; and environment 4: lower UV-A, lower UV-B, lower visible (Table 1).

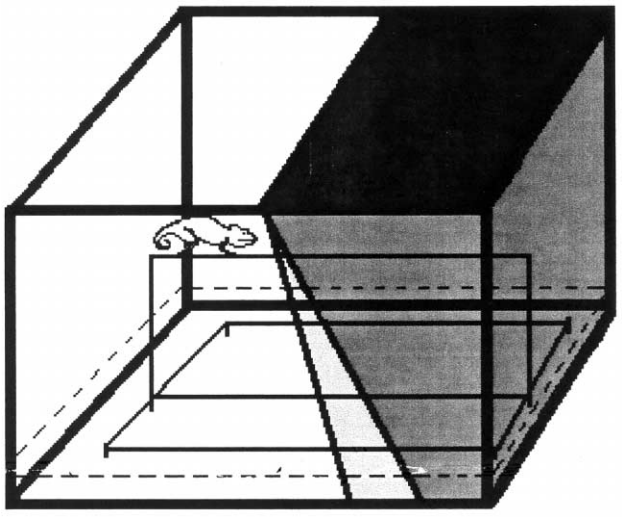

Figure 1. Light gradient established in terrarium housing a chameleon during indoor UV treatments. White region of terrarium represents zone of maximum exposure to visible light and UV irradiance (see Table 1). In cage area above the dashed rectangle, ambient temperature was uniform and close to optimum levels (about 29°C) for chameleon. In the cage area below the dashed rectangle was a gradient above optimum levels (35°–50°C). The warmer area was rarely inhabited by the chameleon during observation periods.

Results for the first 6 mo of the experiment (juvenile phase of the life cycle) are reported here.

For each lizard in each of the four treatments, we calculated the percent of the time that the full (maximum possible) exposure zone was inhabited. The mean percent for a given lizard was calculated for the entire 6-mo period. Terrarium temperature gradients, provided with heat tape underneath the floor of the cage, did not correspond with light gradients (Fig. 1), so during UV treatments, equivalent temperatures were available in both the light and shaded regions of the cage.

Vitamin D_3 was manipulated by feeding crickets experimental grain diets differing only in vitamin D_3 content (Zeigler, Gardners, Pa.; Jones et al. 1996; Ferguson et al. 2002*b*; Table 1). Crickets were then fed to the chameleons. Dietary mass was sufficient to ensure rapid growth and maturity of the chameleons within 6–8 mo.

An additional indoor experiment used 14 hatchling lizards. The setup and procedure were the same as those previously described, but the light environments differed (environments 5–8; Table 2). Effort was made to balance the irradiance of the higher UV-A and UV-B levels and the lower UV-A and UV-B levels better than in the first experiment in order to evaluate the relative attracting value of UV-A and UV-B. Visible light and dietary vitamin D was low for all treatments in this experiment. The experiment was conducted for 8 wk.

After reaching maturity, several chameleons exposed daily to environments 3 and 4 (Table 1), which differed substantially in UV-B, were bled to measure UV-B effects on circulating 25-hydroxyvitamin D_3 (calcifediol). Plasma calcifediol was measured using a competitive-binding assay (Chen et al. 1990). Cricket and grain samples were analyzed for vitamin D_3 content using high-performance liquid chromotography (HPLC; Chen et al. 1992). Patches of skin (0.25 cm^2) were excised from two panther chameleons, which were killed by decapitation followed immediately by brain destruction, and placed on a piece of filter paper soaked in physiological saline. The skin patches were immediately exposed to a Philips sunlamp (90 $\mu W/cm^2$ UV-B) for 0, 20, 40, or 60 min. After exposure, the patches were deep frozen (−70°C) and later analyzed for vitamin D_3 concentration by HPLC (Chen et al. 1992).

In another study, six juvenile panther chameleons initially were maintained indoors with low UV-B irradiance (5 $\mu W/cm^2$) and fed crickets maintained on the low vitamin D_3 grain diet. Beginning 2 mo before being taken to outdoor enclosures, crickets for three of the lizards were dusted by agitation at each feeding with a high vitamin D_3 mineral-based powder (Rep-Cal [Rep-Cal Research Labs, Los Gatos, Calif.] or Miner-all I [Sticky Tongue Farms, Menifee, Calif.]). Crickets dusted with Miner-all I provided 129 IU/g of vitamin D_3 to the lizards. Crickets dusted with Rep-Cal containing vitamin D_3 provided 66 IU/g of vitamin D_3. Crickets for the other three lizards were dusted with pure calcium carbonate or Miner-all 0, neither of which resulted in a concentration in the crickets of more than 3 IU/g of vitamin D_3. The six chameleons were taken to cylindrical outdoor enclosures measuring approximately 2 × 2 m. Each enclosure was constructed from 1.25 × 2.5-cm welded-wire mesh and surrounded one or two chickasaw plum trees, *Prunus angustifolia*, trimmed to prevent the chameleons from reaching and climbing onto the wire. Metal flashing was placed along the inside base of the enclosure to prevent chameleons from climbing the wire from the ground. Black vinyl curtains were placed on top of each enclosure to shade about one-third of the enclosure throughout the day. Each enclosure housed a single chameleon, which was visually isolated from chameleons in the other enclosures. After a week of acclimation in the enclosures, observations began. On the first day, lizard location in the tree was accurately monitored throughout the 12-h day using a coordinate system (K. B. Karsten and G. W. Ferguson, unpublished data). Locations were recorded every 20 min for all lizards. On the following day, a series of four in vitro models (ampoules containing a solution of provitamin D_3; Lu et al. 1992) were used to retrace the previous-day path of the lizard (Carman et al. 2000). A model was attached to the perch site, relocated as necessary, and replaced every 3 h throughout the day. Exposure of the model to UV-B irradiation causes conversion to previtamin D_3 and other photoproducts at a rate

Table 2: Voluntary exposure of juvenile female panther chameleons fed low vitamin D_3 diets to available light in four additional light environments (5–8)

Light Environment (No. of Lizards)	Maximum UV-A ($\mu W/cm^2$)	Maximum UV-B ($\mu W/cm^2$)	Maximum Illuminance (lux)	% Full Exposure with Low Vitamin D Diet
5 (3)	4	67	344	49.6 ± 9.0
6 (4)	63	72	387	43.4 ± 7.8
7 (4)	69	5	344	15.6 ± 7.8
8 (3)	1.4	0	409	17.5 ± 9.0

Note. Percent full exposure values are mean ± 1 SE and represent the mean percent of the observations during a UV treatment period that a lizard located itself in the full exposure region of the light gradient (see Fig. 1). Low vitamin D_3 diet included crickets containing 1 IU/g of vitamin D_3 (Jones et al. 1996). The high UV-B effect was significant.

Table 3: Plasma 25-hydroxyvitamin D_3 (calcifediol) levels and light environment of female panther chameleons exposed in the laboratory to high and low UV gradients

UV Treatment	UV-B Maximum ($\mu W/cm^2$)	UV-A Maximum ($\mu W/cm^2$)	Maximum Visible (lux)	Plasma Calcifediol (ng/mL)
High	70	8.8	538	604.0 ± 77.8 (6)
Low	1	4.4	507	91.8 ± 16.0 (5)

Note. Calcifediol values are mean ± SD (*N*). Calcifediol levels are significantly different. Females were exposed three times weekly for 18 mo.

proportional to irradiance. This procedure provided an indirect measure of the amount of UV-B to which a lizard voluntarily exposed itself. Photoproduct productions for models retracing chameleons fed low and high dietary vitamin D_3 were compared using a *t*-test. The outdoor study was conducted in June and September when midday air temperatures matched or exceeded 32°C. This is the body temperature that the chameleons selected in thermal gradients in the laboratory (K. B. Karsten, unpublished data). Lizards fed both diets were observed throughout the same 12-h period. Available data were compiled in LOTUS 1–2–3 (release 5) files and analyzed using SYSTAT 6.0, SIGMA PLOT 4.0, and SIGMASTAT 2.0. All studies were conducted with the approval of the TCU Institutional Animal Care and Use Committee (protocols 99-5 and 99-10).

Results

UV-B exposure significantly enhanced vitamin D_3 production in the skin and circulating 25-hydroxyvitamin D_3 (calcifediol) levels. In vitro skin patches showed a significant positive relationship between vitamin D_3 concentration and time of exposure ($r = 0.93$, df $= 1,6$, $P < 0.01$). Plasma concentrations of calcifediol were significantly higher in chameleons exposed to high maximum possible UV irradiances than they were in those exposed to low maximum possible UV irradiances in the first indoor study (Table 3; ANOVA: df $= 1,9$, $F = 42.9$, $P < 0.01$).

Panther chameleons exhibited a positive phototaxis to increased light intensity in the first indoor study (Tables 1, 4). Furthermore, each measured component of the light spectrum (visible, UV-A [315–400 nm] and UV-B [290–315 nm]) had an independent positive effect (significant positive coefficient) on voluntary light exposure of prereproductive panther chameleons on the basis of a multiple regression analysis (Table 4). Thus, when visible light was more intense (environments 1 and 2; Table 1), the attraction was clearly stronger. The higher UV environments (1–3; Table 1) were obviously associated with stronger attraction compared with the lowest UV environment (4). Although the significant independent effects of UV-A and UV-B are not as intuitively obvious from Table 1, they were teased apart by the regression analysis (see significant positive coefficients for each in Table 4). Thus, chameleons seemed able to respond positively to both UV-A and UV-B irradiation as well as visible light. Although the regression model suggested that UV-A has had a stronger effect than has UV-B, the range of irradiance among the four environments (1–4) was greater for UV-A than it was for UV-B. Thus, further testing was necessary.

The second indoor study was designed to more precisely address the relative attractiveness of UV-A versus UV-B. When chameleons receiving a low vitamin D_3 diet were provided similar high levels of either UV-A or UV-B, they were attracted to the UV-B significantly more than they were to the UV-A (Table 2; ANOVA: df $= 1,10$, $F = 12.6$, $P < 0.01$).

In contrast to the positive attraction to greater light intensity, higher dietary vitamin D_3 significantly reduced the voluntary exposure of the chameleons to artificial vitamin D_3–generating light and sunlight (Tables 1, 4; Fig. 2). In the indoor study, the significant negative coefficient for vitamin D_3 in the multiple regression analysis demonstrated this effect (Table 4). In the outdoor study, the percent conversion of previtamin D_3 to photoproducts in the in vitro models retracing the chameleon's previous-day activity was significantly lower for chameleons fed high vitamin D_3 than it was for those fed low vitamin D_3 (Fig. 2; *t*-test: df $= 4$, $t = 7.04$, $P < 0.01$). Thus, exposure was less for lizards fed a high vitamin D diet.

Discussion

For more than half a century, studies have focused on thermoregulation of ectothermic vertebrates. However, many findings are difficult to explain. For example, some thermoregulators shift preferred temperature seasonally for unknown reasons (Christian and Bedford 1995; Seebacher and Grigg 1997). Although a shift can be explained as a shift in cost-benefit balance involving energy efficiency or predator avoidance, the phenomenon is widespread and can also be explained as compromises for competing physiological benefits of basking. Thus, seeking a higher body temperature during the breeding season can maximize energy utilization and allow a female lizard to produce more young, reproduce faster, or run faster to escape a predator. But it can also allow an animal to bask longer to attain higher vitamin D_3 levels at a time of maximum vitamin D_3 requirements.

In addition to changes in thermal preference, some thermal conformers bask for unknown reasons. Thus, the Australian freshwater turtle *Emydura signata* is frequently observed to bask, but temperature is not elevated significantly above water

Table 4: Multiple regression analysis of the effects of dietary vitamin D_3 and light variables on voluntary exposure of juvenile female panther chameleons to artificial light in laboratory environments 1–4

Variable	Coefficient	SE	*t*	*P*
Y-intercept of model	.34	.039	8.6	<.001
Vitamin D_3	−.01	.003	−3.5	.002
UV-B	.001	.001	2.3	.034
UV-A	.001	<.001	3.0	.007
Visible	<.001	<.001	3.5	.002

Note. Each of the light variables had a significant ($P < .05$) positive effect on exposure; dietary vitamin D_3 had a significant negative effect. The regression model explained most of the variance of voluntary exposure ($r^2 = 0.84$, $P < .001$).

temperature (Manning and Grigg 1997). Manning and Grigg (1997) suggested that there are functions for basking other than thermoregulation in this species. Vitamin D_3 synthesis has been suggested to be an important factor stimulating turtles to bask (Pritchard and Greenhood 1968; Hutchinson 1989), but the specific role of behaviorally basking for UV-stimulated vitamin D synthesis has not been addressed experimentally before our studies.

Our current understanding of the role, acquisition, and regulation of vitamin D_3 comes from studies of terrestrial vertebrates, mostly endotherms. Vitamin D_3 is an important nutrient complexly involved in calcium and phosphorus metabolism (for summaries, see Holick 1996, 1999*a*, 1999*b*, 1999*c*). Vitamin D_3 may also play critical roles in a number of other poorly understood physiological processes (Bidmon and Stumpf 1996; Holick and Jung 1996, 1999). It can be obtained either in the diet or by endogenous synthesis in the skin. Exposure of the skin to UV-B irradiation converts provitamin D_3 (7-dehydrocholesterol), a steroid widely available in the skin of vertebrates, to previtamin D_3, which is then thermally isomerized to vitamin D_3 or cholecalciferol. Cholecalciferol is transported from the skin by vitamin D–binding protein through the bloodstream first to the liver, where it becomes 25-hydroxyvitamin D_3, or calcifediol (Holick and Clark 1978). Then, it is carried to the kidney, where it is hydroxylated into its most biologically active form, 1,25 dihydroxyvitamin D_3, or calcitriol (Holick et al. 1971). Calcitriol is a hormone whose best-known role is to maintain circulating calcium levels (Holick 1999*b*, 1999*c*). This occurs primarily by promoting absorption of calcium from the gut and resorption from the kidney filtrate. Calcitriol deficiency results in depletion of body calcium and serious bone demineralization. This is mediated principally by a rise in parathyroid hormone, the primary stimulator of calcium resorption from bone (Hurwitz 1989).

The regulation of vitamin D_3 is complex and not fully understood. In endotherms, there is evidence for physiological regulation at several levels (Holick 1999*b*, 1999*c*). First, excess previtamin D_3 production with prolonged UV-B exposure is diverted with the conversion of previtamin D_3 to the biologically inert photoproducts lumisterol and tachysterol (Holick et al. 1981). These compounds can serve as reservoirs of previtamin D_3 since the reaction is reversible. Excess vitamin D_3 remaining in the skin is unstable after exposure to UV radiation, which converts it to relatively inert compounds such as suprasterol I, suprasterol II, and 5,6, transvitamin D (Webb et al. 1989). There is some feedback at the first hydroxylation conversion in the liver (Bell 1985), but this is relatively weak in mammals, and levels of the liver-produced metabolite calcifediol fluctuate substantially with input of vitamin D_3 from the skin and gut. Thus, circulating level of calcifediol is considered a good measure of "vitamin D condition" of an animal (Haddad and Stamp 1974; Haddad and Walgate 1976). Regulation of the hormonally active calcitriol is more precise in the kidney, and circulating levels are relatively constant. Decreased circulating calcium triggers the release of parathyroid hormone, which stimulates the kidney to produce calcitriol. As calcium increases from enhanced absorption from the gut or bone, parathyroid hormone and calcitriol decrease possibly under the direct influence of elevated phosphorus (Holick 1999*b*). Although incompletely studied, much of this scenario seems to apply to lizards (Holick et al. 1995; Liang and Fraser 1999).

Although the complexity of physiological and biochemical regulation of vitamin D_3 is under active investigation, the potential role of behavior remains virtually ignored. Can some vertebrates detect UV-B radiation and adjust their exposure on the basis of internal vitamin D_3 condition? In ectotherms, might this be an important step in vitamin D_3 regulation?

Our data suggest that panther chameleons are able to assess

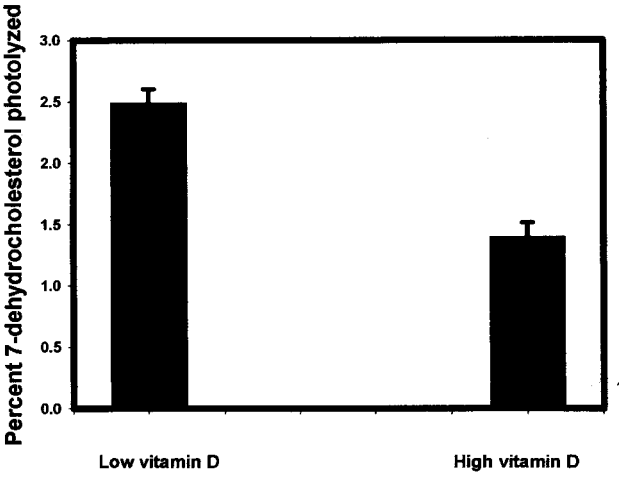

Figure 2. Effect of dietary vitamin D_3 of chameleons in outdoor enclosures on percent conversion of 7-dehydrocholesterol (provitamin D_3) to photoproducts in ampoules retracing their previous-day locations from 10:00 A.M. to 1:00 P.M. Capped lines are standard errors. The diet effect was significant.

their internal vitamin D_3 status, perceive their UV environment, and behaviorally adjust their exposure in a regulatory manner. Existing information suggests that the prerequisites for this ability may exist in lizards such as the panther chameleon. Thus, vitamin D receptors, identified in the brain of *Anolis* lizards (Bidmon and Stumpf 1996), suggest a mechanism for perceiving the level of circulating vitamin D_3. Lizards, including the panther chameleon, have UV-sensitive retinas (Fleishman et al. 1993; E. R. Loew, personal communication). Hence, they should be able to detect UV radiation, provided it is not filtered out completely by the lens of the eye. The greater attraction to UV-B than to UV-A demonstrated in this study does not prove that panther chameleons can directly perceive UV-B. Data such as optic nerve activation in response to UV-B stimulation through an intact eye are needed to verify perceptual acuity. However, greater attraction to UV-B does show that panther chameleons can discriminate a light environment that provides a beneficial physiological effect, that is, enhanced vitamin D_3 condition. Ours is perhaps the first experimental support for the hypothesis that regulation of vitamin D_3 in ectotherms may extend beyond the physiological mechanisms previously described and involve phototactic behavior.

An interesting question is, How would such an ectotherm balance the functions of behavioral thermoregulation and vitamin D_3 photoregulation? Might it involve temporal shifts in thermal preference (Christian and Bedford 1995; Seebacher and Grigg 1997), that is, allowing the body to tolerate more sun exposure and the resulting higher body temperature during periods of high vitamin D_3 requirements? Alternatively, might an ectotherm be able to uncouple these functions? A chameleon may bask to elevate its temperature during the early morning hours when UV irradiation is low (Lu et al. 1992). Then, it might retreat to shady environments to prevent overheating during late morning. If the animal needed to replenish its previtamin D_3, it could expose itself to full or partial sun during midday, when UV irradiance is highest (Lu et al. 1992). However, at midday, bouts of exposure would have to be brief and terminated when body temperature began to elevate. Whether short midday bouts would be sufficient to relieve low vitamin D_3 condition is unknown. One might think that desert-dwelling lizards would be in such a light-rich environment that UV irradiation might never be limited. However, the heat loads in such environments may curtail daytime activity to the extent that it is dangerous to be exposed at times when UV is most readily available.

UV-B limitation suggests another issue. How do lizards adapted to low UV-B light environments obtain vitamin D_3? Must they seek vitamin D–rich foods, or are they still able to generate vitamin D_3 endogenously with low levels of UV-B? We have begun to address this issue (Carman et al. 2000). Noctural/crepuscular house geckos *Hemidactylus turcicus* are active in low UV-B light environments, yet they have skins highly sensitive regarding UV-B-induced vitamin D_3 synthesis. Conversely, diurnal Texas spiny lizards are active in higher UV-B light environments but have skins less sensitive regarding UV-B-induced vitamin D_3 synthesis. The natural dietary levels of vitamin D_3 seem to be lower for the geckos than they are for Texas spiny lizards. We currently do not know whether these species actively show phototactic responsiveness to UV-B, which would suggest that they possess vitamin D–regulating behavior. However, low opportunity may be compensated by enhanced ability. An interesting comparison would be relative opportunity and compensatory ability for UV-B-induced vitamin D_3 production for species or populations within a clade, such as sun-dwelling and shade-dwelling *Anolis* (Hertz 1992*a*, 1992*b*).

In conclusion, the potential role of basking behavior for UV-stimulated vitamin D photoregulation has been virtually unstudied. However, our results clearly show a link between basking behavior and internal vitamin D condition in the panther chameleon. Because vitamin D photosynthetic ability and opportunity may vary among squamate species (Carman et al. 2000), ectotherms may vary in their vitamin D–regulating systems, and these may differ from those of mammals. This previously underemphasized complexity in basking behavior may help explain some of the puzzling findings (e.g., shifts in thermal preference) in previous studies of thermoregulation.

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