Ultraviolet Exposure and Vitamin D Synthesis in a Sun-Dwelling and a Shade-Dwelling Species of Anolis: Are There Adaptations for Lower Ultraviolet B and Dietary Vitamin D$_3$ Availability in the Shade?

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Accepted 7/21/04; Electronically Published 2/25/05

ABSTRACT

We compared the natural ultraviolet B (UV-B) exposure, dietary vitamin D, and skin-generated vitamin D synthesis for adult males of two species of Jamaican anoles. The more shade-tolerant and thermal-conforming Anolis lineotopus merope, rarely exposed to full sun, experienced less UV-B irradiation in its shady environment than the more heliophilic and thermophilic Anolis sagrei, which frequently basked in full sun during the morning hours (0800–1100 hours). Both species obtained detectable levels of vitamin D$_3$ in their diet, but the heliophilic A. sagrei obtained more. To compensate for less availability of UV-B and dietary vitamin D$_3$, the skin of A. lineotopus merope seems to have acquired a greater sensitivity than that of A. sagrei regarding UV-B-induced vitamin D$_3$ photobiosynthesis. We assessed this by observing a greater conversion of provitamin D$_3$ to photoproducts in skin exposed to UV-B from a sunlamp. The reduced skin sensitivity of A. sagrei regarding vitamin D$_3$ photobiosynthesis may reflect a correlated response associated with less need for vitamin D$_3$ photobiosynthesis and greater need for UV-B screening capacity as an adaptation to a more damaging UV-B environment. However, the possibility that adaptations for photobiosynthesis of vitamin D and for protection from skin damage could involve independent mechanisms needs investigation. Also, the ability to behaviorally regulate UV-B exposure, as shown for the panther chameleon, would benefit both species of Anolis and should be investigated.

Introduction

The role of vitamin D in vertebrate physiological systems is under active investigation (Holick 1996, 1999a, 1999b, 2004). The best-known role is its participation, along with other hormones, in the calcium-phosphorus hormonal regulation system. Specifically, 1,25-dihydroxyvitamin D$_3$, or calcitriol, promotes the uptake of calcium from the gut when circulating calcium levels fall. Vitamin D deficiency results in an overall calcium deficiency in the body, which in turn can cause maladies such as rickets, osteomalacia, and reproductive failure (Narbaitz and Tsang 1989; Holick 1999a).

Vitamin D can be obtained from two sources (Holick 1996, 1999a, 1999b). One source is endogenous production by a sequence of photobiochemical events. Initially, provitamin D$_3$, or 7-dehydrocholesterol, a substance widely distributed in the skin of many vertebrates, is converted to previtamin D$_3$ when exposed to UV-B radiation. Previtamin D$_3$ is then thermally isomerized to vitamin D$_3$, which is then transported in the circulation by vitamin D–binding protein to the liver, where it is hydroxylated to 25-hydroxyvitamin D$_3$, or calcidiol. Calcidiol enters the circulation again and is transported to the kidney, where it is hydroxylated again to calcitriol, the hormonally active form of vitamin D$_3$.

The other source of vitamin D is the diet. One form, vitamin D$_2$, or ergocalciferol, is commonly available from some plants, especially fungi and yeasts (Hay and Watson 1977). Vitamin D$_2$ can be utilized by some vertebrates but not by others, for example, New World primates (Hunt et al. 1967). Another form, vitamin D$_3$, or cholecalciferol, is available from animal and plant tissues and is readily used by most vertebrates.

The relative importance of the two sources (endogenous or dietary) of vitamin D varies among species. Animals adapted
to ingesting sources low in dietary vitamin D appear to rely mostly on UV-B-generated endogenous vitamin D, and sometimes appear unable to utilize either form of dietary vitamin D efficiently (e.g., iguanas; Allen et al. 1999). Conversely, animals such as nocturnal carnivores and polar bears with little access to UV-B from sunlight but with rich dietary sources of vitamin D efficiently (e.g., iguanas; Allen et al. 1999). Conversely, an animal species cannot utilize either form of dietary vitamin D efficiently (e.g., iguanas; Allen et al. 1999).

Given that many diurnal animal species can probably utilize both sources of vitamin D, how might species adapted to environments with different availabilities of UV-B and dietary vitamin D compensate? Recently, we showed that the diurnal phrynosomatid lizard *Sceloporus olivaceous* has greater UV-B exposure and dietary vitamin D intake in its natural environment in Fort Worth, Texas, than the sympatric, introduced, nocturnal/crepuscular gekkonid lizard *Hemidactylus turcicus* (Carman et al. 2000). Also, the skin of the former has less sensitivity to UV-B-induced synthesis than that of the latter. Here we investigate the UV-B availability and skin sensitivity regarding vitamin D synthesis of two congenic Jamaican lizards, which inhabit light environments within the extremes shown by *S. olivaceous* and *H. turcicus*. These are the sun-dwelling, thermoregulating *Anolis sagrei* and the partial-shade-dwelling, thermal-conforming *Anolis lineotopus merope*.

*Anolis lineotopus* is a widespread native Jamaican species (Grant 1940). It is ecologically partitioned from other syntopic native anole species and is classified as a “trunk-ground” dweller. It is generally found in habitats of intermediate sun exposure (Schoener and Schoener 1971; Losos and De Queiroz 1997; Jackman et al. 2002). The northern subspecies *A. lineotopus merope* is a thermal conformer, its body temperature closely matching the air temperature in the shade throughout its daily activity (Lister 1976).

*Anolis sagrei*, a native of Cuba, was first reported in Jamaica in 1940 (Grant 1940) near Mandeville on the northwest coast and has since spread across the northern half of the island (Williams 1969; Landwer and Ferguson 2002). Ecologically, it is also a trunk-ground dweller, like *A. lineotopus*, but in Jamaica it inhabits full-sun-exposed ground habitats. It thrives in disturbed habitat and along coastal beaches. In Jamaica it is a thermoregulator, maintaining a daytime body temperature significantly higher than the air temperature (Lister 1976). *Anolis sagrei* is syntopic with *A. lineotopus merope* on the campus of the Hofstra University Marine Laboratory at Priory, where the anole community has been studied since 1983 (Landwer et al. 1995; Landwer and Ferguson 2002).

Our specific goals were (1) to compare the natural UV-B exposure of each species by measuring in vivo synthesis of UV-B photoproducts in the environment of each, (2) to compare the skin sensitivity for vitamin D photobiosynthesis of each species by exposing the skins of each to an artificial UV-B source and measuring photoproduct synthesis, and (3) to compare the availability of dietary vitamin D to each species by analyzing vitamin D concentrations of the stomach contents of free-living animals.

**Material and Methods**

We observed lizards on the campus of the Hofstra University Marine Laboratory at Priory, St. Ann’s Parish, Jamaica, from March 16 to 21, 2000. To obtain data on sun, shade, and ultraviolet exposure, we located individuals as close to 0800 hours as possible and followed them continuously until 1700 hours. The first four coauthors logged 72 observation hours. Four adult males each of *Anolis sagrei* and *Anolis lineotopus merope* were studied. We recorded full-sun, filtered-sun (mosaic of sunny and shady substrate or obvious intermediate illumination), and shade exposures every 5 min and whenever the light exposure changed for an immobile lizard. We marked lizard locations with acrylic paint after each location change of more than a few centimeters. We also noted the exact times spent at each location. We took care to neither disturb the lizard nor cause it to relocate when marking locations. Fortunately, the frequent activity by staff and guests of the Marine Laboratory near the lizards rendered them fairly oblivious of approach by an investigator. We recorded general notes on behavior, such as feeding and social interaction, and notes on environmental changes, such as temporary cloud cover, throughout the observation periods.

Ultraviolet exposure could not be estimated either directly or indirectly when simultaneously observing a lizard without disturbing it and altering its activity or habitat use pattern. Therefore, we assessed UV-B exposure in the field as follows. On a particular day (focal day), we noted the exact locations of a lizard and marked these locations with paint as described above. The sun exposure was noted subjectively as “full sun,” “filtered sun,” or “shade.” On a subsequent day (model-retrace day), we placed in vitro models so as to retrace the locations and times occupied by the lizard on the focal day. In vitro models are ampules constructed of UV-transmitting borosilicate glass and containing a 50-μg sample of provitamin D₃ (7-dehydrocholesterol) dissolved in 100% ethanol. Provitamin D₃ in the in vitro models is converted to previtamin D₃ and other photoproducts proportional to UV-B exposure. Thus, photoproduct concentration reflects exposure. Because photoequilibrium is established in in vitro models after prolonged exposure (G. W. Ferguson, unpublished data), they were replaced every 3 h. For up to 3.5 h, the rate of accumulation is relatively constant (G. W. Ferguson, unpublished data).

In addition to models retracing lizard locations, we placed control in vitro models at fully exposed sites, replaced at 3-h intervals, throughout both focal and model-retrace days. This allowed us to assess homogeneity of the maximum available UV-B environment among the days. To insure that control models assessed the differences between focal days and model-retrace days at the same time for both species, individuals of
each species were watched simultaneously by different observers. Thus, the same focal control and model-retrace control models were used for both species.

All in vitro models were kept wrapped with aluminum foil both before and after use to prevent incidental exposure. In vitro models were shipped to Boston University Medical Center (BUMC) for analysis of provitamin D₃ and previtamin D₃, and its photoproducts by high-performance liquid chromatography (HPLC; Holick et al. 1981; Webb et al. 1988).

While we did not measure UV-B irradiance directly during the 2000 study, we had previously measured the relationship between full-sun UV-B dose and in vitro model conversion of provitamin D₃ to photoproducts (Gehrmann et al. 2004). The resulting standard curve (Fig. 1) was used to estimate the UV-B dose received by in vitro models retracing the lizard locations during the 2000 study.

To assess vitamin D₃ photobiosynthetic ability, we collected and transported to Texas Christian University (TCU) seven A. sagrei and eight A. lineotopus merope adult males. One A. sagrei and three A. lineotopus merope were the same individuals observed in focal observation study described above. We maintained them in the lab and fed them crickets but did not expose them to UV. We euthanized them from eight to 12 days after removal from the field. All were in robust condition at the time. We excised four skin patches 5 × 5 mm in dimension from the dorsum of each animal. Patches were moistened with physiological saline and exposed to 0, 20, 40, or 60 min of irradiation by a Philips FS40 fluorescent sunlamp from a distance of 21 cm (90 μW/cm² irradiance). After exposure, we froze skin samples (−70°C) and sent them to BUMC and to be analyzed by HPLC for provitamin D and vitamin D photoproducts (Chen et al. 1992).

To determine natural levels of dietary vitamin D₃, we removed and froze the stomach contents of 16 A. sagrei and 22 A. lineotopus merope (all sizes and sexes) collected in the field. We made collections on March 15, 19, and 20, 2000, from Saint Ann’s Parish near Priory, Ocho Rios, and Discovery Bay, Jamaica. Stomach contents were removed from euthanized animals within 4 h of capture. Invertebrate prey from the stomachs were identified to order and sometimes family, frozen within 30 min of removal, and sent to BUMC to be analyzed by HPLC for vitamin D₂ and D₃ content. Because of the low volume of each stomach, we combined the samples into two pooled samples for each species.

We reexamined data from a previous study on Hemidactylus turcicus and Sceloporus olivaceous and compared them with the present data on Anolis. Methodology was similar to that presented here and is fully described in Carman et al. (2000).

Data were compiled using LOTUS 123, release 5, and EXCEL 1997 and 2000. Data were graphed and analyzed using SIGMASTAT, version 3.0; SIGMA PLOT 2001; and SYSTAT, version 8.0. Data were transformed when necessary to alleviate violations of normality and variance homogeneity.

![Figure 1. Percent conversion of provitamin D₃ to photoproducts in in vitro models as a function of UV-B dose. In vitro models were exposed to full sun on a cloudless day for 0.5 h at nonoverlapping times of day from 0800 to 1700 hours at Boyd, Texas on September 21, 2002 (Gehrmann et al. 2004). We recorded full-sun UV-B irradiance throughout the day next to the models, using a Gigahertz-Optik P9719 UV-B meter. Dose was calculated as the product of average irradiance in units of mW/cm² and interval time in seconds.](image314x528 to 547x702)

**Results**

There were significant differences between the two Anolis species in voluntary sun exposure. In nine pooled 1-h observation periods, the Anolis sagrei exposed themselves significantly more often to full or filtered sun (41.22% ± 6.3% [mean ± SE] of the observations) than did Anolis lineotopus merope (4.97% ± 2.09%; t = 5.46, df = 6, P = 0.002). In a comparison of the nine observation periods for A. sagrei, the proportion of time spent in the full or filtered sun decreased throughout the day (Fig. 2). The data could not be analyzed with repeated-measures ANOVA because of variance heterogeneity. However, the proportion of time spent in the shade, which increased, did not violate the variance homogeneity assumption and proved to be marginally significant (F = 2.35, df = 3, 8, P = 0.051).

As measured by photoconversion of provitamin D₃, to photobiosynthesis in Anolis, there was a difference between the two species in UV-B exposure (Fig. 3). Models retracing the activity of A. sagrei were exposed to more UV-B than those retracing the activity of A. lineotopus merope. A repeated-measures ANOVA with species as an independent factor and time as a repeated factor revealed a marginally significant difference between species (species effect, F = 5.64, df = 1, 6, P = 0.055). When the time periods were analyzed separately, a t-test revealed that a significant difference between species occurred only during the first time period (t = 6.34, df = 6, P = 0.001). For these comparisons α = 0.017 (Bonferroni-
The three periods was 500 mJ/cm²). Those exposed on the p
received a UV-B dose of 10 mJ/cm² during lineotopus merope
A. sagrei
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atmospheric interference of UV-B on the model-retrace days.
estimated slightly because of more intermittent cloudiness or
B exposure of the lizards on focal days may have been under-
tained more vitamin D₃ than those of
mostly consisting of ants, caterpillars, and grasshoppers, con-
tained more vitamin D, than those of A. lineotopus merope,

determined by conversion of provitamin D₃ to previtamin D₃ and
anoles at the Hofstra University Marine Laboratory. Exposure was
reported previously (Carman et al. 2000). We arranged the two
species in this study was intermediate to that of the two lizards
repeated-measures ANOVA with species as an independent fac-
tor and exposure time as a repeated factor, the time effect was
significant (F = 38.7, df = 2,24, P<0.001). The species effect
was also marginally significant (F = 12.1, df = 1,12, P <
0.053).

The maximum natural UV-B exposure of the two Anolis
species in this study was intermediate to that of the two lizards
reported previously (Carman et al. 2000). We arranged the two
Anolis species and the two lizards from the previous study
according to decreasing maximum UV-B exposure (Table 1).
There was a significant relationship between the amount of
total photoproduct produced upon 1-h exposure of skin to
sunlamp (log-transformed) and decreased natural UV-B ex-
posure measured in the field (y = 3.22 - 0.102x; R² = 0.30,
F = 9.87, df = 1,20, P = 0.005; Fig. 5). Thus, Sceloporus oli-
vaceous, the most UV-B-exposed species, produced the least
photoproduct in their skin. Anolis sagrei, the next most UV-

adjusted α = 0.05/n comparisons). The ANOVA revealed a sig-
nificant time effect (time effect, F = 4.74, df = 2,12, P =
0.030). Overall UV-B exposure decreased throughout the day.

On the basis of the standard equation percent provitamin
D₃ conversion = 0.02 × UV-B dose (Fig. 1), A. sagrei received
a UV-B dose of 65 mJ/cm² during the first time period, 50
during the second time period, and 8 during the third. Their
total dose for the day was approximately 123 mJ/cm². Anolis
lineotopus merope received a UV-B dose of 10 mJ/cm² during
the first time period, 25 during the second time period, and
7.5 during the third. Their total dose for the day was approx-
imately 42.5 mJ/cm².

There was a significant difference between UV-B exposure
of the full-sun control in vitro models exposed on the lizard
focal days and those exposed on the model-retrace days. The
in vitro models exposed on the focal days converted a mean
of 10.0% of provitamin D₃, to photoproducts (mean dose for
the three periods was 500 mJ/cm²). Those exposed on the
model-retrace days converted a mean of 8.5% (425 mJ/cm²;
t = 6.96, df = 7, P<0.001; data log-transformed). Thus, UV-
B exposure of the lizards on focal days may have been under-
estimated slightly because of more intermittent cloudiness or
atmospheric interference of UV-B on the model-retrace days.

Baseline values of dietary vitamin D revealed a possible dif-
ference between the species. The stomach contents of A. sagrei,
mostly consisting of ants, caterpillars, and grasshoppers, con-
tained more vitamin D, than those of A. lineotopus merope, mostly consisting of ants. The average was 37 ng/g of vitamin
D₃ for A. sagrei (n = 2 pooled samples from 16 individuals)
and 9.5 ng/g for A. lineotopus merope (n = 2 pooled samples
from 22 individuals). Presumably because of the low number
of replicates, the difference was not statistically significant
(t = 2.9, df = 1, P = 0.21). No vitamin D₃ was detected in any
of the samples.

The skin of both anole species responded to UV-B irradiation
with photoproduction; that of A. lineotopus merope
responded more strongly (Fig. 4). When the three 20-min time
periods of exposure after time zero were compared using
repeated-measures ANOVA with species as an independent fac-
tor and exposure time as a repeated factor, the time effect was
significant (F = 7.5, df = 2,24, P<0.01). The species effect
was also marginally significant (F = 4.74, df = 1,12, P <
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tained more vitamin D, than those of A. lineotopus merope,
B-exposed species, produced the second-lowest amount of photoproduct. *Anolis lineotopus merope*, the diurnal, shade-dwelling species with the second-lowest UV-B exposure produced the second-most photoproduct. Finally, *Hemidactylus turcicus*, the nocturnal/crepuscular species with the lowest UV-B exposure, produced the most photoproduct. In addition to vitamin D$_3$ and previtamin D$_3$, two of the *H. turcicus* produced substantial amounts of lumisterol, a biologically inert photoproduct (mean 19.7 ng/cm$^2$, 37% of their photoproducts produced).

We measured skin sensitivity not only as total photoproduct produced by a given UV-B dose but also as total photoproducts plotted as a function of initial provitamin D$_3$. A steeper slope indicates greater sensitivity. The analysis of skin photoproduct content after 1-h exposure, with initial provitamin D$_3$ content as a covariate, revealed a significant interaction between species and the covariate for *A. lineotopus merope* and *A. sagrei* (ANOVA, $F = 18.7$, df = 1,11, $P = 0.001$). Thus, the slopes of the regressions of photoproduct versus initial provitamin D$_3$ differed between the species, with that of *A. lineotopus merope* the steeper (Fig. 6). However, despite this significant difference in slopes, we consider this a preliminary finding, because the shallower slope for *A. sagrei* was strongly influenced by the single sample with the highest provitamin D$_3$ content (leverage = 0.875).

To extend the comparison, the skin of *H. turcicus* was significantly more sensitive than that of *A. lineotopus merope*. Thus, analysis of skin total photoproducts content after 1-h exposure, with initial provitamin D$_3$ content as a covariate, revealed a significant difference between these two species when adjusted to the covariate (ANOVA, species effect, $F = 5.6$, df = 1,9, $P<0.05$; covariate effect, $F = 6.5$, df = 1,9, $P<0.05$). The slopes of the regressions of photoproduct versus previtamin D$_3$ differed between the species, with that of *H. turcicus* the steeper (Fig. 7).

To summarize, *H. turcicus* had the most sensitive skin, followed by *A. lineotopus merope*, followed by *A. sagrei*. Finally, *S. olivaceous* had the least sensitive skin. This species has the largest scales of the four tested, and the skin was the most difficult to cut. There was very little photoproduct production by *S. olivaceous* skin under the test conditions (Fig. 5).

Analyzed separately, the initial provitamin D$_3$ concentrations in the skin of *H. turcicus* (75.3 ± 23.2 ng/cm$^2$ [mean ± SE]) and of *S. olivaceous* (151.9 ± 42.3 ng/cm$^2$ [mean ± SE]) were significantly lower than those of *A. lineotopus merope* (1,700 ± 166.5 ng/cm$^2$ [mean ± SE]) and *A. sagrei* (1,459 ± 179.6 ng/cm$^2$ [mean ± SE]; ANOVA $F = 26.81$, df = 3,18, $P<0.01$). The skin concentrations of the two anoles did not differ significantly, nor did that of *H. turcicus* differ significantly from that of *S. olivaceous* ($P>0.50$, least squares means post hoc analyses).

**Discussion**

We have characterized for the first time the UV-B environment for two tropical anoles with different thermal and visible light preferences. On a broader scale, we bring into focus factors

![Figure 4. Vitamin D$_3$ concentration of skin samples of male Jamaican anoles as a function of initial provitamin D$_3$. A steeper slope produced by a given UV-B dose but also as total photoproducts.](image)

**Table 1: Comparison of four lizard species**

<table>
<thead>
<tr>
<th>Species</th>
<th>General Light Exposure Environment</th>
<th>Maximum UV-B Exposure (ng photoproduct/min)</th>
<th>Photoproducts in Skin after 1-h Exposure to UV-B (ng/cm$^2$)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sceloporus olivaceous</em></td>
<td>Sunny</td>
<td>12</td>
<td>8.6 ± 2.02 (4)</td>
<td>Carman et al. 2000</td>
</tr>
<tr>
<td><em>Anolis sagrei</em></td>
<td>Sunny</td>
<td>3.7</td>
<td>15.3 ± 2.81 (6)</td>
<td>This study</td>
</tr>
<tr>
<td><em>Anolis lineotopus</em></td>
<td>Shady</td>
<td>1.1</td>
<td>31.0 ± 6.17 (8)</td>
<td>This study</td>
</tr>
<tr>
<td><em>Hemidactylus turcicus</em></td>
<td>Nocturnal/crepuscular</td>
<td>$1.5 \times 10^{-3}$</td>
<td>32.4 ± 13.6 (4)</td>
<td>Carman et al. 2000</td>
</tr>
</tbody>
</table>

Note. Maximum UV-B exposure was measured by rate of conversion of provitamin D$_3$ to previtamin D$_3$ and photoproducts in in vitro models retracing lizard activity in the field during 3-h period of maximum exposure. Photoproduct data are mean ± SE, with $n$ in parentheses.
that can influence the evolution of either a genetically fixed or a plastic mechanism of reduced or enhanced skin sensitivity to UV-B. Our data suggest that diurnal and crepuscular lizards may adjust the UV-B sensitivity of their skin, resulting in a balance between their ability to avoid UV-B damage and their ability to photosynthesize vitamin D₃.

The more heliophilic and thermophilic Anolis sagrei exposed itself to more sun and less shade than the thermal-conforming Anolis lineotopus merope. As expected, higher sun exposure resulted in higher UV-B exposure in A. sagrei, although A. lineotopus merope still experienced considerable UV-B exposure in its shady habitat at midday. Anolis sagrei also obtained more dietary vitamin D₃ than A. lineotopus merope. Thus, one might expect A. sagrei to have more of a problem avoiding the damaging effects of UV-B exposure, for example, DNA and cell damage (Hays et al. 1995; Blaustein et al. 1998; Miller et al. 2002), than obtaining enough vitamin D. Accordingly, natural selection might favor a mechanism that provides more efficient UV-B screening by their skin. Such a mechanism could cause the correlated response of lower sensitivity to vitamin D photobiosynthesis that we observed. Conversely, with less UV-B exposure and lower dietary vitamin D for A. lineotopus merope, one might expect this species to have a relatively greater problem obtaining sufficient vitamin D. Accordingly, selection might have favored the evolution of a mechanism rendering skin more permeable to UV-B and consequently more sensitive to vitamin D photobiosynthesis, which we observed. Adding the nocturnal/crepuscular Hemidactylus turcicus and more heliophilic Sce-loporus olivaceous to the comparison strengthened our perception of an adaptive balance of damage protection with vitamin D production among lizards in general.

The variation of skin sensitivity to UV-B, whether genetically fixed or adjustable, can involve several mechanisms. These can include increase or decrease in melanogenesis, keratinogenesis, DNA repair capacity, and provitamin D concentration (Tercafs 1963; Porter 1967; Gehrmann 1994; How et al. 1994; Eller et al. 2002). Variation of the first two would result in alteration of UV-B screening. If so, one would expect a correlation between sensitivity to skin damage and photobiosynthetic capacity. Conversely, variation in DNA repair mechanisms, such as photolyase concentration (Blaustein et al. 1994), or variation in provitamin D concentration (How et al. 1994) could cause adaptation to skin damage and vitamin D biosynthesis to vary independently. Our data showing little relationship between provitamin D concentration and photobiosynthetic capacity suggest that variation in photobiosynthetic ability involves something besides provitamin D₃ concentration in lizards. UV-B sensitivity of skin needs further investigation in lizards (Cope et al. 2001).

While overexposure to UV-B can cause skin damage, it is unlikely that this can lead to overproduction of vitamin D and toxicity. Holick (1989, 2004) discovered a mechanism in the skin of vertebrates to protect against the overproduction of vitamin D₃. After several minutes of exposure, the skin contains less previtamin D₃ and more of its biologically inert photoproducts, particularly lumisterol and tachysterol. The synthesis of lumisterol by the skins of two of the house geckos H. turcicus exposed to strong UV-B in the lab suggests that lizards may possess this regulatory mechanism.

Some lizards appear able to assess their internal vitamin D condition and respond by adjusting their voluntary exposure to UV-B (Jones et al. 1996; Ferguson et al. 2003). With limited

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Figure 5. Logarithm of the total photoproduct production in skin of four lizard species exposed to 1 h of UV-B-generating fluorescent sunlamp as a function of maximum natural UV-B exposure measured in the field (see Table 1). The regression is significant ($P = 0.005$); see text for details.

Figure 6. Relationship between photoproduct and provitamin D₃ concentrations in the skin of male Jamaican anoles. Preexposure levels of provitamin D₃ were assessed by adding skin photoproduct and remaining provitamin D₃ after 1-h exposure to UV-B. Previtamin D₃ was the only photoproduct detected. There was a significant interaction between photoproduct and provitamin D for the two species ($P < 0.01$); see text for details.
dietary vitamin D, a mechanism for behavioral regulation of vitamin D condition, as exists in the panther chameleon, would be beneficial. For example, *A. lineotopus merope* could seek out the highest sources of UV-B irradiance in its shady habitat and bask. While attraction to high-UV-B sources may not be as high a priority for *A. sagrei* in Jamaica most of the time, *A. sagrei* could benefit from UV-B photoregulatory ability if dietary vitamin D varies in its availability. Furthermore, on islands lacking a shade-tolerant species, *A. sagrei* invades shady habitats and appears to thermally conform (Lister 1976). Under such circumstances, they could benefit from UV photoregulation in a manner similar to *A. lineotopus merope* in Jamaica. In sunny habitats, thermoregulating *A. sagrei* could utilize UV photoregulatory behavior to seek out heat sources low in UV-B to avoid skin damage. While UV perceptual ability has been documented for this genus (Fleishman et al. 1993, 1997), photoregulatory behavioral ability has not been verified for *Anolis* and warrants further investigation.

**Acknowledgments**

We thank the Hofstra Marine Station officials and personnel, including Eugene Kaplan, Deb Bidwell, and Gorka Sancho, for making this study possible. We thank the officials and personnel of the University of the West Indies Marine Laboratory at Discovery Bay, including George Warner and June Lawrence, for permission to work at the lab. We thank Andrea Donaldson and the Natural Resources Conservation Authority for a research and export permit (ref. no. 18/27). We thank Mrs. Amair of the Ministry of Health for a permit to import the in vitro models. David Cross, John Horner, Jerry Husak, and Day Ligon provided statistical advice. Most of all we thank Dirk the dog and others of his species for efficiently excluding cats and other efficient lizard predators from the field site in Jamaica. Funding was by a grant from the TCU fund for research and creative activities (to G.W.F.) and NIH grant AR 36963 (to M.F.H.). The research methodology was supervised and approved by the TCU Institutional Animal Care and Use Committee (protocol 99-5).

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