Literature review

The Effects of UVb Radiation on Reptiles: a Review of its Usage for Captive Animals

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Abstract

Vitamin D₃, which allows the maintenance and development of bones, is photo-biosynthesised in the skin by UVb radiation. In a captive environment, this radiation is replicated by UVb emitting bulbs which vary in irradiance output, and care must be taken to ensure the correct dosage is offered. Consideration must be taken for the location of bulb, and materials between it and the animals' access. Supplementation may also be taken by certain species as a substitute for UVb radiation, although this may not be a useful alternative for all species.

Key words: Vitamin D_3 , photoregulation, UVb radiation, captive husbandry, reptile, dietary supplementation.

Introduction

As an increasingly more common pet, husbandry of reptiles requires careful consideration. As ectothermic species, temperature is the primary focus when setting up a captive environment for these animals, however, to offer high quality enrichment to these animals, natural habitats should be replicated. Natural lighting may play a large role in the health of captive reptiles.

Ultra-violet radiation (UV) is a large part of natural lighting, and has wavelengths from 400nm to 10nm, shorter than visible light (see figure 1), although wavelengths shorter than UVb are filtered out by the natural ozone layer, and therefore aren't present in natural reptile habitats (Gardiner et al., 2009). This review will therefore focus on UVb radiation and highlight its usage in the herpetocultural hobby. This review aims to evaluate whether UVb lighting is required for the enrichment and healthy living of reptiles, and whether this is worth costs and risks to the animals in a captive setup.

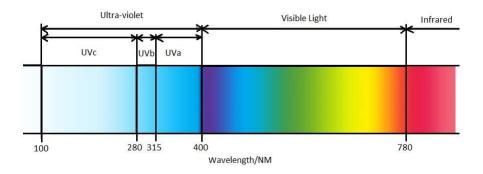


Figure 1 Wavelength spectrum of light.

UVb radiation in a captive environment requires specialised equipment, in the form of fluorescent tubes or compact lights. These bulbs were initially used on reptiles by Laszlo (1969), using the Vita-Lite UV lamp. The study found that reptiles exposed to this bulb fared

better than those without exposure. Since then, studies have found UVb stimulates many biological functions across vertebrate species. These include beta-endorphin production in humans (Holick and Jenkins, 2003), apoptosis (Kulms et al., 1999; Aragane et al., 1998), and increases in lipid peroxides (Dreher and Maiback, 2001; Ichihashi et al., 2000; Shindo et al., 1993). The primary function found in reptilian species is the production of D₃, which is photobiosynthesised in the skin in most animals. However, further studies in usage of UVb within this family may reveal secondary functions. Due to this important function, the usage of UV lighting to replicate natural habitats is recommended in reptile species (Carmel, 2014).

UV radiation does have its side effects however. In mammals, it has been known to cause cancer skin cancer (Soehnge et al., 1997), with a likelihood of it occurring in reptiles (Hannon et al., 2011), however further studies are required to substantiate these claims. Under excessive UVb from artificial lighting, reptiles have been demonstrated to show photo-kerato-conjunctivitis and even, rarely, UV skin "burns" (Baines, 2007; Gardiner et al., 2009).

In a natural environment, exposure to UV radiation from sunlight is often ensured through basking. This behaviour is associated with thermoregulation, which relies heavily on exposure to natural sunlight to allow reptiles to increase body temperature. Due to this, reptiles have evolutionary adaptations to protect themselves from it or increase utilisation efficiency minimising their exposure time. An example of this can be found in the variation of skin thickness found between species, with species with thicker skin having increased UV exposure compared to species with thinner skin (Carman et al., 2000).

The importance of vitamin D₃

Skin exposed to UVb radiation photo-biosynthesises vitamin D_3 (Norman, 1979; Adkins et al., 2003; Holick et al., 1995; Holick, 1995; 2004), a process which occurs in many vertebrate species (Bidmon and Stumpf, 1996; Antwis and Browne, 2009; Hay and Watson, 1976; Hayes et al., 1986). This suggests that it has an early origin of evolution, and is therefore unlikely to be absent in many species. Vitamin D_3 is a secosterol and thus acts as a hormone and is required in reptiles for healthy living (Mader, 1996; Dickinson and Fa, 1997; Brown et al., 2000; Rossie, 2006; Tapley et al., 2015;), with its main role being an important factor in calcium and phosphorus homeostasis (Holick, 1995; 2004; 2007; 2010; Stumpf, 1988; Laing and Fraser, 1999) as this is required to develop and maintain healthy bones.

25-hydoxyvitamin D_3 is the major metabolite of vitamin D_3 , and is probably the storage form in reptiles, like it is in mammals (Laing and Fraser, 1999). This metabolite is found circulating in the blood, allowing a simple method to evaluate vitamin D_3 levels in reptiles through a blood test. Evidence supporting this occurs in many studies, which have shown 25-hydroxyvitamin D_3 activity in their plasma (Henry and Norman, 1975; Aucone et al., 2003), and have vitamin D_3 dependent calcium binding proteins in their tissue (Rhoten et al., 1985).

However, monitoring 25-hydroxyvitamin D_3 to give an indication of current activity may be more complicated. An example of this can be found in a study conducted by Oonincx et al. (2010). The study was conducted over 87 days on Bearded dragons, a species well known for its requirement of UVb for the prevention of metabolic bone diseases (MBD). However, the animals showed no decrease in 25-hydroxyvitamin D_3 plasma concentrations when deprived UVb exposure. This suggests the half-life of vitamin D_3 may be longer than previously expected, or is stored as another form in the body. This is further supported by Ferguson et al. (2013). The study suggested a period of over 6 weeks in *Anolis* lizards. From this evidence, we can assume that vitamin D_3 has a long half-life, which requires studies on dietary or UVb radiation deprivation to occur over a larger time frame.

However, these studies were conducted on adult animals, which may no longer require as much vitamin D_3 for development of the bones. A study on juvenile monitor lizards, *Varanus albigularis*, found a 25 to 35% decrease in plasma 25-hydroxyvitamin D_3 levels after only 87 days deprived of supplementation or UVb exposure (Ferguson et al., 2009). This offers evidence that juvenile animals may require longer doses of vitamin D_3 than their adult counterparts, although further studies would be required to substantiate this hypothesis.

Aucone et al. (2003) studied Chuckwallas, *Sauromalus obesus*, exposed to UVb radiation. The study found no difference in growth rates in Chuckwallas, which may suggest that UVb exposure has no effect on physiological growth. However, the study also recorded 34ng/ml as the lowest 25-hydroxyvitamin D₃ levels, whereas field studies (Gillespie et al., 2000) yielded results from 47ng/ml to 130 ng/ml. This suggests that, despite these being juvenile animals, the pattern shown by adult animals may be occurring here. This may have affected the results, as such a small difference may not have allowed an effect on growth rate.

Embryogenesis

Vitamin D_3 also plays an important role in organ development and embryogenesis (Stumpf, 1988; Laing and Fraser, 1999; Ferguson et al., 2002). Many studies have been conducted on bird embryos showing poor bone formation in embryos and a lowered hatchability of eggs as a result of vitamin D_3 deficiency (Elaroussi et al., 1988; Fraser and Kodicek, 1970; Narabaitz and Tsang, 1989), however it is considered to be used in reptiles as well. Laing and Fraser (1999) found high concentrations of vitamin D_3 in the yolk and embryo of iguanian eggs. Concentrations of vitamin D_3 at 974.1ng/g were found in the yolk of the green iguana (*Iguana iguana*), and 99.5ng/g in the embryo of Eastern water dragons (*Physignathus lesueurii*). This reflects the vitamin D_3 concentrations of 50-100ng/g (Fraser and Emtage, 1976) which are found in the yolk of the domestic chicken. This provides supporting evidence for the usage vitamin D_3 in embryogenesis in reptiles, as well as a similar delivery system of vitamin D_3 to eggs as is found in birds. A study conducted on caucasion green lizard, *Lacerta strigata*, found calcium deficiency can lead to poor bone formation of embryos and lowered hatchability of eggs (Langerwerf, 1980).

Panther chameleons are a prime example of the influence of UVb in embryogenesis, with hatching success and offspring development being reliant on UVb exposure. Ferguson et al. (2002) demonstrated this in a study conducted on chameleons offered high UVb exposure and medium dietary supplementation of vitamin D_3 . This experimental group showed an increase in hatching success rate compared to low exposure and low dietary supplementation. The study also showed the high exposure group and high dietary supplementation had the highest success rate, but also showed mortality in the mothers. This is most likely due to an overdose of D_3 . This was most likely caused by the dietary supplementation as the self-limiting aspect of the photobiosynthesis prevents this.

Deficiency of vitamin D₃

A deficiency of vitamin D_3 in reptiles is shown as similar symptoms as in mammal and bird species (Bernard et al., 1991; Birkett and McCraken, 1990). These most commonly show themselves as MBD, one of the most common disease complexes found in captive reptiles

(Mader, 2006; Kik and Benyen, 2003; Laing and Fraser, 1999). This complex includes nutritional secondary hyperparathyroidism (NSH), osteoporosis (fragility of the bone), osteomalacia (softening of the bone) and rickets (Frye, 1991). These diseases are all caused by an imbalance of calcium and phosphorus, as a result of the deficiency, and causes bone structures to be improperly maintained or developed.

A vitamin D_3 deficiency can occur through either dietary means or lack of UVb exposure. Bearded dragons, *Pogona vitticeps*, are often at risk of these diseases, which can often come as a result of a diet rich in crickets or mealworms (Wright, 2008). These prey items have inverse calcium to phosphorus ratios, resulting in a deficiency in calcium.

Vitamin D₃ absorption through supplementation

Dietary absorption of vitamin D_3 may be a viable alternative to production through UVb radiation for some species of reptiles. The consumption of vitamin D_3 producing prey allows absorption of the vitamin via the intestine. In captive care, supplementation for vitamin D_3 is often used. However, the usefulness of this acquisition by dietary supplementation compared to UVb is controversial (McWilliams, 2005).

A reason for this controversy may be due to lizard prey items generally being low in vitamin D_3 (Barker, 1998). Carman et al. (2000), and Ferguson et al. (2005) conducted stomach content analysis to find the average maximum levels of vitamin D_3 in lizard diets (see table 1 for results).

Species	Vitamin D3 concentrations (IU/kg of food)	Basking behaviour
Anolis sagrei	1500	Thermal regulator
Anolis lineotopus	380	Thermal conformer
Sceloporus olivaceous	279.2	Thermal regulator
Hemidactylus turcicus	117.2	Thermal conformer

Table 1 Stomach content analysis results for vitamin D3 concentrations compared to basking behaviour in four species. Data from Carman et al. (2000) and Ferguson et al. (2005)

Carman et al. found no significant difference between their study animals, *S. olivaceous and H. turcicus*, however, a significant difference was found between the *Anolis* lizards in the study conducted by Ferguson et al. The *Anolis* study suggests a variation in dietary requirements occurs between different basking behaviour types, however, the same is not found in the other study. This suggests the variation is more complex than basking behaviour of the study animals. *A. lineotopus* inhabit an ecological niche with minimal UVb exposure, whereas *H. turcicus* choose shade and thus avoidance of UVb exposure. However, the differences between these niches has a greater effect on the prey these species encounter. Where *A. lineotopus* occur, prey also have minimal UVb exposure, and so photobiosynthesis (and therefore vitamin D₃ concentrations) in these animals is diminished, however, the same cannot be said for *H. turcicus*, whose prey inhabit similar UV conditions as the thermoregulating species.

In captivity, these conditions may be mirrored, as most prey items are farmed in cheap, easy to maintain setups, unlikely to offer UVb radiation for D_3 photobiosynthesis, which may be lower in the vitamin than wild alternatives. Due to this, supplementation of the vitamin is offered instead. Nutrabol is the most commonly used of these vitamin D_3 supplementation products,

and contains 200mg calcium & 150IU vitamin D_3 per gram, with a recommended dosage of a pinch per kilogram of animal. A pinch is not an accurate measurement, which suggests that vitamin D_3 supplementation may be considerably more difficult to quantify in captive care than UVb exposure. However, if we assume a pinch is roughly 10mg, we find 1000IU/kg of animal, similar to the dosages found in stomach content analysis, in animals much smaller than a kilogram. Studies have also been conducted to find the correct dosage of supplementation. Kik and Benyen (2003) recommended vitamin D_3 doses of 260-1800 IU/kg of feed, and Oftedal (1997) suggested 500-1000 IU/kg of feed for captive carnivorous lizards. However, Bernard and Allen (1997) found deficiencies in vitamin D_3 occurred at 2000-3000 IU/kg of food. This may also be due to the inability to quantify it as easily as UVb exposure or the study species being inefficient at absorbing it from the diet.

These estimates appear to be under supplementations when compared to the serum 25hydoxyvitamin D_3 levels found in wild caught specimens, which may be due to the fear of dietary over-supplementation, or hypervitaminosis D, which can be toxic and sometimes lethal in reptiles (Ferguson et al., 1996; Wallach, 1966).

A vitamin D₃ overdose can also lead to hypercalcaemia. This has been found in *Natrix piscator* (Srivastav et al., 1995; Srivastav and Rani, 1989), and the yellow monitor lizard, *Varanus flavescens* (Swatup et al., 1986). Hoby et al. (2010) show the best prevention for these in juvenile veiled chameleons, *Chamaeleo calyptratus*, was locusts gut-loaded with 12% calcium and 250,000 IU/kg (75mg/kg) vitamin A and 25,000 IU/kg (0.624 mg/kg) vitamin D₃ plus low UVB exposure of 3-120 μ W/cm².

Hibma (2004) conducted a study on the effects of dietary supplementation and UVb exposure on the growth rate of the green iguanas, *Iguana iguana*. During the study, 5 animals died. This was thought to be due to overexposure of UVb radiation, however, four of these five animals were given high dietary D_3 supplementation, so death could also be attributed to the previously mentioned high toxicity of d3 supplementation. The study did also find an increase in growth rate of those on dietary supplementation, which suggests that, as long as dosage is considered, supplementation can have a positive effect.

Despite this increase, Bernard et al. (1996) found dietary and high dose injected supplementation of D3 metabolites resulted in a significantly lower 25-hydroxyvitamin D_3 serum concentration than in animals exposed to UVb radiation. This was further demonstrated in Komodo dragons, where higher D_3 blood concentrations were found in animals that had UVb exposure than those with dietary supplementation (Nijboer et al., 2007).

Oonincx et al. (2010) also studied a comparison of exposure to UVb radiation with dietary supplementation. The study monitored the change in vitamin D_3 metabolites in bearded dragons (*Pogona vitticeps*). The study found that at 6 months of age, D_3 concentrations increased in animals exposed to UVb radiation, but those with oral supplementation showed no change. This may provide evidence supporting the usage of UVb over dietary supplementation, however, it may also be due to limitations of the study. The study raised animals in joint terrariums, this resulted in dominance between the animals, resulting in death in one animal and most likely control of resources by a minority of the animals.

These studies suggest dietary supplementation may be ineffective when compared to UVb radiation. This may be because vitamin D_3 can be inactivated in the liver, and then excreted as waste in bile. As such, when large amounts of vitamin D_3 enter the intestine and are absorbed, and enters the liver, large doses are quickly inactivated, making it less efficient than exposure to UVb (Fraser, 1983). This suggest that this mechanism of D_3 acquisition is less useful then UVb.

There is evidence, however, which suggests lizards may be able to regulate their diet based on the nutritional constraints of certain prey items (Eason, 1990). This may extend to include vitamin D_3 selection through dietary regulation. However, further studies on dietary supplementation are therefore required to provide stronger evidence for their usefulness. The rarity of these studies currently occurs as UVb exposure is more easily quantifiable than supplementation (Ferguson et al., 2010).

Exposure to UV radiation in captive care

UVb radiation provides the primary source of vitamin D_3 by enabling photo-biosynthesis in the skin which is exposed to it. Excessive exposure to unnaturally short wavelength UV, namely UVc or low wavelength UVb, can cause eye and/or skin damage, reproduction failure or even death in reptiles (Van Norren, 1991; Gardiner et al., 2009).

Baines (2007) and Gardiner et al. (2009) analysed case studies from reptiles with photokerato-conjunctivitis (see figure 2). These animals exhibited a swelling or closure of eyes, however most recovered in 2-14 days after removal of the UV source, but some resulted in mortality. These cases were found to be most associated with animals with elevated basking levels, such as Bearded dragons, *Pogona vitticeps*, and blue tongued skinks, *Tiliqua* spp., although a severe case was also found in a royal python, *Python regius*, an animal with low levels of basking behaviour.

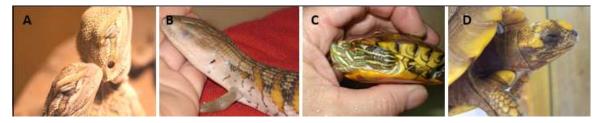


Figure 2 Symptoms of photo-kerato-conjunctivitis (Baines, 2007). A hatchling bearded dragons. B Blue tongued skink. C Red eared slider turtle. D Yellow footed tortoise.

As these symptoms often occurred in private collections using the same bulb type. Due to this, the bulbs were analysed more closely. These lamps contained a "phototherapy" phosphor, the same as those found in fluorescent sun lamps (FS lamps), a lamp found to be a poor choice for use as a sunlight substitute (Brown et al., 2000) for testing the effects of UV. Due to this substance, these lamps were found to emit at a wavelength as low as 275-280nm, a very short wavelength UVb radiation, on the borderline of UVc (see figure 3), which can cause damage and is naturally filtered out by the ozone (Gardiner et al., 2009). This phosphor is no longer used in these brands of lamp.

In a captive setup, various factors must be taken into account to minimise chance of overexposure and to ensure the correct amount of UV reaches the basking spot. These include the output of the bulb, distance between the bulb, and materials between the bulb and the basking spot.

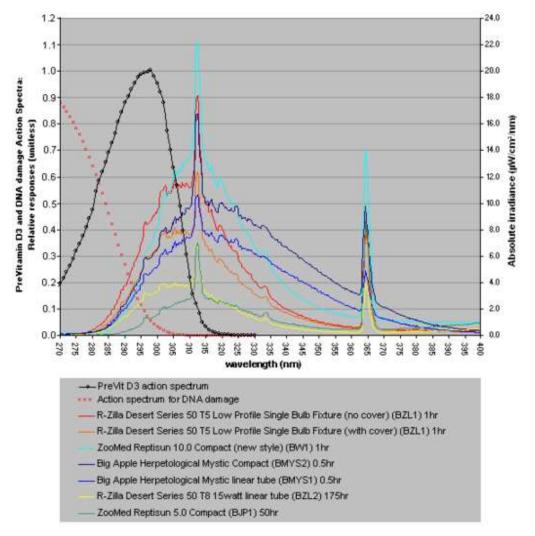


Figure 3 UV wavelength spectrum of reptile UVb lamps with a phosphor similar to those used in FS lamps. (Baines,2007)

UVb emitting bulbs currently fall into four categories, fluorescent tubes (T8 and T5 varieties), mercury vapour lamps and metal halide lamps. Fluorescents are currently the most commonly used UVb emitters in the herpetocultural hobby. It is important to offer reptiles the most suitable dosage, to minimise overexposure risks whilst allowing. Ferguson et al. (2010) offered some insight in this. The study measured UV radiance at locations where reptiles were found basking. The study found variation between taxons in mean exposure, but correlation between ecological niches. These niches fit into four categories of varying degrees of UVb exposure (see table 2). Baines et al. (2016) expanded on this study, and designed a guide based on these zones to suggest lamp usage in the hobby.

-	Characteristics	Zone range UVI	Maximum UVI
Zone 1	Crepuscular or shade dweller, thermal conformer	0-0.7	0.6-1.4
Zone 2	Partial sun/occasional basker, thermoregulator	0.7-1.0	1.1-3.0
Zone 3	Open or partial sun basker, thermoregulator	1.0-2.6	2.9-7.4
Zone 4	Mid-day sun basker, thermoregulator	2.6-3.5	4.5-9.5

Table 2 Ferguson zones offering UVi ranges for species with differing behaviours (Ferguson et al., 2010 and Baines et al., 2016)

Table 3 shows that each UVb emitting bulb offers the same percentage of 7dehydrocholesterol biosynthesised into pre-vitamin D_3 dependant on its dosage, irrespective of variance in irradiance (distance from the bulb) or exposure time (Gehrmann et al., 2004). This also suggests overexposure may also occur due to a lack of locations to hide from the light in the enclosure.

Table 3 Percentage of 7-dehydrocholesterol synthesised into pre-vitamin D_3 with alteration of irradiance and exposure time whilst maintaining dosage levels. UVb source Westinghouse FS 20/T12. Irradiance measured using Solartech 6.2 meter (Gehrmann et al., 2004)

IRRADIANCE (µW/cm ²)	EXPOSURE TIME (min) (mJ/cm ²)	DOSE	% PRODUCT SYNTHESIZED
142	30	255	34.42
70	60	252	34.20
35	120	252	34.14

A further factor effecting UV radiance at the basking point is distance from the bulb. As figure 4 shows, the further away from the source, the greater the loss of UV irradiance, until irradiance diminishes towards zero. This suggests placement of the basking spot is very important, and a higher output lamp would be required for larger animals or larger enclosures (for example, Komodo dragons), since the lamps needs to cover a larger area and/or be positioned at a greater distance from the animal.

The final factor affecting differences in UV exposure at a basking point is whether or not there are materials between the bulb and the basking spot. Burger et al. (2007) found that air-permeable materials, such as wire mesh, gave a transfer of UVb similar to direct transfer and that the percentage transmission was constant, regardless of wavelength, through these materials. The study also found that the UV transmitting acrylics used in the study blocked the shorter wavelengths of UVb, which synthesise D_3 more efficiently, more than the longer wavelengths. As animals also thermoregulate, they also spend varying amounts of time hiding under cover. As such, dosage is also an important factor.

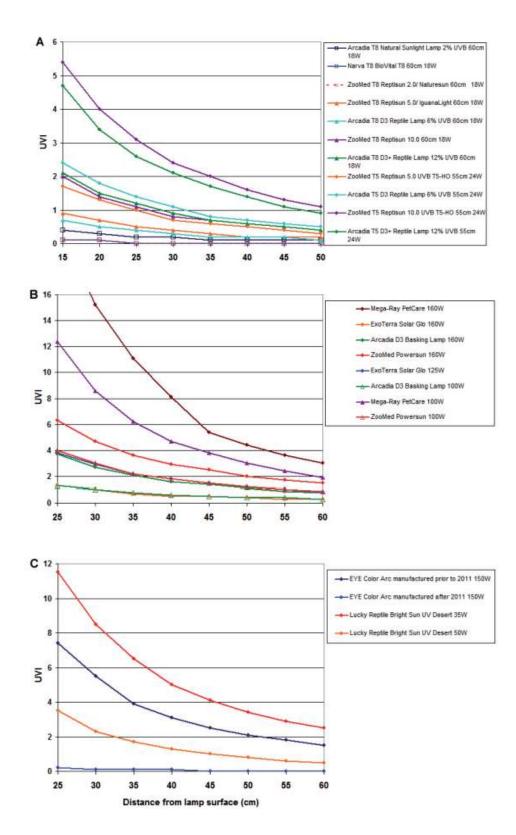
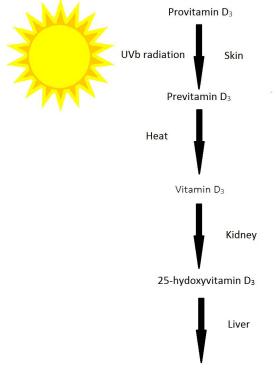


Figure 4 UVi output of bulbs. A) UVb emitting fluorescent tubes (both T8 and T5) B) mercury vapour lamps C) metal halide lamps (Baines et al., 2016)



Production of vitamin D₃

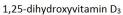


Figure 5 The production of vitamin D₃ (Tian et al., 1993; 1994; Tian and Holick, 1995)

Production of biologically active D_3 begins with photo-biosynthesis in the skin. Due to this, basking is an important mechanism for D_3 synthesis as it allows the skin to absorb UVb, where provitamin D_3 (7-dehydrocholestrol) is photoloysed into previtamin D_3 (Tian and Holick, 1995). This is then thermally isomerised into vitamin D_3 (Tian et al., 1993; 1994; Tian and Holick, 1995), which enters the blood, and becomes hydroxylated in the kidney and then the liver into the biologically active form, 1,25-dihydroxyvitamin D_3 , also called calcitrol (Tian et al., 1993; 1994).

In a natural environment, this process is stimulated by natural sunlight, however, in captivity it can be replicated using UVb bulbs. These bulbs have been suggested to emit a shorter wavelength than found in the natural alternative, and thus stimulate the photobiosynthesis more efficiently (MacLaughlin et al., 1982), however, this may also increase the risk of overradiation so care is needed when positioning the lamps.

Laing and Fraser, 1999, compared agamid and iguanid lizards housed either in indoor enclosures with artificial UVb exposure against those outside (either in captive enclosures or wild caught animals). The study found animals under artificial light had lower vitamin D_3 levels than outdoor animals. This may be due to an increased ability to photoregulate in the outdoor enclosures, or the older style of UVb lamp, which will vary from current standards due to the age of the study.

Laing et al. (2001) also demonstrated this with iguanas. Animals kept outside had 25hydroxyvitamin D₃ concentrations of 105 +/- 70 nmol/L compared to indoor ones under artificial lighting with 44 +/- 25 nmol/L. Those with some natural sunlight exposure had concentrations of 78 +/- 47 nmol/L. This process occurs in many species, however, this may not extend to all species. Some carnivores, such as cats (How et al., 1994), have been shown not to photo-biosynthesise UVb. Another study suggested they may not require vitamin D_3 at all (or at least require a diminished dosage compared to others species), by showing no deficiency after 275 days without a dietary intake of the vitamin (Rivers et al., 1979).

This evidence may have given rise to the opinion that some reptilian species, specifically snakes as generally carnivorous species, do not require UVb. This hypothesis may assume they procure vitamin D_3 through solely dietary means, as carnivore diet offers prey with a higher D_3 yield due to the consumption of D_3 producers.

Evidence supporting this theory may originate from a study on royal pythons. Hedley and Eatwell, 2013, found no change in 25-hydroxyvitamin D_3 concentrations in the blood circulation when exposed to UVb radiation. This can be theorised as being due to their habitat as burrowing species and so they may rely solely on dietary intake. However, the validity of this study must be questioned. The study used a small sample size with an experimental group of only high D_3 concentration females, and a control group consisting predominantly of males with lower concentrations. During the breeding season to aid embryogenesis (Stumpf, 1988; Laing and Fraser, 1999; Ferguson et al., 2002), females have altered blood chemistry. This may, as evidence previously suggested, include higher D_3 concentrations, making male and females non-comparable in this scenario. The study also did not record initial D_3 concentration of D_3 , UVb exposure might not have resulted in further production of vitamin D_3 as a result of it being a self-limiting process (MacLaughlin et al., 1982; Webb et al., 1989). The final limitation of this study is the short time period of 70 days, which may not allow the expiration of the half-life previously suggested.

Contradictory evidence for this theory, suggesting carnivorous snake species can use UVb exposure, was offered by Acierno et al., 2008. The study measured concentrations of 25-hydroxyvitamin D_3 in corn snakes, *Pantherophis guttatus*, and showed an increase of 50 to 196mol/L when exposed to UVb radiation. A further study on a carnivorous reptile, the Komodo dragon, found 25-hydroxyvitamin D_3 concentrations increased by 8 to 60 times when indoor, UV deprived, animals were exposed to sunlight (Gillespie et al., 2000).

Behavioural Adaptation

In a natural habitat, heat is emitted by the sun, and is therefore strongly associated with UV radiation. As such, behavioural adaptions for thermoregulation may simultaneously offer an adaptation for photoregulation. Basking, a critical thermoregulation technique, is one such adaptation. This behavioural adaptation is based on the presence of sunlight, and is found across many species of ectotherms (Young, 1981; Seebacher, 1999; Plummer et al., 2005), and allows the absorption of infrared radiation (heat) from the sun. The behaviour comes with costs (Downes, 2001), including time and exposure to predators, as such, basking behaviours vary between species (Michaels and Preziosi, 2013).

This behaviour falls into one of two categories, allowing optimal exposure to heat with minimal costs: thermoregulators which actively bask in sunlight to absorb heat, and thermal conformers which rely on the ambient temperature to provide optimum body temperatures (Huey, 1982). This raises the question of why bask when ambient temperature may offer a high enough body temperature with fewer costs. This may be due to other possible benefits of basking, such as photoregulation.

Evidence to support this comes from species such as freshwater turtles. Within these species, basking does not always equate to a change in body temperature (Manning and Grigg, 1997; Plummer et al., 2005), suggesting that exposure to natural sunlight offers a further benefit.

Further studies offered more support for this theory. Aucone et al., 2003, found Chuckwalla lizards, *Sauromalus obesus*, basked under heat sources which also offered UVb radiation 40% more frequently than under sources which offer heat alone. Panther chameleons have also been shown to photoregulate (Reichel et al., 1989; Jones et al., 1995; Ferguson et al., 2003; Karsten et al., 2009). This species uses extreme accuracy to increase their UV exposure when on a low D_3 diet. *Anolis sagrei*, another thermoregulating species (Holick, 2007), demonstrates the same behaviours when confronted with a lower D_3 diet (Ferguson et al., 2005; 2013). However, *A. lineoptues*, a shade dwelling thermal conformer (Lister, 1976), showed no change in behaviour under the same circumstances (Ferguson et al., 2005; 2013). This may be due to an adaptation in this species to receiving minimal UV levels in the wild, by having a higher efficacy of photo-biosynthesis in the skin or being less dependent on D_3 . A similar study also showed a thermal conformer, *A. gundlachi*, did not seek light for UVb absorption (Hertz et al., 1994).

Physical Adaptations

Skin

The skin protects the internal organs from harmful UV radiation (Waring, 1963). It uses three ways to maximise D_3 production whilst defending against this damage; colouration of the epidermis, cellular defence, and biochemical defence (Chang and Zheng, 2003).

The utilisation of epidermis colouration in thermoregulation to maximise heat absorbance has been demonstrated in many reptiles previously (Clusella-Trullas et al., 2009). Darker colours absorb heat and lighter colours reflect it. These species display darker colouration pre-basking to maximise absorption and a rapid colour change to a lighter colour to maximise reflectance and prevent overheating (Noris, 1965; Pearson, 1977; Hoppe, 1979; Sherbrooke et al., 1994; Rosenblum, 2005).

The night gecko, however, alters its colour without heat bias (Noris, 1965). Examples like this suggest colouration has functions besides thermoregulation. One of these functions may be UVb reflectance and absorbance, studies support this by finding evidence for melanin pigmentation in the skin altering its ability to absorb UVb (Holick and Jenkins, 2003). Humans display this mechanism, low melanin levels gave 30% UV radiation through the skin, whereas high melanin levels gave 10% (Everett, 1966). In fact, further studies suggest that melanin dispersal may be controlled by light as opposed to heat (Cooper and Greenburg, 1992). This allows melanin dispersal to be utilised for both thermoregulation and photoregulation, as it allows natural sunlight to trigger it.

Overheating during basking is a great concern for these species. This may be combatted election for skin which reflects longer wavelengths (such as infrared), but not shorter wavelengths (such as UV). This would allow the animals to absorb UV more efficiently than heat and minimise the risk of overheating. This was demonstrated in a study using two chameleon species (Walton and Bennet, 1993). These animals reflect longer wavelengths at higher temperatures, but do not demonstrate any extra UV reflectance.

The integument offers further protection in the form of cellular defence. This primarily comes in the form of variations in the thickness of the skin (Porter, 1967; Nietzke, 1990; Carman et

al., 2000; Ferguson et al., 2005) allows varying degrees of protection and ability to photobiosynthesis. This is due to alpha and beta layers limiting UVb diffusion (Chang and Zheng, 2003). Carman et al., 2000, demonstrated this by comparing Texas spiny lizards, and Mediterranean house gecko. As a diurnal species, the spiny lizards had an elevated opportunity for basking and thus photobiosynthesis than the gecko, a crepuscular one. The study also found the geckos possessed a thinner skin, and thus had a higher rate of conversion allowing it to maximise its limited opportunity to photo-biosynthesise. Acierno et al., 2006, found the same effect amongst *Anolis* lizards, although not as pronounced. *Anolis sagrei*, a thermoregulator, was found to have a greater opportunity for UVb absorption than *Anolis lineotopus*, a thermal conformer. The study suggested the thicker skin found on *A. sagrei* was required as a UV defence.

Skin cells (keratinocytes) absorb excess UV radiation and are killed by it. The dying cells can be identified in radiation-damaged skin as "sunburn cells". Because they have absorbed the radiation, it does not reach the internal organs. (Young, 1987; Chang and Zheng, 2003). In reptilian species, shedding is a mechanism already in place, and used for several purpose, which allows the removal of this damaged layer. Without this mechanism, the skin thickness would increase and limit UVb absorption, however, with it the ability to photo-biosynthesise is renewed (Chang and Zheng, 2003).

The final form of protection comes from biochemical defence. D_3 production is self-limiting, as its degrades into inert photoproducts when overexposed to UVb (MacLaughlin et al., 1982; Webb et al., 1989). This minimise the build-up of toxic vitamin D_3 .

Vision

Behavioural photoregulation relies on the ability to identify areas with increase ultra-violet irradiance. This may due to a primitive system, relying on vision within the visible colour spectrum, considered to be used for thermoregulation due to the spectrum of daylight. However, reptiles may further utilise this for photoregulation, which is similarly linked. A further adaption for photoregulation lies in the light sensitive pineal gland under the skull, and the parietal eye or "Third Eye". This gland is presents on the head of some basking lizards, and detects light for basking.

Reptiles may also have more derived adaptations for photoregulation. Studies have found that UVa is visible to many animals (Crescitelli, 1972; Govardovskii and Zueva, 1974; Goldsmith, 1980; Chen et al., 1984; Chen and Goldsmith, 1986; Arnold and Neumeyer, 1987; Mendel and Backhaus, 1991; Perry and McNaughton, 1991; Sillman et al., 1997; Loew et al., 2002; Bowmaker et al., 2005; Brames, 2007; Martin et al., 2014), and is often used to aid social interactions as well as the recognition of prey items and conspecifics. In reptilian species, this may also aid photoregulation.

UVa is currently offered in many light sources, including incandescent and UV florescent bulbs (see figure 6), and small amounts are supplied to reptiles through the usage of incandescent heat bulbs. Herpetoculturists often use non-light emitting bulbs (such as ceramic bulbs or reptile radiators) as a heat source instead of these light sources, and so deny this enrichment aspect to the animal. This is an often overlooked aspect, leading to non-light emitting bulbs being preferred due to the increase heat efficiency and thus lowered costs of use.

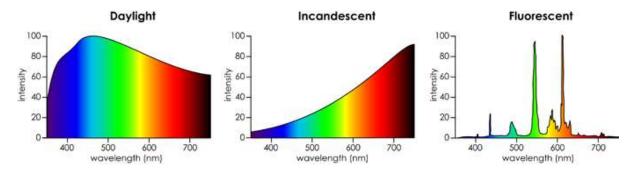


Figure 6 Wavelength spectrums of natural sunlight and typical manufactured household bulbs. (Clark, 2013). Both manufactured bulbs show low intensity UVa. UVb emitting fluorescent bulbs also emit a UVb peak but follow similar wavelength patterns in the visible range to typical manufactured bulbs.

This occurs due to a UV sensitive pigment in cone cells (Chen et al., 1984; Chen and Goldsmith, 1986) which provide a cis-peak or beta band in the vision (Jacobs, 1992). The presence of these pigments is the defining proof of UV vision, as Loew et al., 2002, found in all 17 species of Caribbean anole lizard studied. A peak sensitivity at 380nm has also been found in the red-eared slider, *Trachemys scripta elegans*, (Arnold and Neumeyer, 1987). This suggests further studies on this animal is required to find these cone pigments, and that there is a good chance these are present.

Retina patterns in boid species are considered ancestral (Crescitelli, 1972), so if UV sensitive pigments are present there, it's plausible that most species of snake will have them. To find out if this was the case, Sillman et al. (1999) conducted a study on royal pythons, *Python regius*. The study found both rod and cone cells. The rods were the typical structure found throughout vertebrate. The species also possessed two forms of cone structures. One of these structures is of typical form, and the other, similar to those found in garter snakes (Sillman et al., 1997), which can recognise UV. However, the cones only made up 10% of the photoreceptors, so this vision may be limited.

Conclusion

The evidence suggests that UVb exposure is important for the healthy living of captive reptiles, and more useful than the dietary alternative. The biggest concern presented by UV usage, however, is in translating natural doses and microhabitats into captive setups. As such, offering the correct dosage is important. To ensure animals receive this, the irradiance at the basking point must be monitored as the discussed factors can affect this. Photoregulation is an important factor in allowing animals to receive the correct dosage, and so UVb gradients should be supplied, with UVb refuges to allow the animals to prevent exposure.

The correct dosage relies on field studies of these animals, and therefore not known for every captive species. To ensure damage limitation, animal behaviour should always be monitored after the addition or alteration of an aspect of their captive environment.

References

Acierno, M., Mitchell, M., Roundtree, M. and Zachariah, T. (2006). Effects of ultraviolet radiation on 25-hydroxyvitamin D 3 synthesis in red-eared slider turtles (*Trachemys scripta elegans*). Journal of the American Veterinary Medical Association, 229(11), pp.1794-1794.

Acierno, M., Mitchell, M., Zachariah, T., Roundtree, M., Kirchgessner, M. and Sanchez-Migallon Guzman, D. (2008). Effects of ultraviolet radiation on plasma 25-hydroxyvitamin D 3 concentrations in corn snakes (*Elaphe guttata*). American Journal of Veterinary Research, 69(2), pp.294-297.

Adkins, E., Driggers, T., Ferguson, G., Gehrmann, W., Gyimesi, Z., May, E., Ogle, M. and Oxens, T. (2003). Ultraviolet light and Reptiles, Amphibians. Journal of Herpetological Medicine and Surgery, 13(4), pp.27-37.

Antwis, R. and Browne, R. (2009). Ultraviolet radiation and Vitamin D3 in amphibian health, behaviour, diet and conservation. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 154(2), pp.184-190.

Aragane, Y., Kulms, D., Metze, D., Wilkes, G., Pöppelmann, B., Luger, T. and Schwarz, T. (1998). Ultraviolet light induces apoptosis via direct activation of CD95 (FAS/APO-1) independently from its ligand CD95L. Journal of Dermatological Science, 16, p.S18.

Arnold, K. and Neumeyer, C. (1987). Wavelength discrimination in the turtle *Pseudemys scripta elegans*. Vision Research, 27(9), pp.1501-1511.

Aucone, B., Gehrmann, W., Ferguson, G., Chen, T. and Holick, M. (2003). Comparison of Two Artificial Ultraviolet Light Sources used for Chuckwalla, Sauromalus obesus, Husbandry. Journal of Herpetological Medicine and Surgery, 13(2), pp.14-17.

Baines, F. (2007). UV Lighting for Reptiles: A new problem with high UVB output fluorescent compact lamps and tubes?. [online] Uvguide.co.uk. Available at: http://www.uvguide.co.uk/phototherapyphosphor.htm. [Accessed 13 Apr. 2016].

Baines, F., Chattell, J., Dale, J., Garrick, D., Gill, I., Goetz, M., Skelton, T. and Swatman, M. (2016). How much UVB does my reptile need? The UV-Tool, a guide to the selection of UV lighting for reptiles and amphibians in captivity. Journal of Zoo and Aquarium Research, 4(1).

Barker, D., Fitzpatrick, M. and Dierenfeld, E. (1998). Nutrient composition of selected whole invertebrates. Zoo Biology, 17(2), pp.123-134.

Bernard, J., Allen, M. and Ullrey, D. (1997). Feeding captive insectivorous animals: Nutritional aspects of insects as food. Nutrition Advisory Group Handbook, Fact sheet 3, pp.1-7.

Bernard, J., Oftedal, O. and Ullrey, D. (1996). Idiosyncrasies of vitamin D metabolism in the green iguana (Iguana iguana). Proceedings of the Comparative Nutrition Society Symposium, pp.11-14.

Bernard, J., Oftedal, O., Citino, S., Ulrey, D. and Motali, R. (1991). The response of vitamin D-deficient green iguanas (Iguana iguana) to artificial ultraviolet light. Proc Am Assoc Zoo Vet, 3, pp.147-150.

Bidmon, H. and Stumpf, W. (1996). Vitamin D target systems in the brain of the green lizard *Anolis carolinensis*. Anat Embryol, 193(2).

Birkett, J. and McCracken, H. (1990). Osteodystrophy in an Asian agamid (*Hydrosaurus pustulatus*). Herpetofauna, 20, pp.32-36.

Bowmaker, J., Loew, E. and Ott, M. (2005). The cone photoreceptors and visual pigments of chameleons. J Comp Physiol A, 191(10), pp.925-932.

Brames, H. (2007). Aspects of Light and Reptile Immunity. Iguana, 14(1), pp.19-23.

Brown, D., Peritz, A., Mitchell, D., Chiarello, S., Uitto, J. and Gasparro, F. (2000). Common Fluorescent Sunlamps are an Inappropriate Substitute for Sunlight. Photochemistry and Photobiology, 72(3), pp.340-344.

Burger, R., Gehrmann, W. and Ferguson, G. (2007). Evaluation of UVB reduction by materials commonly used in reptile husbandry. Zoo Biology, 26(5), pp.417-423.

Carman, E., Ferguson, G., Gehrmann, W., Chen, T. and Holick, M. (2000). Photobiosynthetic Opportunity and Ability for UV-B Generated Vitamin D Synthesis in Free-Living House Geckos (*Hemidactylus turcicus*) and Texas Spiny Lizards (*Sceloporus olivaceous*). Copeia, 2000(1), pp.245-250.

Carmel, B. (2014). A guide to health and disease in reptiles & amphibians. Burleigh, Queensland: Reptile Publications.

Chang, C. and Zheng, R. (2003). Effects of ultraviolet B on epidermal morphology, shedding, lipid peroxide, and antioxidant enzymes in Cope's rat snake (*Elaphe taeniura*). Journal of Photochemistry and Photobiology B: Biology, 72(1-3), pp.79-85.

Chen, D. and Goldsmith, T. (1986). Four spectral classes of cone in the retinas of birds. Journal of Comparative Physiology A, 159(4), pp.473-479.

Chen, D., Collins, J. and Goldsmith, T. (1984). The ultraviolet receptor of bird retinas. Science, 225(4659), pp.337-340.

Clark, J. (2013). Indoor Lighting Workshop for Municipalities. 1st ed. [ebook] Available at: http://www.dvrpc.org/EnergyClimate/CircuitRider/pdf/2013-11-19_Jim_Clark_Indoor_Lighting_Basics.pdf [Accessed 17 March. 2016].

Clusella-Trullas, S., Wyk, J. and Spotila, J. (2009). Thermal benefits of melanism in cordylid lizards: a theoretical and field test. Ecology, 90(8), pp.2297-2312.

Cooper, W. and Greenburg, N. (1992). Reptilian coloration and behavior *In* Biology of the Reptilia. pp.298-422.

Crescitelli, F. (1972). The nature of the gecko visual pigment. The Journal of General Physiology, 40(2), pp.217-231.

Dickinson, H. and Fa, J. (1997). Ultraviolet light and heat source selection in captive spinytailed iguanas (*Oplurus cuvieri*). Zoo Biology, 16(5), pp.391-401.

Downes, S. (2001). Trading Heat and Food for Safety: Costs of Predator Avoidance in a Lizard.Ecology, 82(10), p.2870.

Dreher, F. and Maibach, H. (2001). Protective effects of topical antioxidants in humans...

Eason, P. (1990). The Effect of Recent Diet on Prey Choice in Senegalese Chameleons (Chamaeleo senegalensis). Journal of Herpetology, 24(4), p.383.

Elaroussi, M., Forte, L., Biellier, H., Eber, S., Poelling, R. and Krause, W. (1988). Indexes of vitamin D deficiency in Japanese quail embryos. American Journal of Physiology-Endocrinology and Metabolism, 254(5), pp.E639-E651.

Everett, M., Yeargers, E., Sayre, R. and Olson, R. (1966). PENETRATION OF EPIDERMIS BY ULTRAVIOLET RAYS. Photochemistry and Photobiology, 5(7), pp.533-542.

Ferguson, G., Gehrmann, W., Peavy, B., Painter, C., Hartdegen, R., Chen, T., Holick, M. and Pinder III, J. (2009). Restoring vitamin D in monitor lizards: exploring the efficacy of dietary and UVB sources. Journal of Herpetological Medicine and Surgery, 19(3), pp.81-88.

Ferguson, G., Brinker, A., Gehrmann, W., Bucklin, S., Baines, F. and Mackin, S. (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(3), pp.317-334.

Ferguson, G., Gehrmann, W., Chen, T., Dierenfeld, E. and Holick, M. (2002). Effects of Artificial Ultraviolet Light Exposure on Reproductive Success of the Female Panther Chameleon (Furcifer pardalis) in Captivity. Zoo Biology, 21(6), pp.525-537.

Ferguson, G., Gehrmann, W., Karsten, K., Hammack, S., McRae, M., Chen, T., Lung, N. and Holick, M. (2003). Do Panther Chameleons Bask to Regulate Endogenous Vitamin D 3 Production?.Physiological and Biochemical Zoology, 76(1), pp.52-59.

Ferguson, G., Gehrmann, W., Karsten, K., Landwer, A., Carman, E., Chen, T. and Holick, M. (2005). 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?. Physiological and Biochemical Zoology, 78(2), pp.193-200.

Ferguson, G., Jones, J., Gehrmann, W., Hammack, S., Talent, L., Hudson, R., Dierenfeld, E., Fitzpatrick, M., Frye, F., Holick, M., Chen, T., Lu, Z., Gross, T. and Vogel, J. (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(3), pp.279-299.

Ferguson, G., Kingeter, A. and Gehrmann, W. (2013). Ultraviolet Light Exposure and Response to Dietary Vitamin D 3 in Two Jamaican Anoles. Journal of Herpetology, 47(4), pp.524-529.

Fraser, D. (1983). The physiological economy of vitamin d. The Lancet, 321(8331), pp.969-972.

Fraser, D. and Emtage, J. (1976). Vitamin D in the avian egg. Its molecular identity and mechanism of incorporation into yolk. Biochem. J., 160(3), pp.671-682.

Fraser, D. and Kodicek, E. (1970). Unique Biosynthesis by Kidney of a Biologically Active Vitamin D Metabolite. Nature, 228(5273), pp.764-766.

Frye, F. (1991). Biomedical and surgical aspects of captive reptile husbandry.. Malabar: Krieger.

Gardiner, D., Baines, F. and Pandher, K. (2009). Photodermatitis and Photokeratoconjunctivitis in a Ball Python (Python regius) and a Blue-Tongue Skink (Tiliqua spp.). Journal of Zoo and Wildlife Medicine, 40(4), pp.757-766.

Gehrmann, W., Jamieson, D., Ferguson, G., Horner, J., Chen, T. and Holick, M. (2004). A Comparison of Vitamin D-Synthesizing Ability of Different Light Sources to Irradiances Measured with a Solarmeter Model 6.2 UVB Meter. Herpetological Review, 35(4), pp.361-364.

Gillespie, D., Frye, F., Stockham, S. and Fredeking, T. (2000). Blood values in wild and captive Komodo dragons (Varanus komodoensis). Zoo Biology, 19(6), pp.495-509.

Goldsmith, T. (1980). Hummingbirds see near ultraviolet light. Science, 207(4432), pp.786-788.

Govardovskii, V. and Zueva, L. (1974). Spectral sensitivity of the frog eye in the ultraviolet and visible region. Vision Research, 14(12), pp.1317-1321.

Hannon, D., Garner, M. and Reavill, D. (2011). Squamous Cell Carcinomas in Inland Bearded Dragons (*Pogona vitticeps*). Journal of Herpetological Medicine and Surgery, 21(4), pp.101-106.

Hay, A. and Watson, G. (1976). The plasma transport proteins of 25-hydroxycholecalciferol in fish, amphibians, reptiles and birds. Comparative Biochemistry and Physiology Part B: Comparative Biochemistry, 53(2), pp.167-172.

Hayes, M., Guilland-Cumming, D., Russell, R. and Henderson, I. (1986). Metabolism of 25hydroxycholecalciferol in a teleost fish, the rainbow trout (Salmo gairdneri). General and Comparative Endocrinology, 64(1), pp.143-150.

Hedley, J. and Eatwell, K. (2013). The effects of UV light on calcium metabolism in ball pythons (Python regius). Veterinary Record, 173(14), pp.345-345.

Henry, H. and Norman, A. (1975). Presence of renal 25-hydroxyvitamin-D-1-hydroxylase in species of all vertebrate classes. Comparative Biochemistry and Physiology Part B: Comparative Biochemistry, 50(3), pp.431-434.

Hertz, P., Fleishman, L. and Armsby, C. (1994). The Influence of Light Intensity and Temperature on Microhabitat Selection in Two Anolis Lizards. Functional Ecology, 8(6), p.720.

Hibma, J. (2004). Dietary vitamin D3 and UV-B exposure effects on green iguana growth rate: is full-spectrum lighting necessary. Bull. Chic. Herpetol. Soc,, 39(8), pp.145-150.

Hoby, S., Wenker, C., Robert, N., Jermann, T., Hartnack, S., Segner, H., Aebischer, C. and Liesegang, A. (2010). Nutritional Metabolic Bone Disease in Juvenile Veiled Chameleons (Chamaeleo calyptratus) and Its Prevention. Journal of Nutrition, 140(11), pp.1923-1931.

Holick, M. (2004). Vitamin D: importance in the prevention of cancers, type 1 diabetes, heart disease, and osteoporosis. The American journal of clinical nutrition, 79(3), pp.362-371.

Holick, M. (2007). Vitamin D deficiency. New England Journal of Medicine,, 357(3), pp.266-28.

Holick, M. and Jenkins, M. (2003). The UV advantage. New York: Ibooks.

Holick, M., 1995. The role of sunlight in providing vitamin D for bone health *In* Biological Effects of Light, pp.3-12.

Holick, M. ed., 2010. Vitamin D: physiology, molecular biology, and clinical applications. Springer Science & Business Media.

Holick, M., Tian, X. and Allen, M. (1995). Evolutionary importance for the membrane enhancement of the production of vitamin D3 in the skin of poikilothermic animals. Proceedings of the National Academy of Sciences, 92(8), pp.3124-3126.

Hoppe, D. (1979). The influence of color on behavioral thermoregulation and hydroregulation In The behavioral significance of color,. pp.35-62.

How, K., Hazewinkel, H. and Mol, J. (1994). Dietary Vitamin D Dependence of Cat and Dog Due to Inadequate Cutaneous Synthesis of Vitamin D. General and Comparative Endocrinology, 96(1), pp.12-18.

Huey, R. (1982). Temperature, physiology, and the ecology of reptiles. In Biology of the Reptilia.

Ichihashi, M., Ahmed, N., Budiyanto, A., Wu, A., Bito, T., Ueda, M. and Osawa, T. (2000). Preventive effect of antioxidant on ultraviolet-induced skin cancer in mice. Journal of Dermatological Science, 23, pp.S45-S50.

Jacobs, G. (1992). Ultraviolet Vision in Vertebrates. American Zoologist, 32(4), pp.544-554.

Jones, J., Ferguson, G., Gehrmann, W., Holick, M., Chen, T. and Lu, Z. (1995). Vitamin D nutritional status influences voluntary behavioral photoregulation in a lizard *In* Biological effects of light. pp.49-55.

Karsten, K., Ferguson, G., Chen, T. and Holick, M. (2009). Panther Chameleons, Furcifer pardalis , Behaviorally Regulate Optimal Exposure to UV Depending on Dietary Vitamin D 3 Status. Physiological and Biochemical Zoology, 82(3), pp.218-225.

Kik, M. and Benyen, A. (2003). Oorspronkelijk artikel Beoordeling van een aantal commerciele voeders voor leguanen (Iguana iguana), baardagamen (*Pogona vitticeps*) en land-en moerasschildpadden. TIJDSCHRIFT VOOR DIERGENEESKUNDE, 128(18), pp.550-555.

Kulms, D., Poppelmann, B., Yarosh, D., Luger, T., Krutmann, J. and Schwarz, T. (1999). Nuclear and cell membrane effects contribute independently to the induction of apoptosis in human cells exposed to UVB radiation. Proceedings of the National Academy of Sciences, 96(14), pp.7974-7979.

Laing, C., Trube, A., Shea, G. and Fraser, D., 2001. The requirement for natural sunlight to prevent vitamin D deficiency in iguanian lizards. Journal of Zoo and Wildlife Medicine, 32(3), pp.342-348.

Laing, C. and Fraser, D. (1999). The vitamin D system in iguanian lizards. Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology, 123(4), pp.373-379.

Langerwarf, B. (1980). The Caucasian green lizard, Lacerta strigata, Eichwald 1831, with notes on its reproduction in captivity. Br. Herpetol. Bull, 1, pp.23-26.

Laszlo, J. (1969). Observations on two new artificial lights for reptile displays. International Zoo Yearbook, 9(1), pp.12-13.

Lister, B. (1976). The Nature of Niche Expansion in West Indian Anolis Lizards I: Ecological Consequences of Reduced Competition. Evolution, 30(4), p.659.

Loew, E., Fleishman, L., Foster, R. and Provencio, I. (2002). Visual pigments and oil droplets in diurnal lizards a comparative study of Caribbean anoles. Journal of Experimental Biology, 205(7), pp.927-938.

MacLaughlin, J., Anderson, R. and Holick, M. (1982). Spectral character of sunlight modulates photosynthesis of previtamin D3 and its photoisomers in human skin. Science, 216(4549), pp.1001-1003.

Mader, (2006). Metabolic bone diseases. In Reptile Medicine and Surgery.

Mader, D. (1996). Reptile medicine and surgery. Philadelphia: W.B. Saunders.

Manning, B. and Grigg, G. (1997). Basking Is Not of Thermoregulatory Significance in the "Basking" Freshwater Turtle Emydura signata. Copeia, 1997(3), p.579.

Martin, M., Le Galliard, J., Meylan, S. and Loew, E. (2014). The importance of ultraviolet and near-infrared sensitivity for visual discrimination in two species of lacertid lizards. Journal of Experimental Biology, 218(3), pp.458-465.

McWilliams, D. (2005). Nutrition research on calcium homeostasis. I. Lizards (with recommendations). International Zoo Yearbook, 39(1), pp.69-77.

Mendel, and Backhaus, (1991). Colour vision in insects. In The Perception of Colour. Boca Raton: CRC Press.

Michaels, C. and Preziosi, R. (2013). Basking behaviour and ultraviolet B radiation exposure in a wild population of Pelophylax lessonae in northern Italy. Herpetological Bulletin, 124, pp.1-8.

Narbaitz, R. and Tsang, C. (1989). Vitamin D deficiency in the chick embryo: Effects on prehatching motility and on the growth and differentiation of bones, muscles, and parathyroid glands. Calcified Tissue International, 44(5), pp.348-355.

Nietzke, G. (1990). Zur Durchlässigkeit von UV-Strahlen der Reptilien-Hornhaut (Ordnung Squamata). Salamandra, 26(1), pp.50-57.

Nijboer, J., Van Brug, H. and van Leeuwen, M. (2007). UV-B and vitarain D3 metabolism in juvenile Komodo dragons (Varanus Komodoensis)..

Norman, A. (1979). Vitamin D. New York: Academic Press.

Norris, K. (1965). Color adaptation in desert reptiles and its thermal relationships In Lizard ecology. University of Missouri Press.

Oftedal, O., Chen, T. and Schulkin, J. (1997). Preliminary observations on the relationship of calcium ingestion to vitamin D status in the green iguana (Iguana iguana). Zoo Biology, 16(3), pp.201-207.

Oonincx, D., Stevens, Y., van den Borne, J., van Leeuwen, J. and Hendriks, W. (2010). Effects of vitamin D3 supplementation and UVb exposure on the growth and plasma concentration of vitamin D3 metabolites in juvenile bearded dragons (*Pogona vitticeps*). Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology, 156(2), pp.122-128.

Pearson, O. (1977). The effect of substrate and of skin color on thermoregulation of a lizard.Comparative Biochemistry and Physiology Part A: Physiology, 58(4), pp.353-358.

Perry, R. and McNaughton, P. (1991). Response properties of cones from the retina of the tiger salamander. The Journal of Physiology, 433(1), pp.561-587.

Plummer, M., Crabill, T., Mills, N. and Allen, S. (2005). Body temperatures of free-ranging softshell turtles (Apalone spinifera) in a small stream. Herpetological Review, 36(4), pp.371-374.

Porter, W. (1967). Solar Radiation through the Living Body Walls of Vertebrates with Emphasis on Desert Reptiles. Ecological Monographs, 37(4), pp.273-296.

Reichel, H., Koeffler, H. and Norman, A. (1989). The Role of the Vitamin D Endocrine System in Health and Disease. New England Journal of Medicine, 320(15), pp.980-991.

Rhoten, W., Bruns, M. and Christakos, S. (1985). Presence and Localization of Two Vitamin D-Dependent Calcium Binding Proteins in Kidneys of Higher Vertebrates. Endocrinology, 117(2), pp.674-683.

Rivers, J., Frankel, T., Juttla, S. and Hay, A. (1979). Vitamin D in the nutrition of the cat. The Proceedings of the Nutrition Society, 38(2), p.36A.

Rosenblum, E. (2005). The Role of Phenotypic Plasticity in Color Variation of Tularosa Basin Lizards.Copeia, 2005(3), pp.586-596.

Rossie, J. (2006). General husbandry and management In Reptile medicine and surgery. pp.25-41.

Seebacher, F. (1999). Behavioural Postures and the Rate of Body Temperature Change in Wild Freshwater Crocodiles, Crocodylus johnstoni. Physiological and Biochemical Zoology, 72(1), pp.57-63.

Sherbrooke, W., de L. Castrucci, A. and Hadley, M. (1994). Temperature Effects on in vitro Skin Darkening in the Mountain Spiny Lizard, Sceloporus jarrovi: A Thermoregulatory Adaptation?.Physiological Zoology, 67(3), pp.659-672.

Shindo, Y., Witt, E. and Packer, L. (1993). Antioxidant Defense Mechanisms in Murine Epidermis and Dermis and Their Responses to Ultraviolet Light. Journal of Investigative Dermatology, 100(3), pp.260-265.

Sillman, A., Carver, J. and Loew, E. (1999). The photoreceptors and visual pigments in the retina of a boid snake, the ball python (Python regius). Journal of Experimental Biology, 202(14), pp.1931-1938.

Sillman, A., Reihlich, P., Southard, J., Loew, E. and Govardovskii, V. (1997). The photoreceptors and visual pigments of the garter snake (Thamnophis sirtalis): a microspectrophotometric, scanning electron microscopic and immunocytochemical study. Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology, 181(2), pp.89-101.

Soehnge, H., Ouhtit, A. and Ananthaswamy, O. (1997). Mechanisms of induction of skin cancer by UV radiation.. pp.D538-D551.

Srivastav, A. and Rani, L. (1989). Serum calcium and inorganic phosphorus levels of the freshwater snake Sinonatrix piscator (formerly Natrix piscator) in response to calcitonin treatment. Can. J. Zool., 67(5), pp.1335-1337.

Srivastav, A., Srivastav, S., Singh, S. and Norman, A. (1995). Effect of Various Vitamin D Metabolites on Serum Calcium and Inorganic Phosphate in the Freshwater Snake Natrix piscator. General and Comparative Endocrinology, 100(1), pp.49-52.

Stumpf, W. (1988). The endocrinology of sunlight and darkness. Naturwissenschaften, 75(5), pp.247-251.

Swarup, K., Pandey, A. and Srivastav, A. (1986). Calcaemic responses in the yellow monitor, varanus flavescens to vitamin D3 administration. Acta physiologica Hungarica, 70(4), pp.375-377.

Tapley, B., Rendle, M., Baines, F., Goetz, M., Bradfield, K., Rood, D., Lopez, J., Garcia, G. and Routh, A. (2014). Meeting ultraviolet B radiation requirements of amphibians in captivity:

A case study with mountain chicken frogs (Leptodactylus fallax) and general recommendations for pre-release health screening. Zoo Biology, 34(1), pp.46-52.

Tian, X. and Holick, M. (1995). Catalyzed Thermal Isomerization between Previtamin D3 and Vitamin D3 via -Cyclodextrin Complexation. Journal of Biological Chemistry, 270(15), pp.8706-8711.

Tian, X., Chen, T., Matsuoka, L., Wortsman, J. and Holick, M. (1993). Kinetic and thermodynamic studies of the conversion of previtamin D3 to vitamin D3 in human skin. Journal of Biological Chemistry, 268(20), pp.14888-14892.

Tian, X., Chen, T., Lu, Z., Shao, Q. and Holick, M. (1994). Characterization of the translocation process of vitamin D3 from the skin into the circulation. Endocrinology, 135(2), pp.655-661.

Van Norren, D. (1991). Photochemical damage to the eye. Physiology, 6(5), pp.232-234.

Wallach, J. and Hoessle, C. (1966). Hypervitaminosis D in green iguanas. J. Am. Vet. Med. Assoc,, 149(7), pp.912-914.

Walton, B. and Bennett, A. (1993). Temperature-dependent color change in Kenyan chameleons. Physiological Zoology, pp.270-287.

Waring, H. (1963). Color change mechanisms of cold-blooded vertebrates. Academic Press.

Webb, A., Decosta, B. and Holick, M. (1989). Sunlight Regulates the Cutaneous Production of Vitamin D 3 by Causing Its Photodegradation. The Journal of Clinical Endocrinology & Metabolism, 68(5), pp.882-887.

Wright, K. (2008). Two Common Disorders of Captive Bearded Dragons (*Pogona vitticeps*): Nutritional Secondary Hyperparathyroidism and Constipation. Journal of Exotic Pet Medicine, 17(4), pp.267-272.

Young, A. (1987). The sunburn cell. Photo-dermatology, 4(3), pp.127-134.

Young, J. (1981). The life of vertebrates. New York: Oxford University.