Journal of
Zoological and Botanical Gardens

MDPI

Article

The Effects of Artificial UV-B Provision on Positional Sleeping Behaviour and Vitamin D_3 Metabolites of Captive Aye-Ayes (*Daubentonia madagascariensis*)

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Abstract

Zoological environments aim to promote natural behaviours and optimal welfare conditions. Over the past decade, research on the use of artificial ultraviolet-B (UV-B) exposure has improved vitamin D_3 levels and reduced incidences of metabolic bone disease in diurnal primates; however, this has not been investigated in nocturnals. Aye-ayes (*Daubentonia madagascariensis*), nocturnal lemurs often housed indoors in zoos with little to no exposure to natural sunlight, have been reported to have low vitamin D_3 levels. This study aims to investigate the impacts of artificial UV-B as a supplemental healthcare strategy for aye-ayes, examining its influences on vitamin D_3 levels and positional sleeping behaviour. The 25-hydroxy-vitamin D_3 ($25OHD_3$) blood levels were tested before and after exposure to different levels of artificial UV-B and heat sources. Statistical analysis showed no correlation between UV-B and $25OHD_3$ at group parameter levels. However, one individual showed a positive correlation. Sleeping position duration analysis showed a potential basking behaviour with the use of increased ear exposure and other thermoregulatory responses. Despite representing 8.06% of the European captive aye-aye population, these findings highlight the need for further research on vitamin D_3 parameters and responses to UV-B to optimise captive conditions and support the species' long-term health.

Keywords: aye-aye; UV-B; vitamin D; blood serum; basking; thermoregulation; behaviour; nocturnal; primate; lemur

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Received: 14 May 2025
Revised: 12 July 2025
Accepted: 29 July 2025
Published: 6 August 2025

Citation: Walker, D.; Bwye, P.; Richdon, S. The Effects of Artificial UV-B Provision on Positional Sleeping Behaviour and Vitamin D_3 Metabolites of Captive Aye-Ayes (*Daubentonia madagascariensis*). *J. Zool. Bot. Gard.* **2025**, *6*, 39. https://doi.org/10.3390/jzbg6030039

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1. Introduction

Vitamin D is a vital nutrient that plays an important role in calcium absorption and, consequently, the regulation of calcium and phosphorus levels in bones and tissues. Vitamin D is also important for immune system function, with deficiency manifesting a variety of symptoms, including lethargy [1], hair loss [2], impaired growth, skeletal muscle weakness, and weak bones [3] that are prone to fractures and metabolic bone disease. There are two major forms of vitamin D: vitamin D_2 and vitamin D_3. Vitamin D_2 (ergocalciferol) is naturally found in some plant origin items, such as mushrooms; however, there are very few natural sources [4]. Vitamin D_3 (cholecalciferol) is found in animal products, the main sources being fish, egg yolk, and offal [5,6]. Vitamin D_3 can also be naturally synthesised from skin exposure to ultraviolet-B (UV-B), which is a component of sunlight [7]. UV-B

rays penetrate the epidermis, converting 7-dehydrocholesterol to pre-vitamin D_3, which is subsequently isomerised to vitamin D_3 [8].

Skin pigmentation plays a role in vitamin D_3 synthesis, with high concentrations of melanin in the epidermis functioning as a light filter. This reduces the amount of UV radiation that penetrates the outer layers, reducing adverse effects, such as sunburn and immunosuppression [9]. However, this also reduces the amount of vitamin D_3 synthesis [10]. Additionally, studies have shown the effects of the season and latitude on vitamin D_3 skin absorption in humans, showing little to no vitamin D_3 production during the winter months at high latitudes due to a low UV index (UVI) [11]. Further studies have promoted the moderate use of sunbeds in northern countries in order to maintain sufficient vitamin D through this period [12]. While there are potential adverse effects of sunbeds [13], toxic levels of vitamin D cannot occur from extended sun exposure [1]. Another method of countering the seasonal variation of the UV index is through oral supplementation of vitamin D. Studies have shown that this is sufficient to maintain an adequate level of vitamin D over winter [14]. As a result, some foods have been fortified (such as fat spreads and breakfast cereals), and supplements have been developed to correct this environmental deficit. Both vitamins D_2 and D_3 are available; however, these can be toxic in large quantities [1,15]. Studies have shown that vitamin D_3 supplements are significantly better at raising 25-hydroxy-vitamin (25OHD) blood serum levels over vitamin D_2 supplements [16].

In 2012, it was reported that 50% of the human population was thought to have vitamin D insufficiency [17]. However, this is not limited to humans, and vitamin D deficiency is well recognised in domesticated animals, with most cases caused by dietary deficiency [18]. Species vary greatly in their ability to synthesise vitamin D_3, with dogs (*Canis lupus familiaris*) and cats (*Felis catus*) being at the lower end of the spectrum [18]. Carnivorous species have low dermal concentrations of 7-dehydrocholesterol, required to produce vitamin D through UV-B exposure. Therefore, they rely heavily on vitamin D absorption through their diet containing high sources of vitamin D [18,19]. In contrast, some herbivores produce vitamin D_3 in response to ultraviolet radiation, as illustrated by the higher concentration levels of vitamin D_3 in unshorn versus shorn sheep (*Ovis aries*) [18,20]. Llamas (*Lama glama*) and alpacas (*Vicugna pacos*) have also been identified as vulnerable to vitamin D deficiency, as their thick coats and pigmentation have evolved to shield them against intense solar radiation at high latitudes. However, this reduces vitamin D production when housed outside their natural range with lower UV levels [18].

Primates can suffer from similar problems in captivity due to having little or no exposure to UV-B radiation when housed in locations with naturally low UV levels and, subsequently, are routinely given oral vitamin D_3 supplementation [21]. Vitamin D metabolism differs amongst primate orders, with Platyrrhini unable to efficiently utilise vitamin D_2 and, therefore, primarily reliant on vitamin D_3 [22,23]. New World monkeys are extremely tolerant of high doses of dietary vitamin D_3 supplementation compared to other animals, showing fewer adverse effects. Captive cotton-top tamarins (*Saguinus oedipus*) have an abnormally wide range and some very high values of vitamin D compared to their wild counterparts; however, it is uncertain whether there are negative consequences to this [23]. This indicates the importance of establishing normal baseline values from the wild. Multiple factors can influence the range of vitamin D levels observed in captive animals. Recent studies have highlighted the effects of different husbandry and management practices across institutions, including diet and dietary supplementation, natural UV exposure, and artificial UV provision [21,24]. The assessment of serum 25-hydroxyvitamin D concentrations, a form of vitamin D, in two troops of captive gorillas (*Gorilla gorilla gorilla*) predominantly managed indoors in the northern USA, showed concentrations were signifi-

cantly lower than those with near-daily outdoor access, despite both groups being fed a diet with fortified vitamin D_3 [25].

Seasonality and latitude also play roles in vitamin D levels. UV radiation that reaches Earth's surface diminishes as the distance from the equator increases [26]. Vitamin D levels in lemurs (*Lemuroidea*) housed with outdoor access in the United Kingdom, and other countries with similar latitudes, vary with seasonal environmental UV-B light but can remain at adequate levels due to dietary supplementation [27]. Most current primate husbandry guidelines recommend dietary supplementation of vitamin D_3 to maintain acceptable vitamin D levels [28–30]. However, due to the potential toxicity of overdosing on dietary or oral supplementation of vitamin D, the provision of artificial UV-B light is being investigated as an alternative source of supporting vitamin D synthesis. Incorporating UV lighting into primate enclosure design appears to significantly increase vitamin D levels, reducing the risk of metabolic bone disease [24,31]. Additionally, providing artificial lights as a source for vitamin D synthesis may offer secondary benefits through opportunities for animals to express natural basking behaviours. Many animals, particularly reptiles and small mammals, rely on basking behaviours to help them thermoregulate [32,33]. This behaviour is also seen in primates, particularly lemurs, due to their lack of piloerection to raise body hairs, like in other primates [34,35].

To date, research in this area has predominantly focused on diurnal primates. Researchers face distinct challenges when monitoring nocturnal primates due to unsociable hours and limited visibility owing to severely reduced light levels. Blood serums collected from several species of nocturnal primates have shown vitamin D levels similar to or lower than those of their diurnal counterparts [36]. It is uncertain if their vitamin D levels are dependent solely on dietary intake. Some wild nocturnal primates (*Lepilemur edwardsi* and *Aotus azarai azarai*) have been observed to express basking behaviours; however, these are based on personal observations [37,38]. Ancestral mammals were thought to be nocturnal, with some evidence suggesting a morning basking behaviour arose as a method of regaining body heat lost during the cold night [39]. The earliest forms of extant primates are lemuriformes, of which the nocturnal aye-aye (*Daubentonia madagascariensis*) is recognised as the most basal lineage [40].

Within the captive population of aye-ayes, symptoms of low vitamin D have been recorded, despite the use of palatable aqueous vitamin solutions recommended by husbandry guidelines [41]. Aye-ayes are specialised eaters, and even with varying food presentations and contents of diets, large quantities remain uneaten [42], which makes supplementing vitamin D levels through diet difficult. Nutrient intake and diet evaluations have been conducted on wild and captive *Daubentonia* diets; however, vitamin D parameters remain unidentified in this species [43,44]. Furthermore, no serum biochemistry of vitamin D values has been studied for wild aye-ayes.

The majority of aye-aye activity budget data are collected during the night because animals are rarely seen out in the day, except on rare occasions [45,46]. During the day, they usually reside in nests made from branches and leaves. Aye-ayes are found to utilise several different nests within a short timeframe [47,48]. The nests are typically oval-shaped and placed high in the crowns, forks, and tangles in trees, with height varying between nine and seventeen metres [47,48]. Wild aye-aye nests may let in some ultraviolet light due to their construction material and general locations, but this is unknown and unstudied. It is also unknown whether the aye-ayes seek cover from any light theoretically penetrating the nest or if they potentially exhibit basking behaviours for vitamin D synthesis, as seen in observations of other nocturnal primates [45,46].

Due to their nocturnal nature, captive populations of aye-ayes are largely housed indoors, with limited exposure to sunlight [49]. As suggested in the *Daubentonia* husbandry

guidelines, nest boxes should be provided to form a readymade structure that can be used as a nest by itself or be added to by the aye-aye [41]. The indoor nature of these exhibits and nesting areas currently inhibits aye-ayes' ability to express potential basking behaviour. The Zoological Society of London (ZSL) has adapted its practices by giving their captive aye-ayes an additional outdoor space. These aye-ayes are still kept in a reversed lighting system, and an artificial night is created by covering the outdoor space with a tarpaulin, punctuated by several small holes to give minimal light levels [50]. While offering improved natural airflow, UV-B exposure is still likely to be limited. Due to the latitude of the location, ambient UV-B levels would be extremely low compared to those in Madagascar.

Current practices highlight the limited research and understanding of nocturnal mammal UV requirements in both wild and captive populations and the necessity of this knowledge to improve nocturnal mammal welfare in captive settings. The aim of this research is to elucidate the potential effects of the provision of artificial UV-B in captive aye-ayes on basking behaviours and vitamin D serum levels. It is hypothesised that animals provided with UV-B will engage in basking behaviours in areas with UV lamps and that this preference of basking behaviour will increase vitamin D levels found in blood serum. This aim will be achieved by evaluating behavioural data and blood serums before and after UV-B provision in captive aye-ayes. This research will add to the limited discourse on nocturnal mammals' vitamin D requirements, providing guidance for husbandry and improving welfare in these understudied species. Due to the near-complete lack of research on nocturnal primates' UV requirements and appropriate artificial supplementation in captive environments, this study was first trialled on individual animals at the authors' institution. The results and lessons learnt will inform the potential rollout of the initiative to the broader captive population.

In this study, the independent variable was the UV-B exposure level, while the dependent variables were serum 25-hydroxyvitamin D_3 ($25OHD_3$) levels and positional sleep behaviour. The effects of varying levels of artificial UV-B exposure on $25OHD_3$ levels in captive aye-ayes (*Daubentonia madagascariensis*) were investigated, and potential changes in the duration of the positional sleep behaviour were explored under different UV-B and thermal conditions as follows:

1. Effect of UV-B Exposure on Vitamin D_3 Levels

   Null Hypothesis (H_{01}): UV-B exposure has no effect on $25OHD_3$ levels in captive aye-ayes.
   Alternative Hypothesis (H_{11}): UV-B exposure increases $25OHD_3$ levels in captive aye-ayes.

2. Effect of UV-B Exposure on Positional Sleeping Behaviour

Null Hypothesis (H_{02}): UV-B exposure has no effect on positional sleeping behaviour (e.g., increased basking or thermoregulatory postures) in captive aye-ayes.

Alternative Hypothesis (H_{12}): UV-B exposure influences positional sleeping behaviour in captive aye-ayes, leading to increased basking-like behaviour.

2. Materials and Methods

2.1. Location and Date

This study was carried out at the Bristol Zoological Society's Bristol Zoo Gardens site (Clifton, Bristol, UK), where data were collected between 2019 and 2022. Five aye-ayes were observed as the focal animals of this study (Table 1).

Table 1. Study animals housed at the Bristol Zoological Society. * Age at the start of the study. Test subject E was born during the study period.

Test Subject ID	Sex	Birth Status	Date of Birth	Age *
A	Male	Captive Born	29 June 2016	2
B	Female	Captive Born	17 May 2015	3
C	Female	Captive Born	17 May 2015	3
D	Male	Wild Caught	Unknown	~28
E	Male	Captive Born	29 November 2020	0

2.2. Test Subjects

The aye-ayes had access to manmade metal-lined nest boxes with a mesh roof of 2.5 mm quad mesh (Figure 1). Adults were housed separately, and juveniles were housed with siblings or parents. All the individuals were fed on the same diet of commercial primate leaf-eater pellet (Mazuri, Minnesota, USA) mixed with raw egg (commonly known as 'gruel' in aye-aye husbandry), daily vegetables, nuts, and insects. Throughout this study, the aye-ayes were given daily oral supplementation of Zolcal-D (calcium borogluconate (40%), vitamin D_3 (25,000 IU/L), 33.5 mg/mL of calcium, 25 IU of vitamin D_3/mL, plus 2 mg/mL of magnesium) at 1 mL/kg. Details on whether this supplement was given directly or within gruel were recorded, as this affects blood test results for up to six weeks [51].

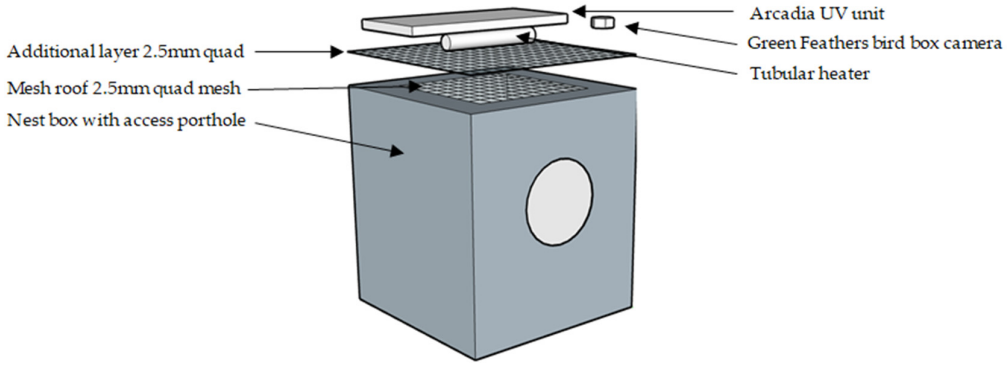


Figure 1. Aye-aye UV-B nest box setup. Two layers of 2.5 mm quad mesh were required to protect the electronic equipment from potentially being damaged by the aye-ayes. The UV unit could be moved closer to and further from the nest box to enable the UVI to be adjusted.

2.3. UV and Thermal Variation

Artificial UV units were installed above nest boxes (Figure 1). UV units were set on a timer for an eight-hour period (00:30–08:30 GMT) to align with the reverse lighting system's artificial day under veterinary recommendations. Guidance on UV units and bulbs used for this study was based on the "UV-tool database of microhabitat requirements and basking behaviour of reptile and amphibian species" [52]. UV lighting units consisted of an Arcadia Reptile D_3+ UV Flood 24w Compact 12% UV-B bulb and an Arcadia Reptile T5 D_3+ reptile lamp with a 12% UV-B bulb (Arcadia Reptile, West Sussex, UK). The mesh layer between UV units affected the UVI output due to light scattering. Therefore, 14% UV-B bulbs and the ability to raise or lower units were used accordingly to adjust UVI levels. Suitable UVI levels for aye-ayes are unknown; therefore, Ferguson zones (Appendix A, Table A1) were used as guidance. Due to any potential risk of adverse effects, such as skin damage, Ferguson zone 1 was used in the first experimental phase (1.1). This is because this is the lowest UVI level on the scale and is thought to most closely match aye-ayes' natural characteristics due to their residing in nests during daylight hours [47,48]. UVI levels were tested once a week with a Solarmeter 6.5 digital UVI Radiometer (Solarlight, Pennsylvania,

USA) by holding the solar meter vertically pointing it towards the UV unit from the bottom centre point of the nest boxes.

In experimental phase 1.1, a 'control nest box' was provided to allow each animal a degree of choice in the nest site, as they are found to use multiple nest sites in the wild [47,48]. This nest box structure was the same manmade metal-lined box with a mesh roof as the UV-B setup. However, no UV-B unit, tubular heater, or camera was installed above. During the six-week exposure, the effect of UV-B on $25OHD_3$ levels was noted when access to this box was given. Each experimental phase was not the same duration (Table 2), as animals were kept in their current phase until blood withdrawals could be taken to check vitamin D_3 levels. Because vitamin D_3 blood tests reflect only recent synthesis and intake—typically from the preceding six weeks [51], individuals spent a minimum of six weeks in each experimental phase immediately prior to blood sampling; therefore, the duration of each phase beyond six weeks would not have affected vitamin D_3 blood results, and animals remained in each experimental phase until a blood sample could be obtained.

Table 2. Duration of experimental phases.

Test Subject ID	Experimental Phase	Duration (Days)
A	1.1	119
	1.2	302
	1.3	574
B	1.1	102
	1.2	234
C	1.1	102
D	1.1	58
	1.3	878
E	1.3	100

Vitamin D_3 was monitored, and the UVI level was increased to the next Ferguson zone if vitamin D_3 serum test results did not show a suitable increase of 10 nmol/L from veterinary recommendation. Experimental phase 1.2, therefore, used the next Ferguson zone (2), and following further vitamin D_3 monitoring at this phase, if there was no increase, experimental phase 1.3 was implemented using Ferguson zone 3.

In the second experimental phase, 30.48 cm long 45 W energy-saving tubular heaters were installed above the nest boxes next to the UV units to investigate if thermoregulatory positions increased under heat exposure (Figure 1). Heat units were added to the same timer as the UV units when used as an additional variable. The heat unit installations did not align with dates of vitamin D_3 serum testing in this study; however, this is recommended in future investigations. Temperature monitoring of the nest box was not possible due to the aye-ayes' destructive nature; therefore, enclosure temperatures were recorded instead with the use of an ambient thermometer.

2.4. Vitamin D_3 Blood Serum Collection and Measurement Protocol

Blood samples (1 mL) were taken from sedated individuals opportunistically by veterinary staff during routine health checks, following animal welfare ethical approval by the Bristol Zoological Society and the University of the West of England (ethical approval code: BZS_2023_057). All the blood collections were conducted prior to other testing (e.g., tuberculosis tests) or medication to prevent any effect on blood parameter measures, as described in Killick et al.'s study [27]. The serum samples were sent to Sandwell and West Birmingham NHS Trust (West Bromwich, UK) for serum 25-hydroxyvitamin D_3 ($25OHD_3$)

testing. Vitamin D deficiency was defined by the Bristol Zoological Society's veterinary staff as 25OHD3 < 50 nmol/L.

2.5. Positional Sleep Behaviour Data Collection

A 1080p HD IP Bird Box Camera (Green feathers, Bristol, UK) was installed above each UV-B nest box beside the UV units (Figure 1) to collect focal continuous data samples with the use of an ethogram of sleeping positions. As there are no previous studies of this type for this species to base an ethogram on, an ethogram was produced by observing three nights of focal continuous data samples for each individual (See Appendix C: Table A8 for the full ethogram). Within other studies, sleep is defined as consolidated circadian periods of immobility in a species-specific posture, resting place, or both [53]. Sleep behaviour varies between species; therefore, a set of criteria was established for *D. madagascariensis* [54]. In this study, 'sleep' was recorded when an individual maintained a sleeping position for a minimum of five minutes within a nest box during artificial daylight hours. With the use of the ethogram, the time spent in each position was recorded until the 'sleep' definition was not followed.

Across a period of 20 nights, 456.52 h of sleep position data were recorded from Test subjects A and B. A total of 106.52 of these hours were recorded under no artificial UV-B lighting, 170 h under only artificial UV-B and 180 h under a combination of artificial UV-B and a heat source. Sleep data were not possible to collect for test subjects C, D, and E.

2.6. Statistical Analysis

2.6.1. Vitamin D_3 Blood Serum Levels

Statistical analyses were carried out using R 4.2.1 [55]. Data normality was assessed using the dplyr package [56] to perform a Shapiro–Wilk test, which indicated the data were not normally distributed. Therefore, Spearman's rank correlation was used, and analyses were carried out on a group and individual census with the RStatix package [57]. A significance threshold of $p = 0.05$ was used for statistical analysis. Results were visualised using a line of best fit, generated in R 4.2.1 [55] with the ggplot2 package [58]. This analysis aimed to evaluate whether there was a relationship between UVI exposure and 25-hydroxyvitamin D_3 ($25OHD_3$) blood serum levels, both at the group level and for individual animals.

2.6.2. Positional Sleep Behaviour

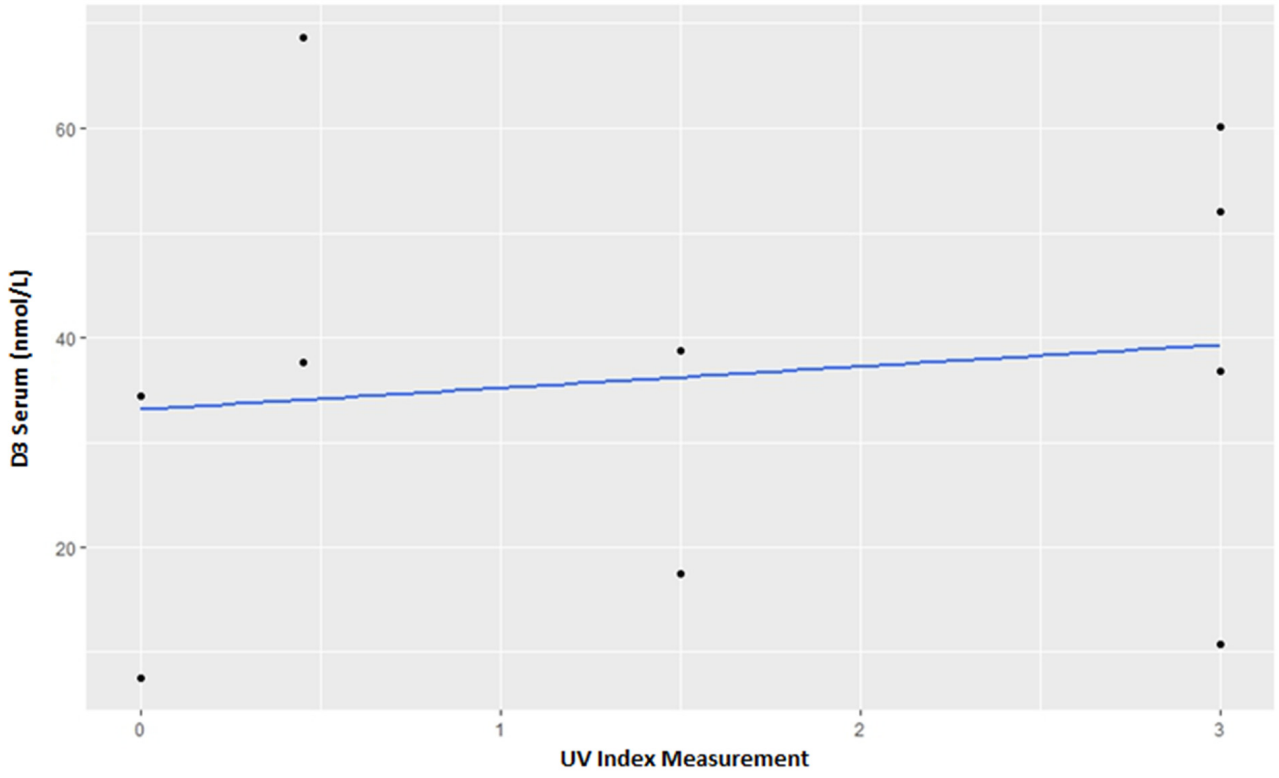
The duration of time spent in each sleeping position was calculated by dividing all the minute data by the total minutes per week, then multiplying it by 60 to obtain an hourly rate (minutes per hour). Data normality was tested as per the previous analysis, and it was found that the data were not normally distributed; therefore, a non-parametric test was used. Statistical analyses were carried out using R 4.2.1 [55] and the RStatix package [57] to run a Fisher's Exact test, followed by post hoc testing of a pairwise Fisher's test. The statistical significance threshold was accepted at $p = 0.05$. Results were visualised as a balloon plot using R 4.2.1 [55] and the ggpubr [59] and ggplot2 packages [58]. To assess the influence of environmental conditions on the positional sleep behaviour, we tested whether the duration of time spent in each defined sleeping position differed significantly across three experimental conditions: (1) no UV exposure, (2) UV exposure only, and (3) UV exposure with heat. These comparisons were conducted separately for each individual to evaluate behavioural responses to UV and heat exposure in relation to the study's aim of identifying potential basking or thermoregulatory behaviours.

3. Results

3.1. Vitamin D_3 Blood Serum Levels

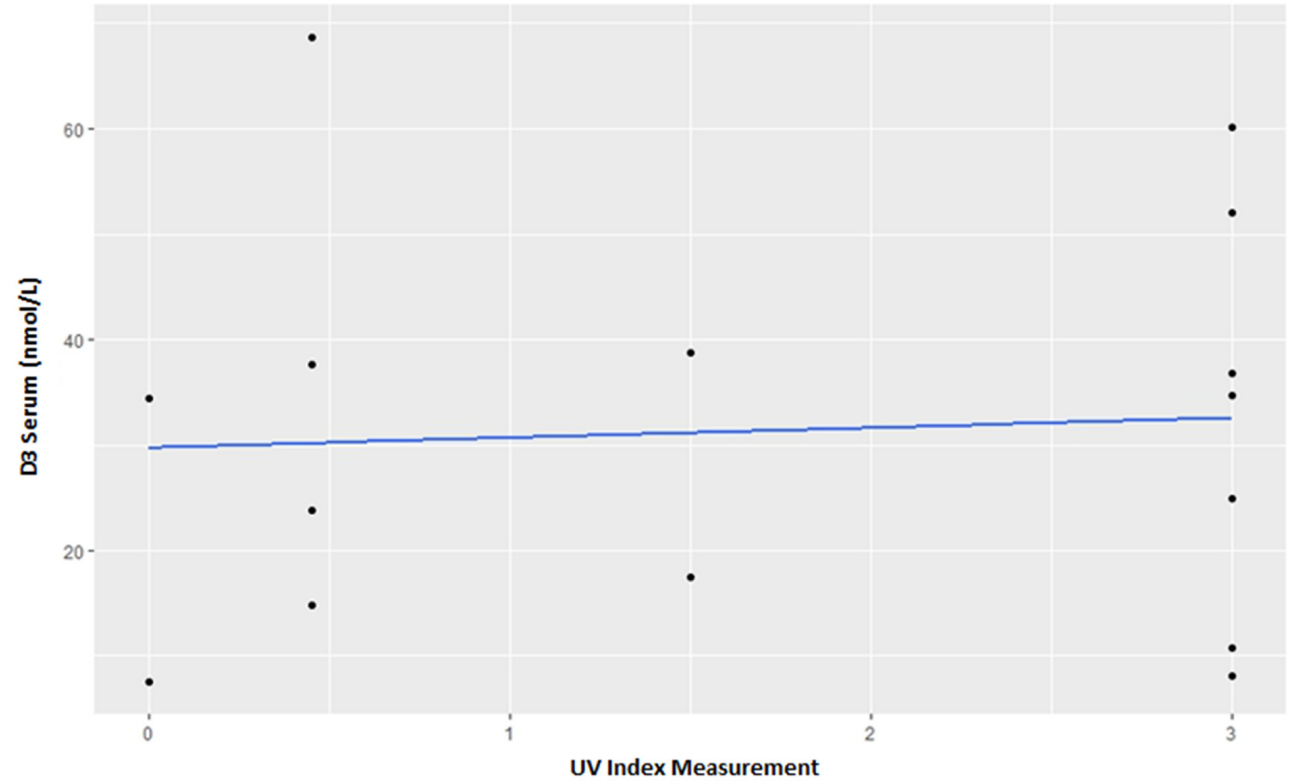
Nineteen blood samples were collected from five individuals at different levels of artificial UV-B exposure between 2019 and 2022 (Appendix D: Tables A9 and A10 for full results and means/ranges). Of these, four samples were excluded due to insufficient serum collection. On a group basis, the analysis showed no significance in vitamin D_3 ($25OHD_3$) parameter levels when exposed to varying levels of UV-B, both with access to the 'control nest box' ($r_s(14) = 0.149$, $p = 0.597$) and without access to the 'control nest box' ($r_s(9) = 0.253$, $p = 0.45$). Due to limited blood sample collection opportunities, only blood samples from three individuals were analysed on an individual basis. These individuals included test subject A with access to the 'control nest box' ($r_s(5) = 0.736$, $p = 0.096$) and without access to 'control nest box' ($r_s(4) = 0.975$, $p = 0.005$), test subject D without access to the 'control nest box' ($r_s(3) = -0.775$, $p = 0.225$), and test subject B with access to the 'control nest box' ($r_s(2) = -1$, $p = 0.333$).

Scatterplots A, B, C, and D (Figure 2) show positive correlations between UVI and nanomoles per litre; however, only scatterplot C showed a significant positive correlation between UVI and D_3 serum levels.

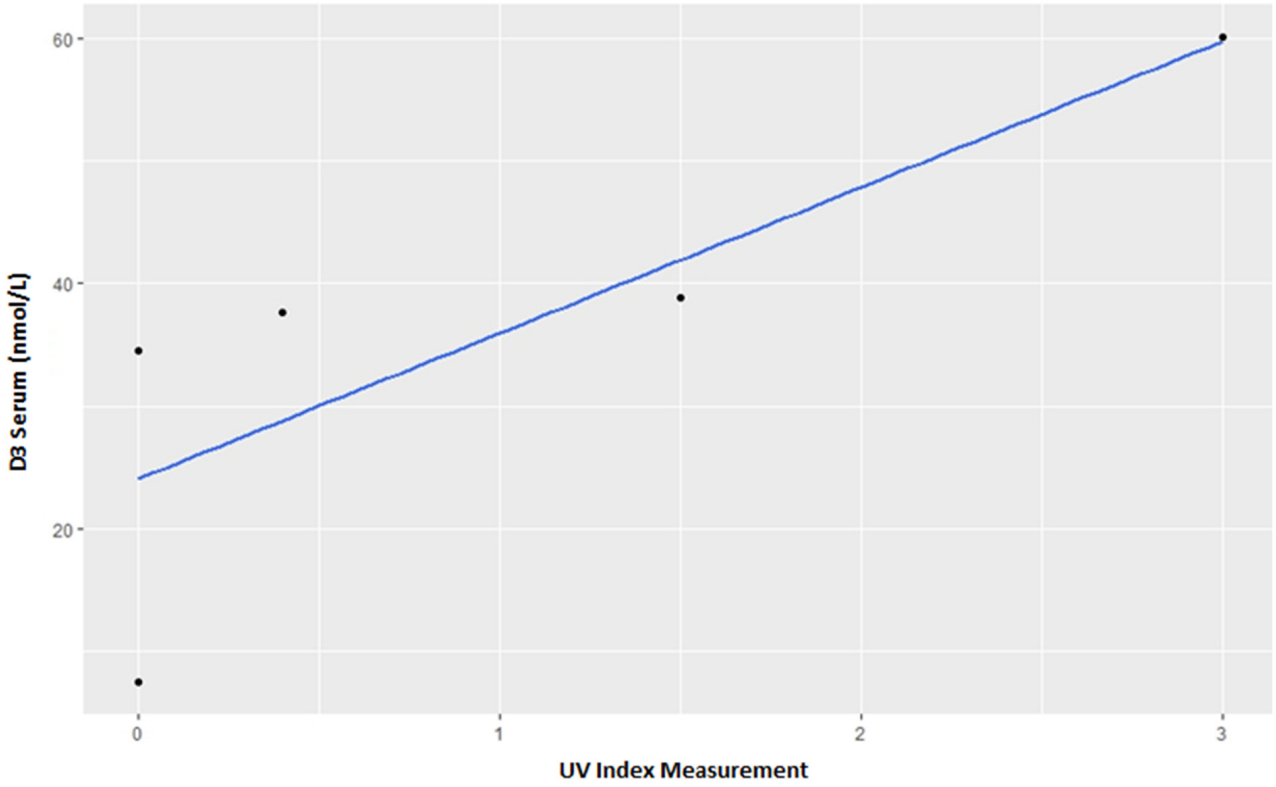


(**a**)

Figure 2. *Cont.*

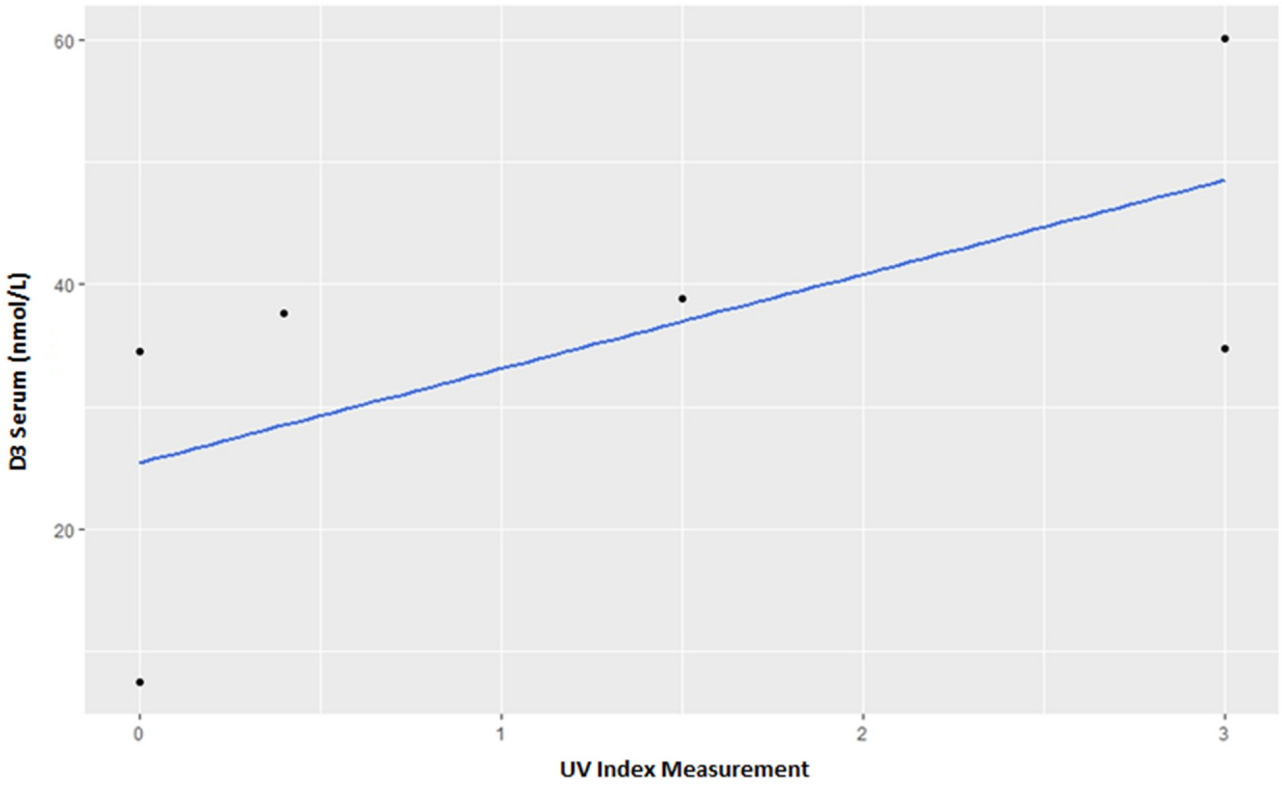


(**b**)

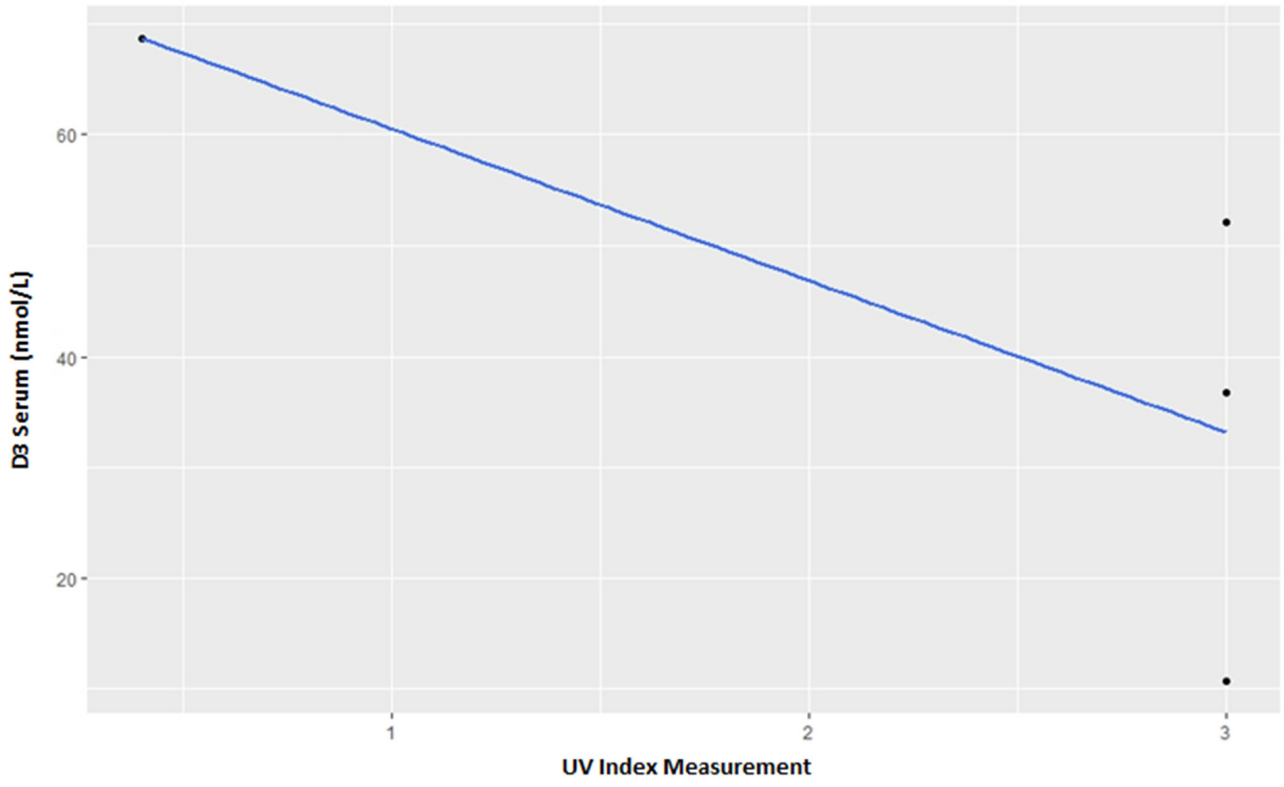


(**c**)

Figure 2. *Cont.*

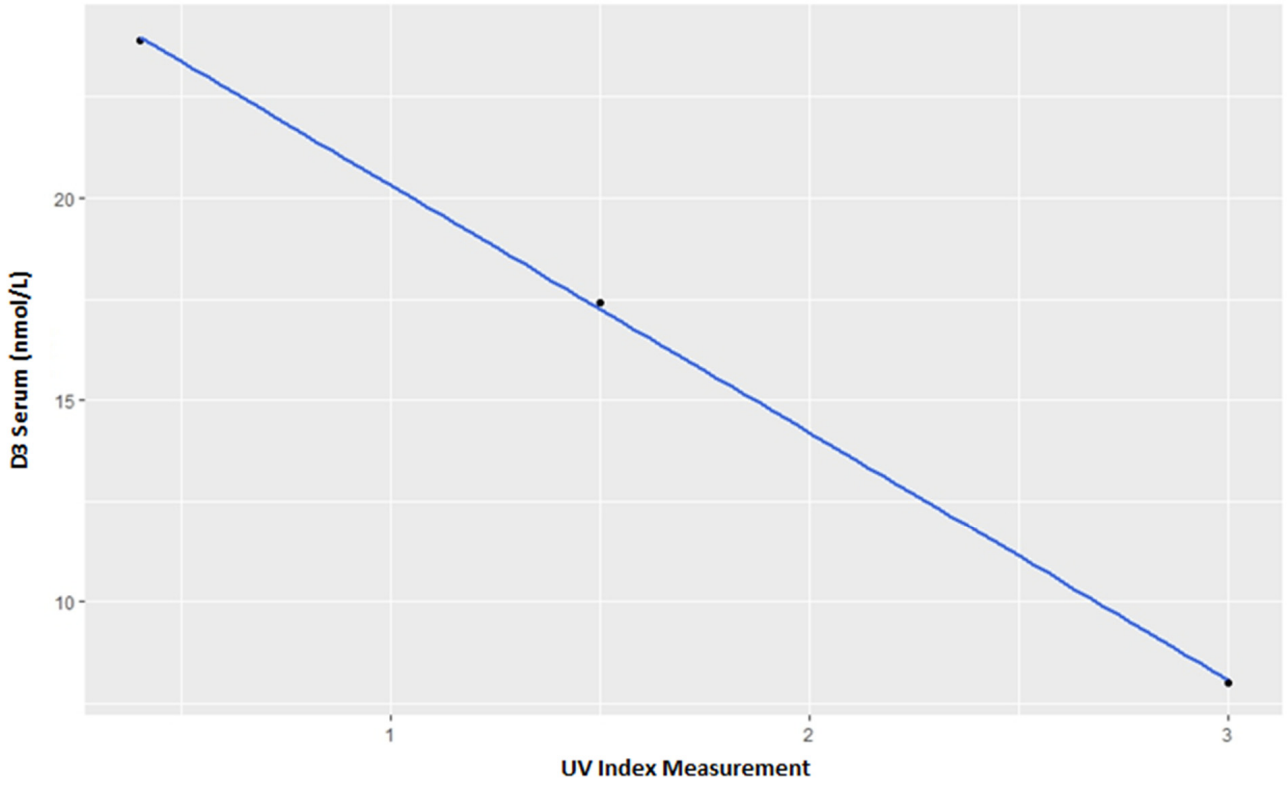


(**d**)



(**e**)

Figure 2. *Cont.*



(**f**)

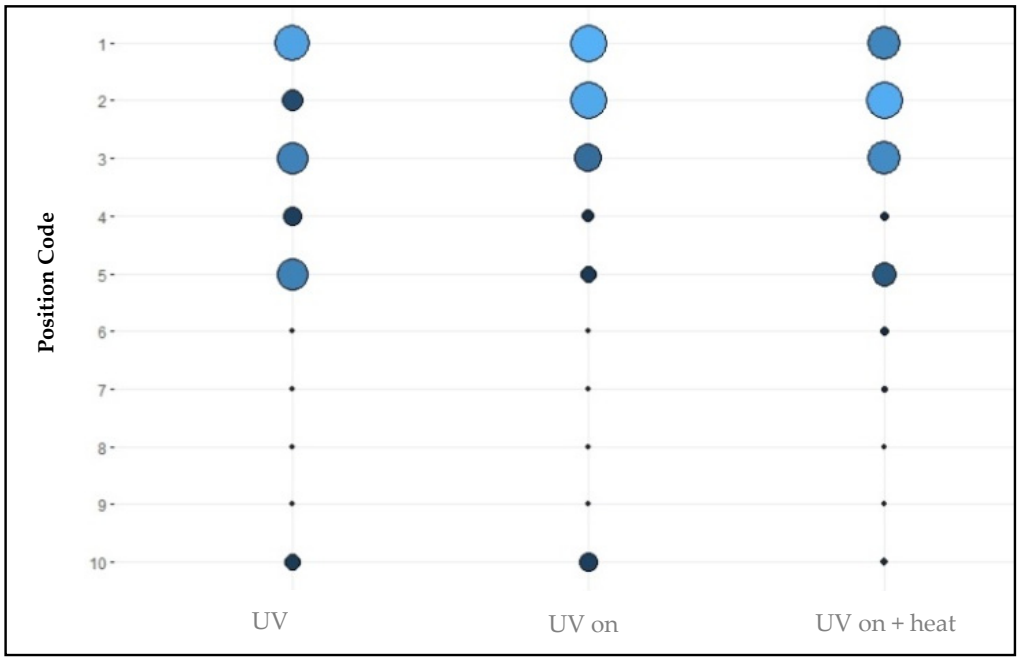
Figure 2. Scatterplots of ultraviolet index (UVI) plotted against D_3 level, with lines of best fit overlaid. (**a**) Group census, excluding results when access to the 'control nest box' was given. (**b**) Group census, including results when access to the 'control nest box' was given. (**c**) Test subject A's vitamin D_3 blood levels, excluding results when access to the 'control nest box' was given. (**d**) Test subject A's vitamin D_3 blood levels, including results when access to the 'control nest box' was given. (**e**) Test subject D's vitamin D_3 blood levels, with no 'control nest box' access. (**f**) Test subject B's vitamin D_3 blood levels, with 'control nest box' access.

3.2. Positional Sleep Behaviour

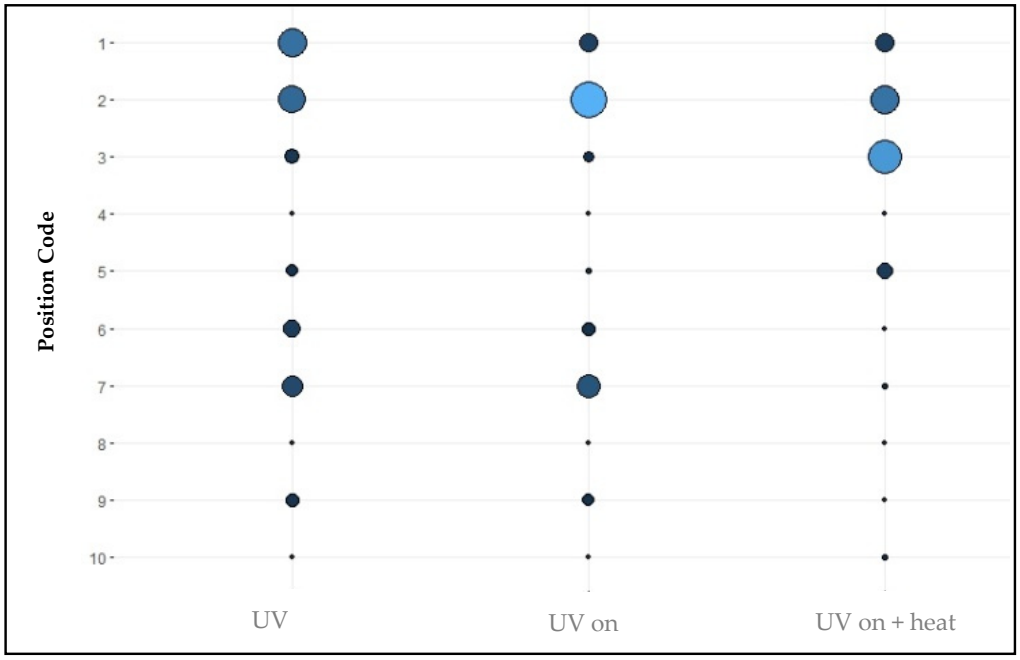
For individual B, significant differences in the duration of time spent in specific sleeping positions were found across UV and heat conditions ($p < 0.001$). Test subject A also showed a significant difference between UV-on vs. UV-off and UV-on with heat vs. UV-off ($p < 0.001$); however, there was lower significance in UV-on vs. UV-on with heat ($p = 0.014$).

The duration of time spent in each position was plotted in a balloon plot (Figure 3). Post hoc pairwise Fisher testing returned non-significant results for most comparisons of duration for each sleeping position, although some significant differences were recorded. Two positions that were 'exposed', positions 1 and 2, showed significant differences between UV-on and UV-off in both individuals ($p < 0.05$), whilst 'exposed' positions 3 and 5 were also significant for one individual (A) under these test conditions ($p < 0.05$).

'Exposed' positions 1, 2, 3, and 5 also showed significant differences between UV-off and UV-on with heat in both individuals ($p < 0.05$). Most positions with a coverage element, 4, 6, 7, 9, and 10, also showed significant differences under these test conditions ($p < 0.05$). Only one individual showed significant differences between variables UV-on and UV-on with heat, including some 'exposed' positions and some positions with a coverage element ($p < 0.05$) (See Appendix B: Tables A2–A7 for the full list of significant results).



(**a**)



(**b**)

Figure 3. Balloon plot of minutes spent per hour in each sleeping position for test subject A (**a**) and test subject B (**b**). Position codes: (1) exposed ball and ears hidden, (2) exposed ball and ears out, (3) exposed stretched out, (4) exposed tail over torso laid on back, (5) exposed laid on back, (6) partial—face exposed, (7) partial—body exposed, (8) under nesting material, (9) under woodwool, and (10) exposed stretched out tail over torso.

4. Discussion

4.1. Vitamin D_3 Blood Serum Levels—Group Census

At present, this study accepts the null hypothesis of no positive correlation between artificial UV-B and $25OHD_3$ levels as a group census. Due to precautionary ethical considerations based on a limited understanding of UV-B effects on aye-ayes at the time, including the potential for adverse UV-B effects on skin, coupled with the UV index output limitations

of the current equipment in a captive setting, the highest UVI level provided was an index of three. In Madagascar, the mean climatological UVI values at local solar noon average 10 UVI units at ground level in the capital of Madagascar, Antananarivo, located in the central highlands of Madagascar at an altitude of 12,501,470 m [60,61]. As previously stated, aye-aye nests are typically located high in the crowns, forks, and tangles in trees, with height varying between nine and seventeen metres. UVI levels within aye-ayes' natural habitat are unknown. Therefore, if UV-B does penetrate nests, UVI readings may be greater than those at ground level; however, varying canopies and cloud coverages will affect this [47,48,62]. With this information, the UVI provided in this study may have been too low to have a significant effect on aye-aye vitamin D_3 blood levels. Husbandry guidelines for ploughshare tortoises (*Astrochelys yniphora*), a ground-dwelling species endemic to Madagascar, suggest a maximum UVI of four to five for juveniles and six to eight for adults in basking areas [63]. These guidelines further suggest that areas outside basking zones (not in full shade) should read between two and four UVIs to still gain benefit. Whilst this may be a terrestrial reptile, the habitat it is living in is very exposed to the sun, much like the upper canopy, where aye-ayes typically nest. Therefore, the levels of UV exposure could be similar, potentially indicating that the UVIs given in this study may have been too low for a tree-dwelling species [63]. However, this cannot be confirmed without data on UV exposure in the aye-ayes' wild habitat.

Previous studies have found nocturnal mammals are able to synthesise vitamin D_3, such as chinchillas and fruit bats, despite them retreating into caves, burrows, trees, and rock crevices during daylight hours [64,65]. The grouped analysis in this study does not reflect these previous findings. This may be due to the small sample size, as, when analysed on an individual basis, one individual's results showed a positive trend. At the time of writing, these individuals made up 8.06% of the captive aye-aye population, indicating a small sample size [66]. The need to work with small sample sizes is common in zoological collections, often stemming from differences in institutional capacity and resources to support multi-zoo research, inconsistent research prioritisation across collections, and variability in animal population sizes.

4.2. Vitamin D_3 Blood Serum Levels—Individual Variations

Blood analysis was only compared in three individuals. As biological samples for research could only be collected opportunistically during veterinary treatments, there were reduced opportunities to collect blood samples from more individuals and obtain repeated samples from the same individuals.

One test subject is thought to be one of the oldest aye-ayes in captivity, test subject D. This individual showed a continued decrease in $25OHD_3$ despite multiple increases of UVI output and not having access to the 'control nest box'. In a study analysing levels of pre-vitamin D_3 produced in the skin of multiple age ranges of humans, it was found that those aged between 77 and 82 had decreased levels by more than twice those aged from 8 to 18 [67], indicating that vitamin D_3 level maintenance may increase in difficulty with age. While direct comparisons should be made cautiously due to interspecies differences in vitamin D metabolism, this finding may offer a useful reference point when considering the decline observed in the older aye-aye individual. Low levels of vitamin D have been reported in cases of liver indices due to pre-vitamin D being hydroxylated to 25-hydroxyvitamin D (25OHD) in the liver [68,69]. However, no clinical signs of liver issues were indicated in this individual, suggesting skin aging may be a factor in this continued vitamin D_3 decline.

Test subject B became pregnant and reared an offspring during this research. Due to this and the aforementioned ethical considerations, only three samples were acquired from

this individual, of which two samples were collected when the individual had access to the 'control nest box'. Multiple factors may have some influence on the insignificant results for this individual. Test subject B was housed with her twin (test subject C) at one of the data points, and they always slept together in the same nest box. From keeper observations, her twin was the dominant individual, potentially affecting sleeping arrangements and, therefore, UV exposure [70]. Despite the twins having access to the same diet, the more dominant individual could have been dominating preferred food items, with potentially varying levels of vitamin D, preventing access for conspecifics, similarly seen in other primate species [71]. This may have been a similar case when a sample was collected from test subject B whilst she was housed with her offspring (test subject E). Moreover, lactation may also impact $25OHD_3$ levels in subject B. Whilst individual E was 14 months old at the time, aye-aye infants have been found to suckle as late as 17 months in the wild [72]. Further research is needed to determine whether lactation has a beneficial or a detrimental effect on $25OHD_3$ levels in either the dam or the infant aye-aye.

We cannot reject the null hypothesis based on the overall data; however, the significant result observed in test subject A indicates that a full 6-week exposure to UV-B had a measurable impact on its $25OHD_3$ levels during experimental phase 1.3. It is possible that similar effects might have been observed in other individuals had they not been in other life stages with varying physiological demands, but these results warrant further investigation.

4.3. Positional Sleep Behaviour

The varied durations of time spent in each sleeping position under different environmental conditions may reflect basking and thermoregulatory behaviours typically associated with natural sunlight exposure.

Many mammals have been recorded to curl into a tight ball when sleeping, and this is thought to be an effective sleeping position for the maximum conservation of heat [73]. The results of this study suggest that the use of 'exposed ball with ears hidden' (position 1) may not be primarily for heat conservation in aye-ayes. Huddling, a similar ball-like position used by ring-tailed lemurs (*Lemur catta*), was found to be associated with the time of day, regardless of the ambient temperature or season [74]. As well as this, the principle of nest housing is to create a microenvironment, preventing environmental changes [73]. This potentially means that ball-like sleeping positions in aye-ayes may not primarily be used for heat retention, as this was not the case for ring-tailed lemurs, and that their nest structure serves this purpose. When further analysing these positions on an individual basis, test subject A's results suggest that ball-type positions could instead be serving some other purpose, such as to block out the light to aid sleep. However, this is not mirrored by test subject B. Aye-ayes may use a ball-like position when in nests to serve as a defence strategy should their nest be infiltrated [75].

In both test subjects, the duration of time spent in position 2 ('exposed ball with ears out') was significantly greater under UV-B conditions compared to UV-off, as reported in the Section 3 ($p < 0.05$), suggesting that this is not a thermoregulatory behaviour and is, instead, in response to the UV-B. This position increases body surface exposure, similar to that seen in other basking mammals that increase their body surface area to maximise sun exposure, which suggests that this may be a basking behaviour [76,77]. Therefore, the null hypothesis that UV-B or heat exposure does not affect the sleep position can be rejected based on the significant increase in time spent in the 'exposed ball with ears out' position under UV-B conditions, indicating a behavioural response to environmental UV-B. However, this position may have derived from the position 'exposed ball with ears hidden' (position 1), as once non-rapid eye-movement (NREM) sleep occurs, muscle retention decreases, potentially allowing the ears to become free of the tight-fisted ball

position [78]. Even with the latter in mind, aye-aye ears may play an important role in UV synthesis. Aye-aye ears and feet have dark skin pigmentation with very few hair follicles, whilst the rest of their body is a much lighter skin pigmentation covered with black hair. Skin pigmentation plays a role in UV synthesis, with high concentrations of melanin in the epidermis functioning as a light filter, reducing adverse effects, such as sunburn [9]. Therefore, these areas have high concentrations of melanin to help with the adverse effects of sun exposure when basking for UV-B.

The results for the position 'exposed stretched out' (position 3) for individual B suggest a thermoregulatory response for this individual. The similar position 'exposed laid on back' (position 5) also appears to be a similar thermoregulatory behaviour for individual A but is negatively affected by the amount of light. Other sleeping positions were favoured to filter out the increased amount of light. However, when the temperature increased, thermoregulation was prioritised. Mammals employ basking for different functions, with multiple studies suggesting a close link between basking for thermoregulation and energy requirements in diurnal and nocturnal mammals [79]. Both positions 'exposed stretched out' and 'exposed laid on back' increase the exposed body surface area of the individuals, resulting in better thermoregulation.

When exposed to heat, test subject B ceased seeking any coverage. In captivity, aye-ayes are supplied with nest housing in the form of nest boxes recommended by the husbandry guidelines, along with the provision of nesting material (woodwool, branches, and leaves). In this case, the nesting material may have been used as a form of heat retention. However, once a heat source was added, these positions were used significantly less, potentially due to the heat retention properties of the nesting material no longer being required. However, test subject A used positions that covered his body with his tail, which also appeared to have the same thermoregulatory effect, as this individual spent significantly more time in these positions under non-heat variables. Therefore, both individuals may be altering their sleep positions to increase thermoregulatory cover when no heat source is provided; however, they have different methods of doing this.

There is a close behavioural link between basking for UV-B and thermoregulation, which could account for the minor changes in test subject A's behaviour under both UV-on conditions [73]. However, this was not mirrored by test subject B. This may be due to the presence of her infant during the sampling period for the heat variable, which changed her thermoregulatory requirements compared to those of a lone individual [73]. Wild counterparts rarely sleep in the same nests as another individual at the same time, though this is common for mother–infant relationships, and the frequency of this decreases with age [72]. Aye-aye infants' protracted development is thought to be likely associated with their specialised foraging behaviour and diet, yet thermoregulation benefits may have a key role in this, as grouping strategies are efficient low-energetic ways of increasing ambient temperatures [73].

Additionally, when aye-ayes had access to multiple nest boxes, they frequently changed sleeping locations across nights. This behaviour, capturing the sleeping site selection, may indicate that the provision of multiple nest boxes supports higher welfare standards, aligning with observations of wild nesting behaviour [80].

4.4. Limitations

This study has some limitations. Small sample sizes increase the risk of the over-estimation or underestimation of probabilities [81]. This small sample size was due to several reasons, including limiting data collection to one zoological institution, ethical considerations, the involvement of keepers, the time constraints of equipment installation, and the restricted opportunities to obtain blood samples. A total of 80% of the individuals

in this study were related; this also may be a limiting factor due to previous human studies having shown the heritability of circulating vitamin D concentrations [82]. Additionally, vitamin D metabolites in nocturnal primates are a relatively new area of study; this study largely relies upon diurnal mammal and reptilian scientific evidence, thus possibly using an inappropriate methodology for nocturnal species.

4.5. Study Applications, Benefits, and Future Research

This study has identified many knowledge gaps regarding wild and captive *Daubentonia madagascariensis*. This study was based on the theory of UV-B penetrating nests due to their natural material structure and their location in trees; however, there is still limited research in these areas. Further research is needed into the structure, function, and locations of aye-aye nests to enhance the welfare of captive counterparts and further conservation efforts. Vitamin D levels can also be affected by food intake. Nutrient intake and diet compositions have been studied in wild and captive populations, though with little emphasis on vitamin D levels in either plant or insect matter. One paper reported no vitamin D levels were found during food analysis; however, only four food items were analysed [43]. It was also suggested that aye-ayes were similar to naked mole rats (*Heterocephalus glaber*), having an extremely efficient digestive system that allowed them to exploit limited food resources due to their highly efficient modes of mineral uptake; however, this has not been investigated [43].

Despite the small number of significant results for the effects of artificial UV-B on vitamin D blood levels, further research into the provision of artificial UV-B should be carried out by collections with aye-ayes under veterinary supervision. Research should comprise a larger population sample size, with varying life stages. Investigation is also needed into wild aye-aye serum levels. Despite low vitamin D levels and its symptoms being recorded in captive aye-ayes, these are presumed deficiencies based on data from diurnal lemurs, which may naturally have higher levels due to their diurnal rhythms. The combination of artificial UV-B and a heat source allowed the aye-ayes to express basking behaviours. Based on this, collections with aye-ayes should supply their animals with these to help to expand their natural behaviour repertoire. Excessive exposure to UV-B does not cause vitamin D intoxication; however, there may be long-term risks, as shown in the considerable research on UV rays causing skin damage in humans [26,83]. Therefore, time under UV exposure should be limited and provided at a low strength until further research into the appropriate conditions has been fully investigated.

Artificial UV-B is passive and does not need intervention to administer. This method of administration also allows animals the choice to cooperate and self-regulate with their own healthcare whilst exhibiting naturalistic behaviours. In comparison, palatable aqueous vitamin D_3 solutions are commonly added to 'gruel', as per husbandry guidelines [41]. This method requires intervention, with varying amounts being consumed daily, and needs dosage rates to be adjusted on a regular basis, depending on the physical weight changes of the animal. This solution can also be given directly by keepers via syringe administration for more accurate administration measures; however, this requires an increase in keeper time and an increased level of non-naturalistic involvement and is subject to individual animal acceptance. Injectable vitamin D can also be used; however, it can be costly and labour intensive and increase animal stress levels. Although there is an initial setup cost of artificial UV-B and the cost of the replacement of bulbs (six months on average), this does not require daily intervention. The results within this study tentatively suggest that artificial UV-B could be sufficient to sustain aye-aye vitamin D_3 blood levels; however, supplementation of palatable aqueous vitamin D_3 solutions may still be needed for those

in specific life stages, such as old age and pregnancy, indicating further need for research to reach a definitive conclusion.

The role of UV exposure in aye-aye health remains poorly understood. Further research is required to clarify its physiological effects and to inform the development of captive husbandry practices that may optimise potential health benefits for the species.

5. Conclusions

This study highlights that aye-ayes, a nocturnal primate, do exhibit basking behaviours but that the extent to which they absorb UV-B is not fully understood. A range of potential basking behaviours were exhibited, and the time spent in positions where body surface area exposure increased was the most prominent under conditions that mimic sunlight. Individuals favoured balled-up positions throughout, highlighting the importance of this behaviour for either comfort or physical defence. Once UV-B was added, there was a significant increase in the exposure of ears whilst remaining in a ball, potentially showing a response to light that may be a basking behaviour for UV absorption. Once heat was added, further thermoregulatory responses were seen through the exposure of the torso from the body posture, tail, and nesting coverage changes.

The null hypothesis that UVI exposure does not increase vitamin D_3 levels in the blood of aye-ayes could not be entirely rejected. Due to the small sample size of the population, the individual life stages may have a strong effect on the overall results. The presence of an aged individual and a lactating individual are mitigating factors that could be reducing their serum D_3 levels. The only significant change under UVI conditions was found in the adult male with access only to the UV nest box; however, the limited samples mean that no strong conclusions can be drawn either way about UVI exposure effects in aye-ayes. The complexities of investigating management methods of captive animals with varying life and reproductive states meant that strict experimental protocols could not be enforced for all the individuals throughout the length of the experiment. To mitigate this, further experiments need to take this into account when deciding on study population sizes and durations of sampling to mitigate against individual life stages and welfare requirements.

Author Contributions: Conceptualisation, P.B.; methodology and execution of the procedure in this work, D.W. and P.B.; statistical analysis, D.W. and S.R.; writing—original draft preparation, D.W.; writing—review and editing, D.W. and P.B.; supervision, S.R.; funding acquisition, D.W. and P.B. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Association of British and Irish Wild Animal Keepers' (ABWAK) Live Your Legacy Grant.

Institutional Review Board Statement: The animal study protocol was approved by the Ethics Committee of the Bristol Zoological Society (BZS_2023_057) for studies involving animals.

Data Availability Statement: The data supporting this study are available upon request addressed to the corresponding author.

Acknowledgments: First: we would like to extend thanks to ABWAK for awarding the 'Live Your Legacy Grant' funding. Without this, the vital research into nocturnal animal welfare would not have been carried out. Thanks to the staff at the Bristol Zoological Society (BZS), with emphasis on the 'Twilight World' keepers, the Mammal Department managers, and the Senior Curator of Animals at the time of research and to BZS's IT and Maintenance Department for their technical assistance. We would like to recognise the British and Irish Association of Zoos and Aquariums (BIAZA) for awarding this research an award at the Annual BIAZA Awards, 2022. Lastly, we would like to deeply acknowledge Rowena Killick and Frances Baines for their expertise, providing invaluable knowledge and support for the research.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of the data; in the writing of the manuscript; or in the decision to publish the results.

Abbreviations

The following abbreviations are used in this manuscript:

UV-B Ultraviolet-B
UVI Ultraviolet index

Appendix A. Ferguson Zones

Table A1. Ferguson zones, summarised from Baines et al. 2016 [52].

Zone	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	1.1–3.0
Zone 3	Open or partial sun basker, Thermoregulator	1–2.6	2.9–7.4
Zone 4	Mid-day sun basker, Thermoregulator	2.6–3.5	4.5–9.5

Appendix B. Pairwise Fisher's Exact Test Results

Appendix B.1.

Table A2. Pairwise Fisher's exact test results for test subject B: Differences in duration of sleeping positions between UV-off and UV-on conditions. *P*. adj. signif. values of *** $\leq$ [0.0001–0.0005]; ns = non-significant.

UV-Off and UV-On	UV-Off and UV-On	N	*p*	*P*. Adj.	*P*. Adj. Signif.
position 1	position 2	130.070936	1.31×10^{-5}	5.9×10^{-4}	***
position 1	position 3	52.780741	1.00×10	1.00000×10	ns
position 1	position 4	43.249530	1.00×10	1.00000×10	ns
position 1	position 5	47.431244	5.60×10^{-1}	1.00000×10	ns
position 1	position 6	56.551378	7.30×10^{-1}	1.00000×10	ns
position 1	position 7	77.724120	5.75×10^{-3}	1.2900×10^{-1}	ns
position 1	position 8	43.249530	1.00×10	1.00000×10	ns
position 1	position 9	51.689233	4.19×10^{-1}	1.00000×10	ns
position 1	position 10	43.249530	1.00×10	1.00000×10	ns
position 2	position 3	96.352616	3.59×10^{-2}	3.2300×10^{-1}	ns
position 2	position 4	86.821405	1.00×10	1.00000×10	ns
position 2	position 5	91.003119	1.53×10^{-2}	2.2900×10^{-1}	ns

Table A2. *Cont.*

UV-Off and UV-On	UV-Off and UV-On	N	*p*	*P*. Adj.	*P*. Adj. Signif.
position 2	position 6	100.123253	2.84×10^{-2}	3.2000×10^{-1}	ns
position 2	position 7	121.295995	4.05×10^{-1}	1.00000×10	ns
position 2	position 8	86.821405	1.00×10	1.00000×10	ns
position 2	position 9	95.261108	2.72×10^{-1}	1.00000×10	ns
position 2	position 10	86.821405	1.00×10	1.00000×10	ns
position 3	position 4	9.531210	1.00×10	1.00000×10	ns
position 3	position 5	13.712924	5.05×10^{-1}	1.00000×10	ns
position 3	position 6	22.833058	1.00×10	1.00000×10	ns
position 3	position 7	44.005800	1.65×10^{-1}	1.00000×10	ns
position 3	position 8	9.531210	1.00×10	1.00000×10	ns
position 3	position 9	17.970913	6.50×10^{-1}	1.00000×10	ns
position 3	position 10	9.531210	1.00×10	1.00000×10	ns
position 4	position 5	4.181714	1.00×10	1.00000×10	ns
position 4	position 6	13.301847	1.00×10	1.00000×10	ns
position 4	position 7	34.474590	1.00×10	1.00000×10	ns
position 4	position 8	0.000000	1.00×10	1.00000×10	ns
position 4	position 9	8.439703	1.00×10	1.00000×10	ns
position 4	position 10	0.000000	1.00×10	1.00000×10	ns
position 5	position 6	17.483561	5.19×10^{-1}	1.00000×10	ns
position 5	position 7	38.656304	4.71×10^{-2}	3.5300×10^{-1}	ns
position 5	position 8	4.181714	1.00×10	1.00000×10	ns
position 5	position 9	12.621417	2.28×10^{-1}	1.00000×10	ns
position 5	position 10	4.181714	1.00×10	1.00000×10	ns
position 6	position 7	47.776437	1.93×10^{-1}	1.00000×10	ns
position 6	position 8	13.301847	1.00×10	1.00000×10	ns
position 6	position 9	21.741550	6.62×10^{-1}	1.00000×10	ns
position 6	position 10	13.301847	1.00×10	1.00000×10	ns
position 7	position 8	34.474590	1.00×10	1.00000×10	ns
position 7	position 9	42.914293	7.10×10^{-1}	1.00000×10	ns
position 7	position 10	34.474590	1.00×10	1.00000×10	ns
position 8	position 9	8.439703	1.00×10	1.00000×10	ns
position 8	position 10	0.000000	1.00×10	1.00000×10	ns
position 9	position 10	8.439703	1.00×10	1.00000×10	ns

Appendix B.2.

Table A3. Pairwise Fisher's exact test results for test subject B: Differences in duration of sleeping positions between UV-on and UV-on with Heat. *P*. adj. signif. values of * = $p \leq$ [0.01–0.05], ** $\leq$ [0.001–0.005], *** $\leq$ 0.0001–0.0005, and **** $\leq$ [0–0.00005]; ns = non-significant.

UV-On and UV-On with Heat	UV-On and UV-On with Heat	n	*p*	*P*. Adj.	*P*. Adj. Signif.
position 1	position 2	112.72657952	4.56×10^{-1}	1.00×10	ns
position 1	position 3	72.94662309	2.22×10^{-5}	2.50×10^{-4}	***
position 1	position 4	21.49346405	1.00×10	1.00×10	ns
position 1	position 5	29.26361656	1.16×10^{-2}	4.35×10^{-2}	*
position 1	position 6	25.77015251	1.25×10^{-1}	4.02×10^{-1}	ns
position 1	position 7	41.40522876	4.79×10^{-4}	3.08×10^{-3}	**
position 1	position 8	21.45642702	1.00×10	1.00×10	ns
position 1	position 9	24.96623094	1.25×10^{-1}	4.02×10^{-1}	ns
position 1	position 10	21.62309368	1.00×10	1.00×10	ns
position 2	position 3	142.76034858	1.06×10^{-12}	2.38×10^{-1}	****
position 2	position 4	91.30718954	1.00×10	1.00×10	ns
position 2	position 5	99.07734205	5.58×10^{-4}	3.14×10^{-3}	**
position 2	position 6	95.58387800	2.94×10^{-1}	8.27×10^{-1}	ns
position 2	position 7	111.21895425	6.96×10^{-4}	3.48×10^{-3}	**
position 2	position 8	91.27015251	1.00×10	1.00×10	ns
position 2	position 9	94.77995643	2.94×10^{-1}	8.27×10^{-1}	ns
position 2	position 10	91.43681917	1.00×10	1.00×10	ns
position 3	position 4	51.52723312	1.00×10	1.00×10	ns
position 3	position 5	59.29738562	1.00×10	1.00×10	ns
position 3	position 6	55.80392157	9.53×10^{-5}	7.15×10^{-4}	***
position 3	position 7	71.43899782	5.68×10^{-15}	2.56×10^{-13}	****
position 3	position 8	51.49019608	1.00×10	1.00×10	ns
position 3	position 9	55.00000000	9.53×10^{-5}	7.15×10^{-4}	***
position 3	position 10	51.65686275	1.00×10	1.00×10	ns
position 4	position 5	7.84422658	1.00×10	1.00×10	ns
position 4	position 6	4.35076253	1.00×10	1.00×10	ns
position 4	position 7	19.98583878	1.00×10	1.00×10	ns
position 4	position 8	0.03703704	1.00×10	1.00×10	ns
position 4	position 9	3.54684096	1.00×10	1.00×10	ns
position 4	position 10	0.20370370	1.00×10	1.00×10	ns
position 5	position 6	12.12091503	2.02×10^{-3}	8.26×10^{-3}	**
position 5	position 7	27.75599129	3.22×10^{-7}	4.83×10^{-6}	****
position 5	position 8	7.80718954	1.00×10	1.00×10	ns
position 5	position 9	11.31699346	2.02×10^{-3}	8.26×10^{-3}	**
position 5	position 10	7.97385621	1.00×10	1.00×10	ns
position 6	position 7	24.26252723	1.00×10	1.00×10	ns
position 6	position 8	4.31372549	1.00×10	1.00×10	ns
position 6	position 9	7.82352941	1.00×10	1.00×10	ns
position 6	position 10	4.48039216	1.00×10	1.00×10	ns
position 7	position 8	19.94880174	1.00×10	1.00×10	ns
position 7	position 9	23.45860566	1.00×10	1.00×10	ns
position 7	position 10	20.11546841	1.00×10	1.00×10	ns
position 8	position 9	3.50980392	1.00×10	1.00×10	ns
position 8	position 10	0.16666667	1.00×10	1.00×10	ns
position 9	position 10	3.67647059	1.00×10	1.00×10	ns

Appendix B.3.

Table A4. Pairwise Fisher's exact test results for test subject B: Differences in duration of sleeping positions between UV-off and UV-on with heat conditions. *P*. adj. signif. values of * = $p \leq$ [0.01–0.05], ** $\leq$ [0.001–0.005], *** $\leq$ [0.0001–0.0005, and **** $\leq$ [0–0.00005]; ns = non-significant.

UV-Off and UV-On with Heat	UV-Off and UV-On with Heat	n	*p*	*P*. Adj.	*P*. Adj. Signif.
position 1	position 2	103.97398563	4.24×10^{-3}	2.07×10^{-2}	*
position 1	position 3	97.64893232	1.10×10^{-10}	4.18×10^{-9}	****
position 1	position 4	42.31162175	1.00×10	1.00×10	ns
position 1	position 5	53.87133148	1.23×10^{-2}	5.03×10^{-2}	ns
position 1	position 6	51.26270655	1.76×10^{-1}	4.95×10^{-1}	ns
position 1	position 7	57.20778052	4.89×10^{-2}	1.69×10^{-1}	ns
position 1	position 8	42.27458472	1.00×10	1.00×10	ns
position 1	position 9	47.20448338	5.69×10^{-1}	1.00×10	ns
position 1	position 10	42.44125138	1.00×10	1.00×10	ns
position 2	position 3	117.07374852	5.35×10^{-5}	6.02×10^{-4}	***
position 2	position 4	61.73643795	1.00×10	1.00×10	ns
position 2	position 5	73.29614768	5.30×10^{-1}	1.00×10	ns
position 2	position 6	70.68752275	2.71×10^{-3}	1.52×10^{-2}	*
position 2	position 7	76.63259671	7.57×10^{-5}	6.81×10^{-4}	***
position 2	position 8	61.69940091	1.00×10	1.00×10	ns
position 2	position 9	66.62929957	5.34×10^{-2}	1.72×10^{-1}	ns
position 2	position 10	61.86606758	1.00×10	1.00×10	ns
position 3	position 4	55.41138464	1.00×10	1.00×10	ns
position 3	position 5	66.97109437	9.42×10^{-2}	2.83×10^{-1}	ns
position 3	position 6	64.36246944	3.58×10^{-7}	5.37×10^{-6}	****
position 3	position 7	70.30754341	1.86×10^{-10}	4.18×10^{-9}	****
position 3	position 8	55.37434761	1.00×10	1.00×10	ns
position 3	position 9	60.30424627	1.33×10^{-4}	9.98×10^{-4}	***
position 3	position 10	55.54101427	1.00×10	1.00×10	ns
position 4	position 5	11.63378380	1.00×10	1.00×10	ns
position 4	position 6	9.02515887	1.00×10	1.00×10	ns
position 4	position 7	14.97023284	1.00×10	1.00×10	ns
position 4	position 8	0.03703704	1.00×10	1.00×10	ns
position 4	position 9	4.96693570	1.00×10	1.00×10	ns
position 4	position 10	0.20370370	1.00×10	1.00×10	ns
position 5	position 6	20.58486860	4.60×10^{-3}	2.07×10^{-2}	*
position 5	position 7	26.52994257	2.23×10^{-4}	1.43×10^{-3}	**
position 5	position 8	11.59674677	1.00×10	1.00×10	ns

Table A4. *Cont.*

UV-Off and UV-On with Heat	UV-Off and UV-On with Heat	n	*p*	*P*. Adj.	*P*. Adj. Signif.
position 5	position 9	16.52664543	2.94×10^{-2}	1.10×10^{-1}	ns
position 5	position 10	11.76341343	1.00×10	1.00×10	ns
position 6	position 7	23.92131764	1.00×10	1.00×10	ns
position 6	position 8	8.98812184	1.00×10	1.00×10	ns
position 6	position 9	13.91802050	1.00×10	1.00×10	ns
position 6	position 10	9.15478850	1.00×10	1.00×10	ns
position 7	position 8	14.93319580	1.00×10	1.00×10	ns
position 7	position 9	19.86309446	1.00×10	1.00×10	ns
position 7	position 10	15.09986247	1.00×10	1.00×10	ns
position 8	position 9	4.92989866	1.00×10	1.00×10	ns
position 8	position 10	0.16666667	1.00×10	1.00×10	ns
position 9	position 10	5.09656533	1.00×10	1.00×10	ns

Appendix B.4.

Table A5. Pairwise Fisher's exact test results for test subject A: Differences in duration of sleeping positions between UV-off and UV-on conditions. *P*. adj. signif. values of * = $p \leq$ [0.01–0.05], and **** $\leq$ [0–0.00005]; ns = non-significant.

UV-Off and UV-On	UV-Off and UV-On	n	*p*	*P*. Adj.	*P*. Adj. Signif.
position 1	position 2	109.561584	7.96×10^{-3}	7.16×10^{-2}	ns
position 1	position 3	109.383293	4.31×10^{-1}	1.00×10	ns
position 1	position 4	75.546192	2.62×10^{-1}	1.00×10	ns
position 1	position 5	95.236908	2.71×10^{-3}	4.07×10^{-2}	*
position 1	position 6	66.955979	1.00×10	1.00×10	ns
position 1	position 7	66.955979	1.00×10	1.00×10	ns
position 1	position 8	66.955979	1.00×10	1.00×10	ns
position 1	position 9	66.955979	1.00×10	1.00×10	ns
position 1	position 10	78.095938	1.00×10	1.00×10	ns
position 2	position 3	85.032920	1.57×10^{-3}	3.53×10^{-2}	*
position 2	position 4	51.195818	5.98×10^{-3}	6.73×10^{-2}	ns
position 2	position 5	70.886534	5.82×10^{-7}	2.62×10^{-5}	****
position 2	position 6	42.605605	1.00×10	1.00×10	ns
position 2	position 7	42.605605	1.00×10	1.00×10	ns
position 2	position 8	42.605605	1.00×10	1.00×10	ns
position 2	position 9	42.605605	1.00×10	1.00×10	ns
position 2	position 10	53.745565	1.34×10^{-1}	7.54×10^{-1}	ns
position 3	position 4	51.017528	4.50×10^{-1}	1.00×10	ns

Table A5. *Cont.*

UV-Off and UV-On	UV-Off and UV-On	n	*p*	*P*. Adj.	*P*. Adj. Signif.
position 3	position 5	70.708244	3.85×10^{-2}	2.85×10^{-1}	ns
position 3	position 6	42.427315	1.00×10	1.00×10	ns
position 3	position 7	42.427315	1.00×10	1.00×10	ns
position 3	position 8	42.427315	1.00×10	1.00×10	ns
position 3	position 9	42.427315	1.00×10	1.00×10	ns
position 3	position 10	53.567274	5.18×10^{-1}	1.00×10	ns
position 4	position 5	36.871142	6.39×10^{-1}	1.00×10	ns
position 4	position 6	8.590213	1.00×10	1.00×10	ns
position 4	position 7	8.590213	1.00×10	1.00×10	ns
position 4	position 8	8.590213	1.00×10	1.00×10	ns
position 4	position 9	8.590213	1.00×10	1.00×10	ns
position 4	position 10	19.730172	3.52×10^{-1}	1.00×10	ns
position 5	position 6	28.280929	1.00×10	1.00×10	ns
position 5	position 7	28.280929	1.00×10	1.00×10	ns
position 5	position 8	28.280929	1.00×10	1.00×10	ns
position 5	position 9	28.280929	1.00×10	1.00×10	ns
position 5	position 10	39.420888	4.43×10^{-2}	2.85×10^{-1}	ns
position 6	position 7	0.000000	1.00×10	1.00×10	ns
position 6	position 8	0.000000	1.00×10	1.00×10	ns
position 6	position 9	0.000000	1.00×10	1.00×10	ns
position 6	position 10	11.139959	1.00×10	1.00×10	ns
position 7	position 8	0.000000	1.00×10	1.00×10	ns
position 7	position 9	0.000000	1.00×10	1.00×10	ns
position 7	position 10	11.139959	1.00×10	1.00×10	ns
position 8	position 9	0.000000	1.00×10	1.00×10	ns
position 8	position 10	11.139959	1.00×10	1.00×10	ns
position 9	position 10	11.139959	1.00×10	1.00×10	ns

Appendix B.5.

Table A6. Pairwise Fisher's exact test results for test subject A: Differences in duration of sleeping positions between UV-on and UV-on with heat conditions. *P*. adj. signif. values of ns = non-significant.

UV-On and UV-On with Heat	UV-On and UV-On with Heat	n	*p*	*P*. Adj.	*P*. Adj. Signif.
position 1	position 2	127.47167756	0.37400	1.000×10	ns
position 1	position 3	104.71350763	0.11200	7.59×10^{-1}	ns
position 1	position 4	63.27995643	1.00000	1.000×10	ns

Table A6. *Cont.*

UV-On and UV-On with Heat	UV-On and UV-On with Heat	n	*p*	*P*. Adj.	*P*. Adj. Signif.
position 1	position 5	77.95315904	0.03160	3.56×10^{-1}	ns
position 1	position 6	60.87254902	0.42600	1.000×10	ns
position 1	position 7	60.26143791	1.00000	1.000×10	ns
position 1	position 8	60.22440087	1.00000	1.000×10	ns
position 1	position 9	60.22440087	1.00000	1.000×10	ns
position 1	position 10	66.79411765	0.07540	6.79×10^{-1}	ns
position 2	position 3	111.73638344	0.43900	1.000×10	ns
position 2	position 4	70.30283224	1.00000	1.000×10	ns
position 2	position 5	84.97603486	0.11800	7.59×10^{-1}	ns
position 2	position 6	67.89542484	1.00000	1.000×10	ns
position 2	position 7	67.28431373	1.00000	1.000×10	ns
position 2	position 8	67.24727669	1.00000	1.000×10	ns
position 2	position 9	67.24727669	1.00000	1.000×10	ns
position 2	position 10	73.81699346	0.02710	3.56×10^{-1}	ns
position 3	position 4	47.54466231	0.56700	1.000×10	ns
position 3	position 5	62.21786492	0.39600	1.000×10	ns
position 3	position 6	45.13725490	1.00000	1.000×10	ns
position 3	position 7	44.52614379	1.00000	1.000×10	ns
position 3	position 8	44.48910675	1.00000	1.000×10	ns
position 3	position 9	44.48910675	1.00000	1.000×10	ns
position 3	position 10	51.05882353	0.00847	1.91×10^{-1}	ns
position 4	position 5	20.78431373	0.24700	1.000×10	ns
position 4	position 6	3.70370370	1.00000	1.000×10	ns
position 4	position 7	3.09259259	1.00000	1.000×10	ns
position 4	position 8	3.05555556	1.00000	1.000×10	ns
position 4	position 9	3.05555556	1.00000	1.000×10	ns
position 4	position 10	9.62527233	0.33300	1.000×10	ns
position 5	position 6	18.37690632	1.00000	1.000×10	ns
position 5	position 7	17.76579521	1.00000	1.000×10	ns
position 5	position 8	17.72875817	1.00000	1.000×10	ns
position 5	position 9	17.72875817	1.00000	1.000×10	ns
position 5	position 10	24.29847495	0.00343	1.54×10^{-1}	ns
position 6	position 7	0.68518519	1.00000	1.000×10	ns
position 6	position 8	0.64814815	1.00000	1.000×10	ns
position 6	position 9	0.64814815	1.00000	1.000×10	ns
position 6	position 10	7.21786492	0.14300	8.04×10^{-1}	ns

Table A6. *Cont.*

UV-On and UV-On with Heat	UV-On and UV-On with Heat	n	*p*	*P*. Adj.	*P*. Adj. Signif.
position 7	position 8	0.03703704	1.00000	1.000×10	ns
position 7	position 9	0.03703704	1.00000	1.000×10	ns
position 7	position 10	6.60675381	1.00000	1.000×10	ns
position 8	position 9	0.00000000	1.00000	1.000×10	ns
position 8	position 10	6.56971678	1.00000	1.000×10	ns
position 9	position 10	6.56971678	1.00000	1.000×10	ns

Appendix B.6.

Table A7. Pairwise Fisher's exact test results for test subject A: Differences in duration of sleeping positions between UV-off and UV-on with heat conditions. *P*. adj. signif. values of * = $p \leq$ [0.01–0.05], ** $\leq$ [0.001–0.005], ns = non-significant.

UV-Off and UV-On with Heat	UV-Off and UV-On with Heat	n	*p*	*P*. Adj.	*P*. Adj. Signif.
position 1	position 2	100.71953587	0.000465	1.050×10^{-2}	*
position 1	position 3	107.07719317	0.442000	1.00000×10	ns
position 1	position 4	64.08105011	0.225000	8.4400×10^{-1}	ns
position 1	position 5	93.54300788	0.520000	1.00000×10	ns
position 1	position 6	57.75009632	0.448000	1.00000×10	ns
position 1	position 7	57.13898521	1.000000	1.00000×10	ns
position 1	position 8	57.10194817	1.000000	1.00000×10	ns
position 1	position 9	57.10194817	1.000000	1.00000×10	ns
position 1	position 10	62.30182045	0.075600	4.8600×10^{-1}	ns
position 2	position 3	93.59283270	0.008940	8.050×10^{-2}	ns
position 2	position 4	50.59668965	0.001820	2.050×10^{-2}	*
position 2	position 5	80.05864741	0.000185	8.32×10^{-3}	**
position 2	position 6	44.26573585	1.000000	1.00000×10	ns
position 2	position 7	43.65462474	1.000000	1.00000×10	ns
position 2	position 8	43.61758770	1.000000	1.00000×10	ns
position 2	position 9	43.61758770	1.000000	1.00000×10	ns
position 2	position 10	48.81745999	0.001170	1.760×10^{-2}	*
position 3	position 4	56.95434695	0.105000	5.9100×10^{-1}	ns
position 3	position 5	86.41630471	0.189000	7.7300×10^{-1}	ns
position 3	position 6	50.62339315	1.000000	1.00000×10	ns
position 3	position 7	50.01228204	1.000000	1.00000×10	ns
position 3	position 8	49.97524500	1.000000	1.00000×10	ns
position 3	position 9	49.97524500	1.000000	1.00000×10	ns

Table A7. *Cont.*

UV-Off and UV-On with Heat	UV-Off and UV-On with Heat	n	*p*	*P*. Adj.	*P*. Adj. Signif.
position 3	position 10	55.17511729	0.053000	3.9700×10^{-1}	ns
position 4	position 5	43.42016166	0.396000	1.00000×10	ns
position 4	position 6	7.62725009	0.250000	8.6500×10^{-1}	ns
position 4	position 7	7.01613898	1.000000	1.00000×10	ns
position 4	position 8	6.97910195	1.000000	1.00000×10	ns
position 4	position 9	6.97910195	1.000000	1.00000×10	ns
position 4	position 10	12.17897423	1.000000	1.00000×10	ns
position 5	position 6	37.08920786	0.378000	1.00000×10	ns
position 5	position 7	36.47809675	1.000000	1.00000×10	ns
position 5	position 8	36.44105972	1.000000	1.00000×10	ns
position 5	position 9	36.44105972	1.000000	1.00000×10	ns
position 5	position 10	41.64093200	0.160000	7.5200×10^{-1}	ns
position 6	position 7	0.68518519	1.000000	1.00000×10	ns
position 6	position 8	0.64814815	1.000000	1.00000×10	ns
position 6	position 9	0.64814815	1.000000	1.00000×10	ns
position 6	position 10	5.84802043	0.167000	7.5200×10^{-1}	ns
position 7	position 8	0.03703704	1.000000	1.00000×10	ns
position 7	position 9	0.03703704	1.000000	1.00000×10	ns
position 7	position 10	5.23690932	1.000000	1.00000×10	ns
position 8	position 9	0.00000000	1.000000	1.00000×10	ns
position 8	position 10	5.19987229	1.000000	1.00000×10	ns
position 9	position 10	5.19987229	1.000000	1.00000×10	ns

Appendix C. Ethogram of Aye-Aye Positional Sleep Behaviour

Appendix C.1.

Table A8. Ethogram of aye-aye positional sleep behaviour.

Position	Code	Description
Exposed ball and ears hidden	1	The aye-aye is in a fully closed ball-like position, lying laterally on their side. Their tail either follows their curved body on the side or is placed on top of their body. The arms, legs, and face are fully tucked within the body. The ears are curled over and appear flattered to the body. Less than 20% of the body is covered by nesting or woodwool material.
Exposed ball and ears out	2	The aye-aye is in a fully closed ball-like position, lying laterally on their side. The tail either follows their curved body on the side or is placed on top of their body. The arms, legs, and face are fully tucked within the body. The face may be fully or partially tucked within the body. The ears are protruding and appear fully erect. Less than 20% of the body is covered by nesting or woodwool material.

Table A8. *Cont.*

Position	Code	Description
Exposed stretched out	3	The aye-aye is lying laterally on their side. The arms, legs, head, and ears are free from the torso and can be easily identified. The tail is also free from the torso but may be covering some of the legs. Less than 20% of the body is covered by nesting or woodwool material.
Exposed tail over torso laid on back	4	The aye-aye is lying posteriorly, and the underbelly can be clearly seen. The tail comes up between the back legs covering the torso. The arms are lying either at the side of or perpendicular to the torso. The legs are splayed out apart. The head is lying recumbently or laterally. Less than 20% of the body is covered by nesting or woodwool material.
Exposed laid on back	5	The aye-aye is lying posteriorly, and the underbelly can be clearly seen. The tail lies away from the body. The arms are lying either at the side of or perpendicular to the torso. The legs are splayed out apart. The head is lying recumbently or laterally. Less than 20% of the body is covered by nesting or woodwool material.
Partial—face exposed	6	From 20% to 70% of the body is covered in nesting or woodwool material. The face and top of the torso are exposed.
Partial—body exposed	7	From 20% to 70% of the body is covered in nesting or woodwool material. The tail, legs, and hips are exposed.
Under nesting material	8	Approximately 80% of the body is covered by nesting material, and the position cannot be determined.
Under woodwool	9	Approximately 80% of the body is covered by woodwool, and the position cannot be determined.
Exposed stretched out tail over torso	10	The aye-aye is lying laterally on their side. The arms, legs, head, and ears are free from the torso and can be easily identified. The tail is either fully or partially covering the torso. Less than 20% of the body is covered by nesting or woodwool material.

Appendix D. Raw Vitamin D3 Serum Blood Results

Appendix D.1.

Table A9. Raw vitamin D_3 serum blood results for all the test subjects.

Test Subject ID	UVI Measurement	nmol/L	Control Box Access
A	0	7.5	N/A
	0	34.5	N/A
	0.4	37.6	N
	1.5	38.8	N
	3	60.1	N
	3	34.8	Y
B	0.4	23.9	Y
	1.5	17.4	N
	3	8	Y
C	0.4	14.8	Y
D	0.4	68.7	N
	3	52.1	N
	3	36.8	N
	3	10.7	N
E	3	25.02	Y

Appendix D.2.

Table A10. Means and ranges for all the raw vitamin D_3 serum blood results.

UVI Measurement	Control Box Access	n	Mean (nmol/L)	Range (nmol/L)
0	N/A	2	24.75	7.5–34.5
0.4	Yes	2	19.35	14.8–23.9
0.4	No	2	53.15	37.6–68.7
1.5	Yes	-	-	-
1.5	No	2	28.6	17.4–38.8
3	Yes	3	22.61	8–34.8
3	No	4	39.93	10.7–60.1

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