

Vitamin D Status in European Zoo-Housed Great Apes

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Abstract

Vitamin D is crucial for physiological homeostasis and cardiovascular health. Zoo-housed great apes in Europe face significant risks of vitamin D deficiency due to limited ultraviolet B (UVB) exposure, potentially exacerbating conditions such as idiopathic myocardial fibrosis. This multi-centre observational study evaluated 25-hydroxyvitamin D (25-OHD) concentrations using liquid chromatography-tandem mass spectrometry in 480 opportunistic serum and plasma samples from 334 individuals across five great ape species (bonobo, chimpanzee, Western lowland gorilla, Sumatran orangutan, and Bornean orangutan) housed in 56 European zoos. Mixed-effects models were utilised to investigate the impact of individual, environmental, and husbandry factors on 25-OHD status. Using human reference intervals, 45.7% of samples were classified as deficient or insufficient (≤ 50 nmol/L). Insufficiency was most prevalent in bonobos (71.4%) and orangutans (58.6%). Local UVB irradiance and dietary fortification via commercial pellet in the diet emerged as the strongest positive predictors of 25-OHD levels. Unrestricted outdoor access also correlated with significantly higher concentrations. Chimpanzees exhibited the highest baseline levels among the species studied. There is a high prevalence of inadequate vitamin D status among European zoo-housed great apes. Husbandry interventions, including maximising UVB exposure, providing unrestricted outdoor access, and ensuring targeted dietary supplementation, are important to mitigating deficiency risks and safeguarding long-term cardiovascular and systemic health. This is the first study which describes vitamin D status in all commonly kept non-human great ape species in human care across a broad geographical range.

Introduction

Non-human great apes (*Hominidae*) share close genetic and physiological similarities with humans, suggesting comparable vitamin D requirements and metabolism [1, 2]. Maintaining adequate vitamin D status in human care, however, can be challenging due to limited ultraviolet B (UVB) exposure and dietary differences compared with natural habitats. Enclosure design, geographic latitude, and seasonal variation constrain cutaneous synthesis of cholecalciferol (vitamin D₃), while dietary sources of ergocalciferol (vitamin D₂) may be insufficient to compensate [3].

Vitamin D is essential for calcium and phosphorus homeostasis, immune function, and cardiovascular health, with deficiency associated with hypertension, endothelial dysfunction, and increased cardiovascular risk in humans [4–10]. Cholecalciferol (vitamin D₃) is synthesised in the skin following UVB-mediated conversion of 7-dehydrocholesterol, whereas ergocalciferol (vitamin D₂) is obtained from plant and fungal sources [11]. Both forms are hydroxylated to 25-hydroxyvitamin D (25-OHD), the principal circulating biomarker for vitamin D status with a half-life of approximately 2–3 weeks [12, 13].

The active metabolite, 1,25-dihydroxyvitamin D, exerts pleiotropic effects via the vitamin D receptor (VDR), influencing musculoskeletal, immune, and cardiovascular systems [6, 7, 9, 10]. Vitamin D may have a cardioprotective role by modulating pro-inflammatory and oxidative stress pathways relevant to cardiac fibrosis [14], including idiopathic myocardial fibrosis (IMF), a common cardiac disease specific

to non-human great apes [15]. Reduced UVB exposure and downstream vitamin D deficiency is also implicated in the pathogenesis of hypertension via effects on the renin–angiotensin system, endothelial function, and vascular inflammation [4, 5].

In European zoos, great apes may face multiple risk factors for deficiency: darker skin pigmentation reduces the efficiency of cutaneous vitamin D synthesis due to the UV-absorbing properties of melanin [16–20]; northerly latitude limits natural UVB irradiation in winter months, especially above $\sim 37^{\circ}\text{N}$ [21]; and lower ambient temperatures may reduce time spent outdoors [22]. Moreover, the prevalence of cardiovascular disease, particularly IMF, appears higher in zoo-housed apes than in wild populations or in animals living in range country sanctuaries [3, 15].

Published research on vitamin D deficiency in great apes in human care remains limited. Cases of rickets in juvenile chimpanzees raised without outdoor access underscore the risks of insufficient UVB exposure, while greater sunlight access is associated with higher serum vitamin D in captive chimpanzees [23, 24]. In gorillas, individuals housed indoors without direct sunlight had lower 25-OHD than those with outdoor access despite comparable diets [25], suggesting diet alone is ineffective at maintaining adequate status [26]. In sanctuary chimpanzees living in range countries, median vitamin D status also varied by sex, age, and sunlight exposure [27].

Building on the first large multi-zoo study in European chimpanzees that identified widespread insufficiency and highlighted predictors such as season, health status, and outdoor access [28], the present multi-species study aimed to: (i) evaluate 25-OHD concentrations in bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), Western gorillas (*Gorilla gorilla*), Bornean orangutans (*Pongo pygmaeus*), Sumatran orangutans (*Pongo abelii*), and hybrid orangutans (*Pongo* sp.); (ii) determine the prevalence of deficient, insufficient, adequate, and optimal vitamin D status using human reference intervals; and (iii) investigate associations between vitamin D status and individual (e.g., age, sex, health status, coat coverage), environmental (e.g., UVB irradiance, season), and modifiable husbandry factors (e.g., outdoor access, diet).

Results

Overall 25-OHD status

All but three samples had a total 25-OHD ($25\text{-OHD}_2 + 25\text{-OHD}_3$) that was equivalent to their 25-OHD_3 concentration, because the concentration of 25-OHD_2 was below the limit of detection (5 nmol/L) (exceptions: two gorillas ($25\text{-OHD}_2 = 9.60$ and 5.51 nmol/L) and one bonobo ($25\text{-OHD}_2 = 23.97$ nmol/L)). Therefore, the key outcome variable is total 25-OHD level (in nmol/L). A histogram showed evidence of skew, but a log transformation did not result in a more symmetrical distribution of values. Accordingly, the uncorrected total 25-OHD levels were used as the outcome score, reflecting overall vitamin D levels.

The median 25-OHD concentration across all samples was 53 nmol/L (range: 5-159 nmol/L). Of all samples, 46% fell into the deficient or insufficient reference interval categories, however, species-specific differences were substantial. While 36% of chimpanzee samples showed inadequate vitamin D status, this was 50% in gorilla, 59% in orangutan and 71% in bonobo samples. Within the 10% of samples with lowest 25-OHD concentrations, gorillas (n = 21, 44%) and bonobos (n = 13, 27%) were overrepresented, while the highest 10% was dominated by chimpanzees (n = 32, 67%). Species-specific 25-OHD data, as well as the number and proportion of samples per species in each vitamin D reference interval category are shown in Table 1.

Table 1

Species-specific 25-OHD levels in nmol/L, and number (percentage) of samples in each reference interval category: deficient (< 25 nmol/L), insufficient (25–50 nmol/L), adequate (51–75 nmol/L), optimal (> 75 nmol/L) [22, 72]. Level of detection: 5 nmol/L, samples lower than that were analysed as 5 nmol/L.

Species	Median (nmol/L)	Min (nmol/L)	Max (nmol/L)	Deficient (n (%))	Insufficient (n (%))	Adequate (n (%))	Optimal (n (%))
Bonobo	37	5.0	108	17 (35%)	18 (37%)	11 (22%)	3 (6%)
Chimpanzee	58	5.0	151	16 (6%)	74 (29%)	93 (37%)	68 (27%)
Gorilla	51	5.0	159	32 (30%)	21 (20%)	28 (26%)	25 (24%)
Orangutan	46	5.9	123	22 (30%)	22 (30%)	18 (24%)	12 (16%)
Total	53	5.0	159	87 (18%)	135 (28%)	150 (31%)	108 (23%)

Local UVB irradiance (in W/m²) during the 60-day window prior to taking the sample, as described in the methods, was the other key variable. The distribution also exhibited some right-hand skew, but a log transformation did not lead to a more symmetrical distribution. Therefore, the raw UVB irradiance scores were used for further analysis.

Main effects

Using a stepwise forward procedure, all significant predictor variables for 25-OHD levels were entered as fixed main effects into a mixed effects model. No interactions were included. A random effect for each individual was included to account for repeated measures.

Season (4 levels: spring, summer, autumn, winter) dropped out of significance (p > 0.17 for all contrasts) when the continuous variable UVB irradiance (t(245) = 7.9, p < 0.0001) was added into the same model, indicating that the measured UVB irradiance explains the variance in vitamin D levels much better than the 4-level season proxy. The effect size for UVB irradiance was scaled for the observed range of UVB

values, which ranged from 0 to 0.45 W/m². Over the 0.45 W/m² range, 25-OHD levels were 47 nmol/L higher, the strongest individual effect size of all included predictors.

The model also included the main effect of species on 25-OHD levels as a categorical variable, with chimpanzees set as the baseline level. Bonobos had significantly lower 25-OHD levels (-17 nmol/L, $t(221) = -2.7$, $p = 0.007$). There were non-significant trends for lower levels in Orangutans (-9 nmol/L, $t(213) = -1.6$, $p = 0.11$) and Gorillas (-7 nmol/L, $t(201) = -1.6$, $p = 0.12$).

Dietary vitamin D supplementation via pellet in the diet was related to significantly higher 25-OHD levels with a strong effect size (+ 25 nmol/L, $t(263) = 2.7$, $p = 0.008$). Access to outdoor areas was also related to significantly higher 25-OHD levels (+ 8 nmol/L, $t(275) = 2.3$, $p = 0.02$). Poor health (binary variable) showed a trend for lower 25-OHD levels (-6 nmol/L, $t(278) = -1.8$, $p = 0.07$).

Overall, this demonstrated good predictive value of the fixed effects for 25-OHD levels with a marginal $R^2 = 25\%$, which captures the variance explained exclusively by the fixed main effects listed here.

However, the conditional R^2 , which captures the variance explained by the random effects (i.e. due to variation between individuals), was considerably more substantial at 71%. The high conditional R^2 implies significant between-individuals variance in 25-OHD levels, and that individuals are quite consistent over time. This supports the mixed-effects modelling approach and suggests that predictive models should incorporate individual random effects.

Sensitivity analysis

Dietary vitamin D supplementation via pellet in the diet had missing values for 57 observations, equating to 17% of the data. Including this variable in the regression models thus reduced the sample count from 344 to 287, which is likely to affect the significance levels and effect size estimates of key effects in the main model presented above. To assess this impact, we repeated the model without including dietary supplementation.

Effect sizes and significance estimates for all predictors of total vitamin D levels in this regression model are shown in Table 2. Each previously significant main effect became more significant whilst effect sizes remained broadly stable. UVB irradiance ($t(279) = 8.4$, $p < 0.0001$) was still the strongest individual predictor with an effect size of 45 nmol/L for a 0.45 W/m² change in irradiance (observed range). The main effect of species became more pronounced: compared with chimpanzees, all other great ape species had significantly lower 25-OHD levels. Bonobos had the lowest levels (-20 nmol/L, $t(262) = -3.3$, $p = 0.001$), followed by Orangutans (-10 nmol/L, $t(247) = -2.1$, $p = 0.04$) and Gorillas (-8 nmol/L, $t(240) = -2.0$, $p < 0.05$). A boxplot of the uncorrected 25-OHD levels per species is shown in Fig. 2.

Table 2

Effect sizes (per 1-unit absolute change in the predictor) and significance estimates for all predictors of total vitamin D levels in the main model. For the species effect (4-level categorical), chimpanzee was set as the baseline species. The UV-B effect size refers to a change of 0.45 W/m², the highest level seen in our data.

Predictor	Effect size	df	t	p
UV-B irradiation (0.45 W/m ²)	45 nmol/L	280	8.4	<< 0.0001
Species: Bonobo	-20 nmol/L	263	-3.3	0.001
Species: Gorilla	-8 nmol/L	240	-2.0	0.049
Species: Orangutan	-10 nmol/L	247	-2.1	0.038
Outdoor access	7 nmol/L	331	2.3	0.02
Health score	-6 nmol/L	315	-2.2	0.03

The effect of access to outdoor areas was almost unchanged (+ 7 nmol/L, $t(331) = 2.3$, $p = 0.02$). The effect size of poor health on 25-OHD also remained stable at -6 nmol/L for those with poor health, but it crossed the significance threshold with the larger sample ($t(315) = -2.2$, $p = 0.03$).

Seasonal vitamin D levels

Although season was removed from the main model since UVB irradiance was the better predictor of 25-OHD levels, it provides a very useful proxy for UVB irradiance and the resulting 25-OHD changes when direct measurement of UVB irradiation is not available. There was also a significant effect of season when included as the only predictor of 25-OHD. Vitamin D levels were lowest in winter (median = 39 nmol/L, $p = 0.004$), highest in summer (median = 71 nmol/L, $p < 0.0001$), and intermediate in spring (mean = 54 nmol/L, reference level) and autumn (median = 49 nmol/L), with no significant difference between spring and autumn ($p = 0.14$).

UVB effect

The continuous UVB irradiance scores were the strongest individual predictor of vitamin D levels. We analysed this effect further, isolated from the other variables. A cubic spline for UVB irradiance was included to detect any potential non-linearity in the relationship, which may indicate saturation at higher levels of UVB irradiation. However, the non-linear effect was not significant ($p = 0.59$), which implies that there was no saturation effect for UVB irradiation (Fig. 3).

Non-significant predictors

Reproductive status (contraception, pregnancy, lactation), provision of artificial UVB lighting, and the presence of UV-permeable materials in the animal’s enclosure were not analysed due to small sample size for these factors. All other variables were also tested for main effects on vitamin D levels in separate mixed effects models containing no other co-variates (Table 3). They exhibited significant effects in some cases when used as the only predictor but were excluded from the main model because they had no significant effects when competing with the other significant predictors.

Table 3

Non-significant predictors of vitamin D levels. This includes variables which were significant individual predictors of 25-OHD, but dropped out of significance when added into the main model (marked with *). Effect sizes are only included for at least marginally significant ($p < 0.1$) effects.

Variable	Valid n	P	Effect size
Storage time (months)	480	0.08 *	-0.04 nmol/L / month
Sex	480	0.87	
Age	480	0.92	
Latitude	480	0.003 *	-0.8 nmol/L / degree
Sample type (plasma/serum)	480	0.64	
Body condition score (1–9 scale)	312	0.16	
Coat quality (3 levels)	285	0.17	
Dietary vitamin D supplementation other than pellet	318	0.59	

Discussion

This is the first comprehensive study to quantify 25-OHD concentrations across all great ape species commonly housed in human care across a large geographical range, evaluating the discrete impacts of individual, environmental and modifiable husbandry factors on their vitamin D status.

In the context of European zoo populations, this study included samples from the equivalent of 27% of all bonobos (from 46% of bonobo-holding zoos), 23% of all chimpanzees (from 37% of chimpanzee-holding zoos), 21% of all gorillas (from 12% of gorilla-holding zoos), and 15% of all orangutans (from 14% of orangutan-holding zoos) [29].

Overall 25-OHD status

Across all samples, 46% were classified as vitamin D deficient or insufficient (≤ 50 nmol/L) using human reference intervals, indicating a risk of widespread vitamin D inadequacy in the zoo-housed great ape population in Europe. This raises concerns about potential implications, particularly given vitamin D's

important role in immune function, musculoskeletal and cardiovascular health, among other physiological processes [7–10, 30, 31].

Bonobos exhibited the highest proportion of vitamin D deficient and insufficient samples, followed by orangutans, gorillas, and chimpanzees. The relatively higher vitamin D levels in chimpanzees may reflect better alignment of husbandry practices with their physiological requirements or higher UVB exposure. However, this observation could also be influenced by the larger sample size and broader geographic representation for chimpanzees. It is also important to note that all bonobo holding zoos are located in Northwestern Europe with naturally limited UVB irradiation, while chimpanzees are housed across a wider geographical range, including a larger number of zoos in Southern Europe where UVB irradiance may be seasonally higher. There is currently no scientific evidence indicating species-specific biological differences in vitamin D metabolism across great apes species. However, in other closely related species it has been shown that species-specific differences exist, and these may be linked to the degree of colouration of the skin [32].

While these data highlight a potential widespread issue in the European zoo-housed great ape population, the reliance on human reference intervals necessitates a cautious interpretation. However, species-specific reference intervals for wild non-human great apes are currently unknown. In traditionally-living East African human populations, the mean 25-OHD serum concentration was 115 nmol/L (range: 58–171 nmol/L), with 72% of the samples being > 100 nmol/L (0% <50 nmol/L, 13% <80 nmol/L) [33]. Sanctuary chimpanzees living in range countries were found to have a median 25-OHD concentration of 46.24 nmol/L (range: 17.10–109.23 nmol/L) [34], more similar to our findings. A group of zoo-housed chimpanzees moved from mainland USA to Hawaii increased their average 25-OHD concentration from 31 nmol/L to 97 nmol/L [24]. Based on these studies, it is plausible to expect that normal chimpanzee (and possibly other great ape) reference intervals fall into a similar range. However, direct comparison between the current study and previous results using different vitamin D quantification methods is challenging, due to well-known biases and imprecisions of various measurement methods [35].

Sample storage time and sample type

Sample storage time showed no correlation with 25-OHD concentrations, supporting previous research demonstrating that vitamin D is considered highly stable in serum and plasma, even during long-term storage [36–39].

No significant differences were observed between serum and plasma samples, supporting the validity of using both sample types in vitamin D assessments, as reported elsewhere [36, 40].

Individual factors

Health status was significantly associated with 25-OHD concentrations, with healthy individuals exhibiting higher 25-OHD than those with reported abnormal health. This finding is consistent with

human literature, where low vitamin D correlates with an array of systemic health issues [8, 30, 41–45]. However, as a cross-sectional observational study, the directionality of this relationship cannot be established.

While vitamin D deficiency may not directly cause conditions like IMF, it could exacerbate underlying cardiovascular pathology by contributing to hypertension, endothelial dysfunction, and vascular inflammation [15, 46]. Furthermore, chronic vitamin D deficiency is associated with (lung) fibrosis via the over-activation of the renin-angiotensin system, increasing extracellular matrix changes independent of hypertension [47]. To understand if vitamin D deficiency acts as an exacerbating factor for IMF or other cardiovascular pathologies, or if it is a consequence of poor health (e.g. due to reduced outdoor activity), future research should move from cross-sectional data to controlled, longitudinal studies that pair serological profiles with post-mortem cardiovascular histopathology.

Other individual characteristics, including sex, age group, body condition score, and coat condition were not significantly associated with vitamin D levels in this study. This contrasts with findings from previous research in chimpanzees in range-country sanctuaries [27], which reported that female chimpanzees had higher 25-OHD concentrations than males, and adults had higher concentrations than infants. In humans, elderly individuals typically have lower serum 25-OHD [48, 49], and higher body fat composition is also associated with lower vitamin D status [50]. The lack of statistically significant findings for body condition and coat condition may partly reflect the small sample size in our study due to lack of available information from participating zoos, which likely reduced statistical power. However, this study had complete coverage for sex and age category data.

Pregnancy and lactation are known to influence vitamin D status in humans, with links to deficiency [51, 52]. Similarly, the use of hormonal contraception has been associated with increased 25-OHD concentrations [53]. Similar differences due to reproductive status and obesity have also been described in other primate species [54–56]. In this study, it was not possible to ascertain the effect of contraception, pregnancy and lactation due to the sample size for these factors.

Environmental factors

UVB irradiance emerged as key determinant of vitamin D status. The majority of our samples were collected under relatively low natural UVB exposure. Average annual UVB irradiance in the natural ranges of great apes is typically $\geq 0.3 \text{ W/m}^2$ (NASA LaRC POWER Project, Data Access Viewer v2.0.0). Only 5.6% of samples in this study were from individuals exposed to comparable UVB levels in the 60 days prior to sampling. This highlights the potential inadequacy of solar UVB irradiance in Europe compared with the natural ranges of great ape species. The most southerly samples were collected at a zoo in Tenerife, which provide a valuable addition to this dataset. These samples were collected under UVB irradiance levels closer to those found in great ape natural habitats. Although only 11 samples originated from there ($n = 6$ chimpanzees; $n = 5$ gorillas), the mean UVB irradiance was 0.28 W/m^2 , double than the average of 0.14 W/m^2 across all other samples. This highlights the importance of obtaining more samples from locations that more closely match the species' natural ranges. It also supports the idea

that UVB irradiance could be a more important variable than season alone for evaluating vitamin D status, as UVB exposure can vary substantially within the same season depending on geographic location. As research expands to include a wider geographic range, including the Southern Hemisphere where seasonality patterns are reversed, UVB irradiance will provide a consistent and biologically relevant measure of solar exposure.

Seasonal effects were also significant when analysed separately, with higher concentrations observed in summer compared with autumn, winter and spring. This finding aligns with well-established knowledge about the role of UVB exposure in cutaneous vitamin D synthesis and the seasonal variability of UVB availability [21, 57]. A key challenge for European zoological institutions is also linked to seasonality: cutaneous vitamin D synthesis is not possible for part of the year at latitudes north of approximately 37°N [21]. This period may last up to two months annually at 40°N and approximately four months at 50°N [58]. Given that the median latitude of the sampling locations in our dataset was 52.2°N (range: 28.1–58.2°N), seasonal limitations on vitamin D synthesis are likely to affect a substantial proportion of zoological institutions across Europe.

Modifiable husbandry factors

While environmental and individual factors are important, these cannot readily be controlled by the institutions caring for great apes. Therefore, modifiable husbandry factors offer the highest potential to improve the health and welfare of great apes in human care.

Of these, outdoor access was significantly associated with 25-OHD concentrations: individuals provided with unrestricted outdoor access exhibit higher vitamin D levels than those with restricted access, confirming our previous, similar finding in chimpanzees [28]. Unrestricted outdoor access is increasingly recommended for non-human great apes, as it provides welfare benefits beyond those associated with sunlight exposure. For example, the EAZA Best Practice Guidelines for Chimpanzees [59] highlights the importance of outdoor access. Furthermore, the United Kingdom's recently updated Standards of Modern Zoo Practice [60] requires zoos to provide great apes with enclosures that “allow continuous 24-hour access to indoor, outdoor, and off-show areas, except for routine husbandry and in exceptional circumstances”. Providing great apes with unrestricted outdoor access is a low-cost, potentially high-impact husbandry intervention that may improve vitamin D status while conferring additional welfare benefits.

The provision of commercial pellet in the diet was another important factor for vitamin D status. This is the first study to demonstrate a clear positive impact of dietary vitamin D supplementation via pellet on vitamin D status in zoo-housed great apes, underscoring the importance of dietary fortification, particularly in regions with limited UVB availability. There is ongoing discussion in the literature regarding both the benefits and drawbacks of pellet feeding. While fortified pellets provide essential nutrients, including vitamin D, their use has also been associated with behavioural issues such as increased regurgitation and reingestion in great apes [61–64]. Consequently, some zoos have moved towards pellet-free diets, which may inadvertently compromise vitamin D status. It is highly challenging to

quantify dietary vitamin D intake at the individual level, as zoo-housed great apes are typically fed as a group, making it difficult to determine exact consumption. While this study demonstrates an overall potential benefit of supplementation via pellet, further research is needed to provide insights into its specific impact on vitamin D status. Controlled dietary studies focusing solely on changes in vitamin D intake, while minimising other husbandry changes, would be valuable for confirming these findings and guiding evidence-based management practices.

The limited data on the use of other (not pellet based) vitamin D supplements (14% of all samples) and UV-related interventions, including UV lighting and UV-permeable materials (1.3% of all samples) makes it difficult to assess the effectiveness of these interventions. However, this does not rule out their potential importance in influencing vitamin D status in zoo-housed great apes. While no published studies have explored UVB lighting or UV-permeable materials in great apes, studies in other zoo-housed taxa have demonstrated their efficacy in improving vitamin D status [65, 66]. As the awareness and implementation of various strategies to improve vitamin D status become more widespread, these are also likely to emerge as more prominent determinants of vitamin D concentrations in future research. It is important to note that the implementation of artificial UVB lighting poses significant logistical challenges, including maintenance, space constraints, and cost [67, 68], which may make it prohibitive for many, especially older, great ape facilities.

Oral supplementation, on the other hand, is a more feasible and cost-effective approach [69]. That said, results from human studies remain mixed regarding the efficacy of vitamin D oral supplementation [70–74]. It may hold potential especially in regions with limited UVB availability and in animals that are fed a pellet-free diet, though more work is needed to clarify this.

Future directions

Future research should prioritise the development of species-specific 25-OHD reference intervals and explore longitudinal changes in vitamin D status to better understand its clinical relevance to health outcomes in these species. Additionally, controlled trials investigating the efficacy of a pellet-based diet, additional dietary vitamin D supplementation, UVB lighting, and UVB permeable materials in enclosure design would offer valuable insights into evidence-based husbandry practices.

To improve the conclusions drawn for bonobos and orangutans, a higher number of samples, as well as a broader range of holding institutions from these species would be beneficial. Challenges, however, remain due to the small population size and geographical distribution of zoos holding some of the great apes species. For instance, the bonobo samples originated from five different zoos, all of which were situated in Northern Europe (latitudes $> 46^{\circ}\text{N}$), which inevitably influenced results. However, there are no zoos in Southern Europe (latitudes $< 46^{\circ}\text{N}$) currently holding this species. Expanding the geographic scope of this research to include zoos outside of Europe and incorporating range-country populations could provide a more comprehensive perspective on naturalistic vitamin D concentrations and their determinants, but only if the same methodology is used between studies in order to facilitate accurate comparisons [35, 75, 76].

Due to the potential impact of inadequate vitamin D status on health outcomes in these species, and the high prevalence of cardiovascular pathology including IMF, the relationship between cardiovascular health and vitamin D status should be more closely examined.

Conclusions

This multi-centre study is the first large scale assessment of vitamin D status in all great ape species commonly housed in human care, across a broad geographical range. Our findings demonstrate a high prevalence of inadequate vitamin D status (measured as 25-OHD serum concentration) among European zoo-housed great apes, based on the application of human reference intervals. The data confirm that modifiable husbandry parameters, especially unrestricted outdoor access, and the use of vitamin D fortified pellet in the diet, are significantly and positively associated with improved vitamin D status. These findings offer a clear evidence base for refining management practices. Bonobos and orangutans appear particularly vulnerable to low 25-OHD levels under managed care, which may necessitate targeted interventions to improve their wellbeing. Future research must focus on longitudinal monitoring to disentangle the complex relationships between systemic health, cardiovascular disease, and vitamin D metabolism in non-human great apes. Establishing species-specific reference intervals remains a priority.

Methods

Study design and setting

We conducted a multi-centre observational study using opportunistically collected serum and plasma samples from non-human great apes housed in European zoos and wildlife sanctuaries.

Study population and sampling

The study included bonobos, chimpanzees, Western gorillas, and orangutans (comprising Sumatran orangutans, Bornean orangutans, and hybrids of the two species) from 56 European zoos. Repeated samples from the same individual were included only if collected at least 60 days apart.

Sample collection occurred during routine health checks or veterinary procedures at participating institutions. Samples were frozen (-20°C to -80°C) at the zoo of origin prior to submission to this study, following which samples were stored at -80°C until analysis. All analyses were performed at the same laboratory and, where feasible, in consolidated batches to minimise analytical variability [75–77].

Sample size and demographics

480 samples from 334 individuals were retained for analysis. Table 4 shows the species-specific distributions of individuals, samples, median age and the number of zoos from which samples were collected. Of these, data from 245 chimpanzee samples were previously analysed in a single-species assessment of vitamin D status [28], while the remaining data has not been previously published.

Table 4
Species-specific counts of samples, individuals, their median ages, and origin zoos.

Species	Samples (n)	Individuals (n)	Median age (years)	Origin zoos (n)
Bonobo	49	43	18.0	5
Chimpanzee	251	147	28.0	31
Gorilla	106	85	14.5	22
Orangutan	74	59	23.0	18
Total	480	334	24.0	56

Ethical considerations and permits

Ethical approval

was obtained via the Committee for Animals and Research Ethics at the School of Veterinary Medicine and Science, University of Nottingham, UK (approval numbers SVMS 3064 200106 and 2253 18322). This research used scientific samples from zoo-housed great apes taken opportunistically while animals were anaesthetised for other clinical reasons. No animal was anaesthetised or harmed in any way for the purposes of this study. Convention on International Trade in Endangered Species (CITES) permits were obtained from the relevant authorities prior to international movement of samples as required. All methods were performed in accordance with the relevant guidelines and regulations.

Vitamin D measurement

Serum and plasma 25-hydroxyvitamin D₂ (25-OHD₂) and 25-hydroxyvitamin D₃ (25-OHD₃) were quantified using liquid chromatography–tandem mass spectrometry (LC-MS/MS) at a UK Accreditation Service-participating laboratory (Clinical Biochemistry, Manchester University NHS Foundation Trust, M13 9WL). Total 25-OHD was defined as the sum of 25-OHD₂ and 25-OHD₃. Analysis was performed using either Transcend II liquid chromatography with TurboFlow online sample preparation and a TSQ Endura tandem quadrupole mass spectrometer (Thermo Fisher Scientific), as previously described [28, 78], or using an updated analytical method in the same laboratory. For the later method, samples were prepared by adding 100 µL of Internal Standard solution (25-OHD₂-d3 and 25-OHD₃ in isopropanol/methanol (1:3.5)) to 150 µL of serum before extraction of 25-OHD₃ and 25-OHD₂ using hexane liquid-liquid extraction on an Integra Viaflo 96-well semi-automated pipetting station. Twenty microliters of the dried down and

reconstituted (66% methanol) sample extract was then injected by the Acquity Ultra-Performance Liquid Chromatography (Waters™) system and analytes separated using a Waters™ Acquity UPLC BEH phenyl (1.7µm, 2.1 x 50mm) column. Aqueous and organic mobile phases were 2 mM ammonium acetate and 0.1% formic acid in water and in methanol respectively. Mass spectrometric detection was performed using a Xevo TQD triple quadrupole mass spectrometer (Waters™) with atmospheric pressure chemical ionisation at 500°C. Reported coefficients of intermediate precision for 25-OHD₃ measurements in matrix matched quality control material were 3.8% at 34.8 nmol/L, 5.2% at 81.7 nmol/L and 4.0% at 121.0 nmol/L. The lower limit of quantitation for both 25-OHD₃ and 25-OHD₂ was 5 nmol/L.

Continuity of results between the methods was confirmed during validation of the new method with sample comparison studies and analysis of prior samples from the External Quality Assessment Schemes together with ongoing performance assessment.

Clinical interpretation adopted human reference intervals due to the absence of great ape-specific reference intervals: deficient (< 25 nmol/L), insufficient (25–50 nmol/L), adequate (51–75 nmol/L), optimal (> 75 nmol/L) [22, 79].

Animal and environmental data

For each sample, data was collected on individual animal characteristics (name/ID, species, sex, age, coat quality, health status, reproductive status (contraception, pregnancy, lactation), body condition score (BCS, on a scale of 1–9, with 1 being emaciated and 9 being morbidly obese, 5 marking ideal BCS) and modifiable husbandry factors (whether the diet included commercial pellet (pre-formulated, typically nutritionally complete animal feed made of compressed ground ingredients), other oral vitamin D supplementation, provision of artificial UVB lighting, presence of UV-permeable materials in the animal's enclosure). Due to the sample size, all orangutan data were analysed as a single species.

Mean UVB irradiance (Daily All Sky Surface UVB irradiance, W/m²) at the sampling location for the 60 days preceding sampling was obtained from NASA's Langley Research Center Prediction of Worldwide Energy Resources (POWER) Project Data Access Viewer using zoo-specific latitude and longitude (from Species360 ZIMS). The starting date for each 60-day window was determined using an online date calculator (Time and Date AS, 1995–2024). For mapping of sample origins relative to global annual mean UVB (J/m²; 2004–2013), gridded data were downloaded [80] and visualised in QGIS Desktop v2.18.28. Distribution of samples and the corresponding average UVB irradiation is shown on Fig. 4.

Seasons were defined as spring (21 March–20 June), summer (21 June–21 September), autumn (22 September–20 December), and winter (21 December–20 March). Age groups were defined as juvenile (< 15 years), adult (15–34 years), and elderly (> 34 years), consistent with great ape life-history literature [15, 81–84].

Data analysis

Data were collated using Microsoft Excel. Values reported below the assay limit of detection (< 5 nmol/L) were assigned 5 nmol/L to conservatively enable inclusion while avoiding underestimation.

To account for the repeated measures of vitamin D levels within the same individuals, we used mixed effects models with a random effect for each individual. The analyses were performed with R version 4.4.1 and the lme4 package for mixed effects models, which were optimised via the restricted maximum likelihood (REML) criterion. There is no requirement for normality of the outcome variable for these models, instead normality of the model residuals was assessed to establish model fit. Package lmerTest was used for significance testing and degrees of freedom estimation, using the conservative Satterthwaite method [85].

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Declarations

Data availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Conflict of interest statement

The authors declare no competing interests.

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Author contribution statement

M.L. and K.B. conceived the original idea and designed the study. R.J.M. managed sample collection and was responsible for general project management. S.B. provided the statistical analysis. C.R. conducted the laboratory analysis. P.D., M. L. and S. M collected samples. R.J.M. and M.L. drafted the manuscript. All authors substantively revised the work, approved the final submitted version, and have agreed to be personally accountable for their own contributions. Furthermore, all authors ensure that questions related to the accuracy or integrity of any part of the work are appropriately investigated, resolved, and the resolution documented in the literature.

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Figures

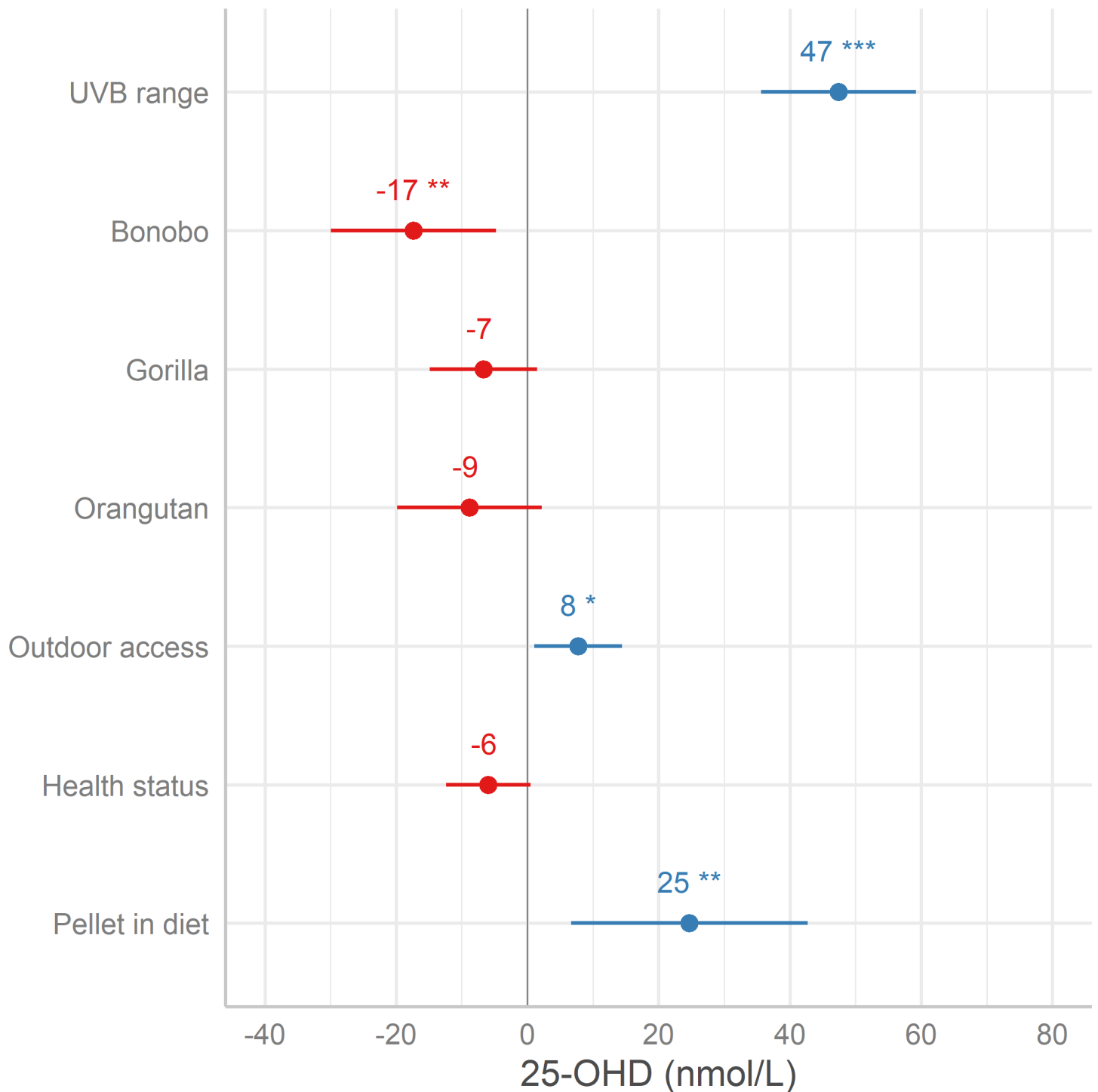


Figure 1

Main effects (filled circle with effect size above) and 95% confidence intervals (horizontal bands) of the key predictors of 25-OHD levels. For the species comparison, chimpanzees were used as the reference value (not shown). The effect size for UVB is over the entire range of measured values, i.e. the difference between lowest and highest UVB exposure in the sample (0.45 W/m^2).

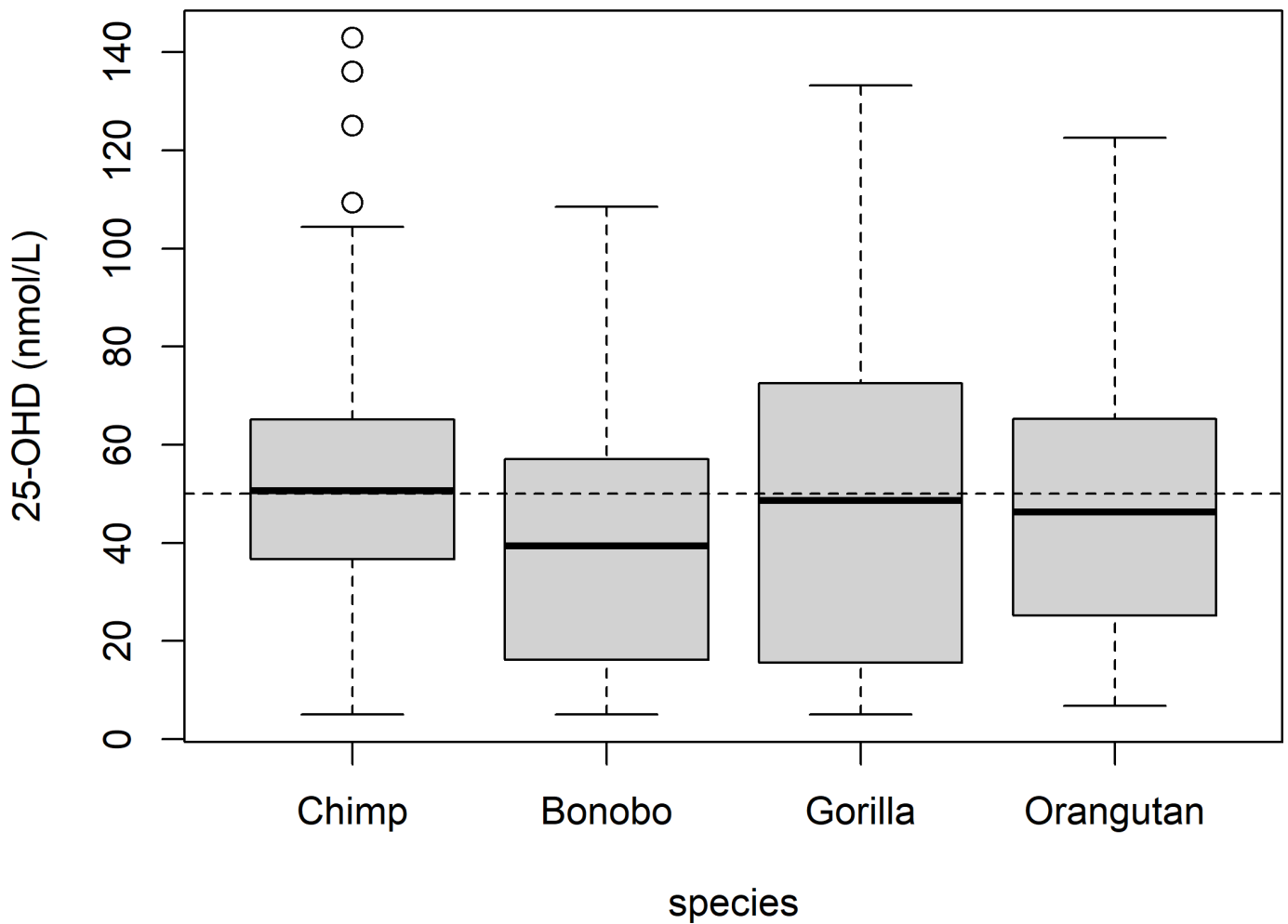


Figure 2

Uncorrected seasonal 25-OHD levels per species. The dashed horizontal line indicates the hypothetical reference level of 50 nmol/L, below which vitamin D status was considered inadequate (deficient or insufficient).

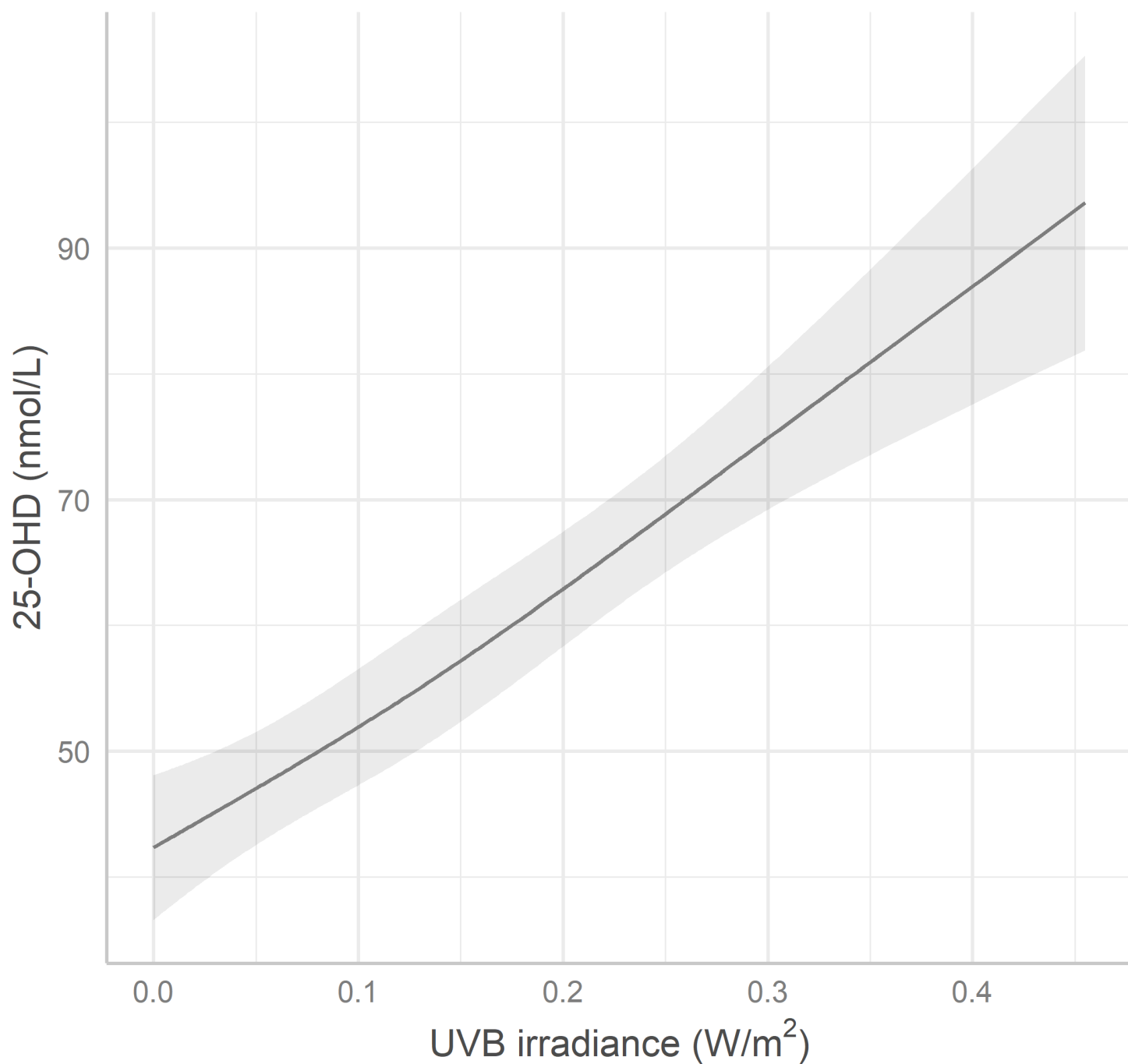


Figure 3

The relationship between UVB irradiation and 25-OHD levels. Even though a non-linear term was included, it was not significant, and there is no indication of a plateau at higher UVB irradiation levels.

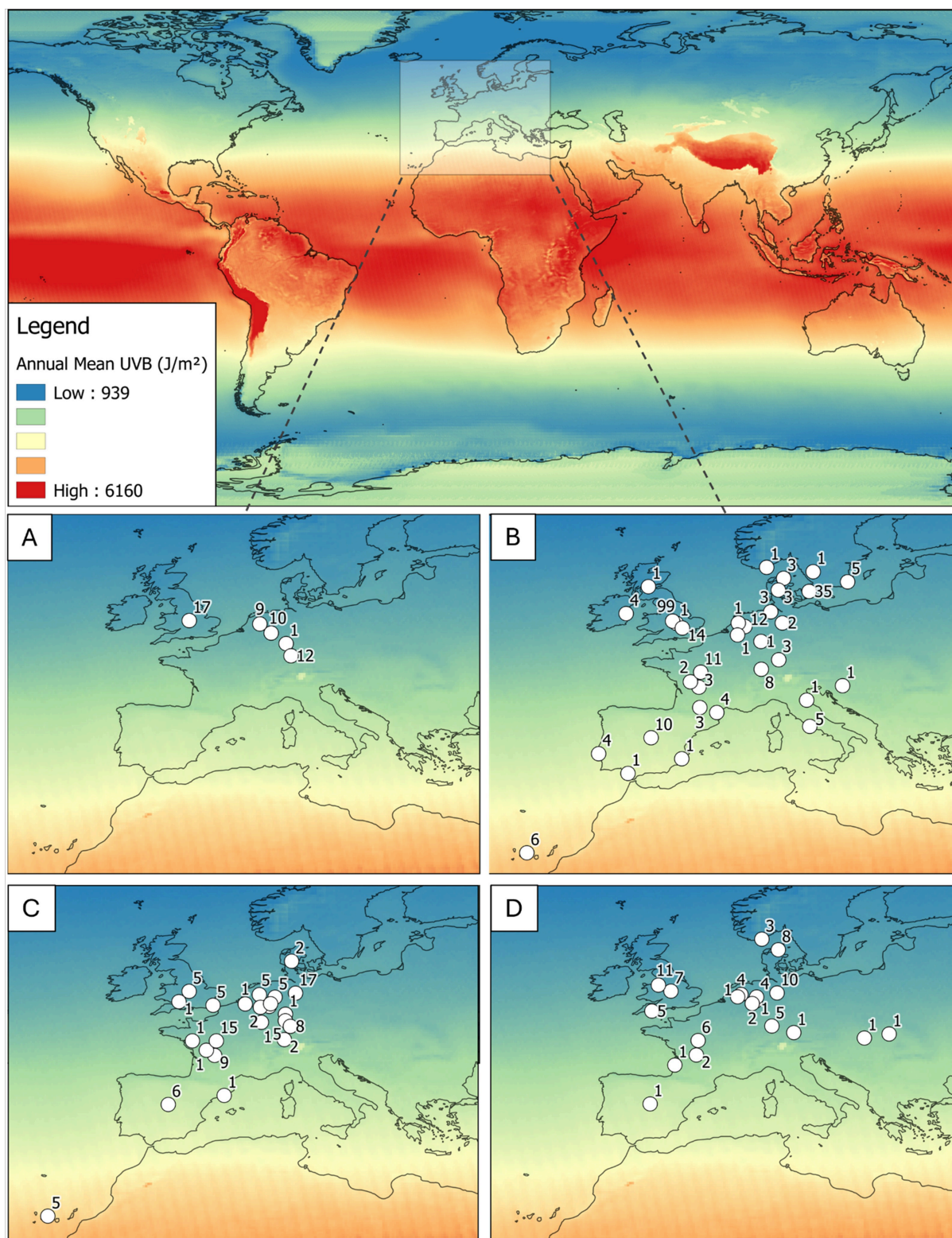


Figure 4

Distribution of sampling locations and sample sizes for each location in relation to the global annual mean ultraviolet B irradiation (J/m²; 2004–2013). Numbers next to each sampling location indicate sample size from that location.