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DIVERSITY, DISTRIBUTION, AND MICROCLIMATIC CONDITIONS EXPERIENCED BY THE CHAMELEONS OF THE VOHIMANA RESERVE, MADAGASCAR

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***Abstract*.—Madagascar harbors exceptional chameleon diversity, yet detailed ecological and microclimatic data remain scarce for many species. We conducted an extensive field survey of chameleons in the Vohimana Reserve, eastern Madagascar, combining species inventories, habitat characterization, and fine-scale microclimatic measurements across primary forest, secondary forest, and Eucalyptus plantations. Over 195 survey days, we recorded 577 individuals representing at least 12 species from three genera (*Brookesia*, *Calumma*, and *Furcifer*), including the first confirmed record of the Panther Chameleon (*Furcifer pardalis*) for the reserve. Species showed pronounced differences in habitat use: *Brookesia* species, the Forked Chameleon (*Calumma furcifer*), and, to a lesser extent, the Pinocchio Chameleon (*C. pinocchio*) were strongly associated with undisturbed primary forest, characterized by higher and less variable Normalized Difference Vegetation Index (NDVI) values, whereas other taxa were more prevalent in secondary habitats. Microclimatic conditions measured at observation sites varied seasonally but differed only modestly among the most abundant species, suggesting that habitat structure and vegetation integrity may be more influential than microclimate alone in shaping species distributions. Nevertheless, species associated with dense forest were consistently exposed to lower temperatures and UV indices. Seasonal variation in detectability further emphasized species-specific ecological strategies. Together, our results highlight the importance of preserving intact primary forest, fine-scale habitat heterogeneity, and microclimatic stability for chameleon conservation, and provide critical baseline data for habitat suitability modeling and future in situ and ex situ conservation planning.**

Key Words.—*Brookesia*, *Calumma*, *Furcifer*, habitat preference, microclimate

Résumé.—Madagascar abrite une diversité exceptionnelle de caméléons, mais les données écologiques et microclimatiques détaillées restent rares pour de nombreuses espèces. Nous avons mené une vaste étude de terrain sur les caméléons dans la réserve de Vohimana, à l'Est de Madagascar, combinant l'inventaire des espèces, la caractérisation des habitats et des mesures microclimatiques dans la forêt primaire, la forêt secondaire et les plantations d'*Eucalyptus*. Au cours de 195 jours d'étude, nous avons recensé 577 individus représentant au moins 12 espèces appartenant à trois genres (*Brookesia*, *Calumma* et *Furcifer*), dont la première observation confirmée du Caméléon panthère (*Furcifer pardalis*) dans la réserve. Les différentes espèces ont présenté des différences marquées dans leur utilisation de l'habitat : les espèces du genre *Brookesia*, le Caméléon fourchu (*Calumma furcifer*) et, dans une moindre mesure, le Caméléon pinocchio (*C. pinocchio*) étaient fortement associés à la forêt primaire intacte, caractérisée par des valeurs plus élevées et moins variables de l'indice de végétation par différence normalisée (NDVI), tandis que les autres taxons étaient plus répandus dans les habitats secondaires. Les conditions microclimatiques mesurées sur les sites d'observation variaient selon les saisons, mais ne différaient que modérément entre les espèces les plus abondantes, ce qui suggère que la structure de l'habitat et l'intégrité de la végétation peuvent avoir une influence plus importante que le microclimat seul sur la répartition des espèces. Néanmoins, les espèces associées à la forêt dense étaient systématiquement exposées à des températures et à des indices UV plus faibles. Les variations saisonnières de la détectabilité observées soulignent les stratégies écologiques spécifiques à chaque espèce. D'une manière générale, nos résultats soulignent l'importance de préserver la forêt primaire intacte, l'hétérogénéité fine de l'habitat et la stabilité microclimatique pour la conservation des caméléons, et fournissent des données de référence essentielles pour la modélisation de l'adéquation des habitats et la planification future de la conservation in situ et ex situ.

Mots-clefs.—*Brookesia*, *Calumma*, *Furcifer*, préférence d'habitat, microclimat

INTRODUCTION

The relationship between environmental factors and physiological mechanisms in ectotherms is complex and multifaceted (Huey 1991; Rozen-Rechels 2019; Sokolova 2021). Temperature, relative humidity, light intensity, and substrate composition are just a few of the environmental variables that exert potential profound effects on ectotherm physiology, specifically reptiles and amphibians, influencing metabolic rates, reproductive behavior, immune function, and overall fitness (Huey 1982, 1991; Angilletta et al. 2002; Angilletta 2009). Temperature governs aerobic metabolism and performance (Huey 1982), while humidity dictates thermo-hydroregulation, forcing dehydrated reptiles to lower their body temperature to limit evaporation (Sannolo and Carretero 2019). Skin permeability plastically can be adjusted according to variations in humidity (Weaver et al. 2023) and water stress can trigger muscle catabolism to release internal water (Dezetter et al. 2023). Finally, visible light can strongly influence behavior and hormonal balance in reptiles and amphibians (Bagnara and Hadley 1970; Tosini and Menaker 1998). Moreover, UV-B radiation (290–315 nm) exposure is vital for many reptiles for vitamin D3 endogenous synthesis, which activates immunity and regulates hormonal cycles (Brames 2007). To ensure the survival of the individual, these parameters must fall between a minimum and maximum value beyond which the physiological function of the individual is compromised (Angilletta 2009; Baines et al. 2016; Weaver 2023). High and low limits are specific to each species and sometimes different between populations of the same species (Marquis et al. 2008; Cocciardi 2024; Schultz 2024).

Beyond these physiological limits, the spatial and temporal variations of these climate parameters are strong environmental constraints constituting important evolutionary forces, which can lead to strict habitat preferences and local adaptations. For example, the Labord's Chameleon (*Furcifer labordi*) synchronizes its egg laying and hatching with rainfall, and juvenile growth can accelerate in response to seasonal delays of rain (Raselimanana et al. 2021). Also, the Asp Viper (*Vipera aspis*) selects humid refuges to counteract drought (Dezetter et al. 2023) and Blackbelly Garter Snake (*Thamnophis melanogaster*) exploits the thermal inertia of water to stabilize its temperature with less metabolic effort than terrestrial snakes (Figueroa-Huitrón et al. 2024). Preferences for certain habitats and microhabitats are the consequence of the selection of very specific environmental conditions essential to the life of the animal (Hyslop et al. 2009; Scheffers et al. 2014; Hecker et al. 2020) and certain species can have very specific environmental requirements that must be understood to properly comprehend their environmental preferences and understand how they could react to environmental changes.

Arboreal species with low dispersal capacities such as chameleons are subjected to local ambient climate more than terrestrial species that can use burrows or can hide under stones or logs (Hyslop et al 2009; Guillon et al 2014; Hecker et al 2020). Indeed, chameleons can have strict habitat preferences (Houniet 2007, 2009) with strong local adaptations to microhabitat (Randrianantoandro et al. 2007; da Silva et al. 2014; Ebrahim 2022; Barends et al 2025) but information about the microclimatic conditions corresponding to these microhabitats are few. Knowing the species-specific climatic needs is crucial for helping to identify suitable habitats (Stark and Fridley 2022), predicting the potential distribution of one species across different regions (Strangas 2019), informing how these species may respond to shifts in local climatic conditions (Böhm 2016; Seebacher 2023), and establishing protected areas (Anderson and Chapple 2026). Also, building healthy and sustainable captive populations for *ex-situ* conservation programs requires a detailed understanding of the environmental needs of species (Loughman 2020).

With at least 98 endemic species of chameleons, Madagascar hosts 44% of the total diversity of this group (Tolley et al. 2013; http://www.reptile-database.org), many of which remain poorly known, some yet to be described (Antonelli et al. 2022), and all endemic to the island (Roll et al. 2017). These reptiles have evolved intricate physiological and behavioral adaptations to thrive in diverse habitats, including forests, savannas, and even urban environments. Unfortunately, this unique diversity is largely threatened by habitat destruction (Mondanaro et al. 2024) and climate change (Dubos et al. 2025). It is therefore important and urgent to study the ecological specificities of the different species to better understand their needs, an essential prerequisite for species protection. Selecting study areas in regions where the diversity of chameleon species is high is the fastest and most efficient way to obtain maximum information in minimum time.

The mid-elevation humid forests of central-eastern Madagascar are especially rich in herpetofauna.

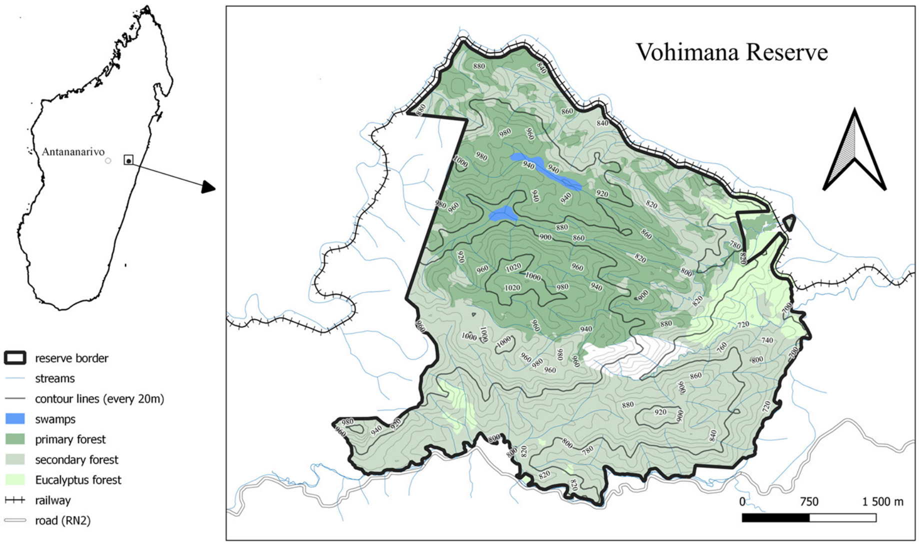

Figure 1. Location of the Vohimana Reserve in eastern Madagascar. (Map drawn with Qgis software, version 3.16 Hannover).

Situated within the Ankeniheny-Zahamena forest corridor, one of the largest remaining contiguous rainforests in the mid-eastern region of Madagascar (Portela 2012), the area around Andasibe, including Vohimana Reserve, is particularly known for its amphibian and reptile species richness including chameleons (Jenkins et al. 2014; Brown et al. 2016; Antonelli et al. 2022) and therefore constitutes an ideal study area. By highlighting the complex interaction between chameleons and their microenvironments, we aim to contribute to a deeper understanding of the ecological needs of these emblematic Malagasy reptiles and underscores their vulnerability to rapid environmental change. Our main objectives are: (1) to complete the inventory of chameleon species present in the Vohimana reserve; (2) to collect initial data on their distribution and possible habitat preferences; and (3) to collect reference values for three key climatic factors (i.e., temperature, relative humidity and ultraviolet index) specific to each of the chameleon species found in the Vohimana reserve.

MATERIAL AND METHODS

Study site.—We studied chameleons in Vohimana Reserve (18.9289S, 48.4996E), a 1,500 ha protected area in eastern Madagascar at 800–1,000 m elevation (Fig. 1). The reserve contains one 600 ha zone of preserved primary forest in the center surrounded by 840 ha of secondary forest patches that were previously heavily logged and 108 ha of fragmented non-native Eucalyptus (Fig. 1). The main core forest is dense and situated on an inclined succession of ridges and valleys perpendicular to the east coast. The satellite patches of secondary forest typically contain a high proportion of introduced trees, shrubs, and herbaceous plants (pers. obs.).

This specific region of Madagascar is relatively cool and humid all year round. The climate of the Vohimana Reserve is characterized by an absence of a real dry season with an average annual precipitation of 1,850 mm and an average annual temperature of 20.4° C (Klanderud et al. 2010). Historical meteorological data extraction from the U.S. National Aeronautics and Space Administration (NASA) website (https://power.larc.nasa.gov) show two seasons can be distinguished: a cold winter with low rainfalls from May to October (mean monthly temperature between 2001 and 2020 = 19.7° C), alternating with a summer when temperatures rise and rainfall intensifies from October to May (mean monthly temperature between 2001 and 2020 = 23.8° C).

Study species and identification.—As no published inventory of the Chameleons of the Vohimana Reserve currently exists, we only had a partial idea of the species present in the reserve, based on two previous inventories carried out in 2016 and between November 2018 and February 2019 (Oscar Hadj-Bachir, unpubl. data). Thanks to these preliminary data, we expected to potentially encounter 12 species of chameleons: Brown Leaf Chameleon (*Brookesia superciliaris*), Permet Leaf Chameleon (*B. therezieni*), Domergue's Leaf Chameleon (*B. thieli*), Ramanantsoa's Leaf Chameleon (*B. ramanantsoai*), Short-horned Chameleon (*Calumma*

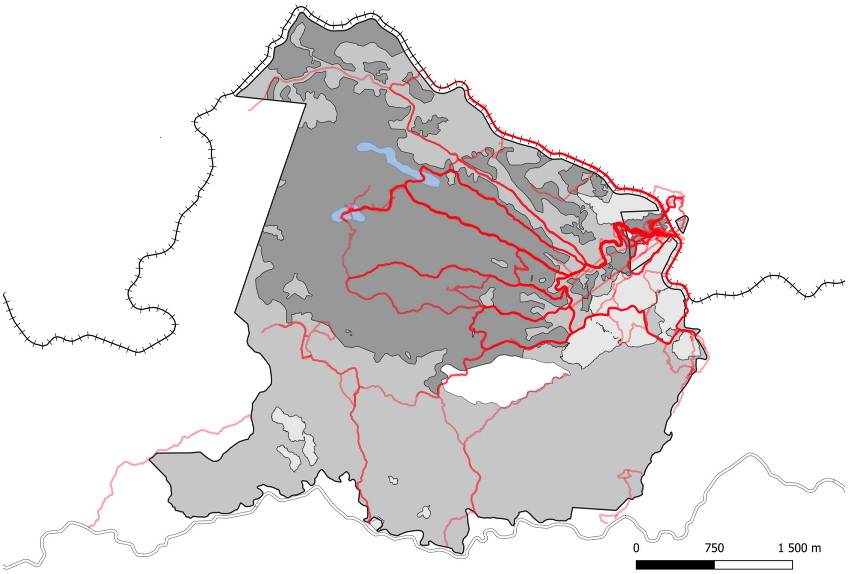

Figure 2. GPS tracks recorded during this study in the Vohimana Reserve in eastern Madagascar. The intensity of the color indicates the frequency of use of the path during the surveys. (Map drawn with Qgis software, version 3.16 Hannover).

brevicorne), Forked Chameleon (*C. furcifer*), Lance-nosed Chameleon (*C. gallus*), Perinet Chameleon (*C. gastrotaenia*), Nose-horned Chameleon (*C. nasutum*), Parson's Chameleon (*C. parsonii*), Fork-nosed Chameleon (*Furcifer bifidus*) and Canopy Chameleon (*F. willsii*). It must be taken into consideration that *C. gallus* has recently been divided into *C. gallus* and the Pinocchio Chameleon (*C. pinocchio* ; Glaw et al. 2025). Individuals previously identified as *C. gallus* in the Vohimana region are now considered *C. pinocchio*. During fieldwork, local staff photographed each chameleon and recorded preliminary species identifications based on their field expertise and helped by the literature (Glaw and Vences 2007; Prötzel et al. 2020; Glaw et al. 2025). We then reviewed all photographs to confirm species-level assignments. As the distinction between certain species based on field pictures can be challenging with regard to the *C. nasutum* group (Prötzel et al. 2020; Glaw et al. 2025) or between *B. superciliaris* and *B. therezieni* (Ratsoavina et al. 2010) some identifications were conservatively assigned to species groups to avoid misclassification. As a result, we grouped all species resembling *C. nasutum* under the term *C. nasutum* group and all species resembling *B. superciliaris* under the term *B. superciliaris* group (potentially including *B. superciliaris* and *B. therezieni*).

Data collection.—We conducted Visual Encounter Surveys during day and night with help of experienced selected team of local guides. Existing paths in both the core forest and the fragmented forest patches were used as transects to search for chameleons. Due to the density of the forest, we assumed that the vegetation along the paths was representative of the whole forest. Each survey session consists of a 2–8 h walk depending on how far we had to go in the reserve randomly selected among the possible main paths crossing the reserve. We used GPS to record tracks used during the field sessions (Fig. 2), which represented a total of approximately 350 km of walking, each track being used multiple times. Due to the difficulty of accessing certain remote paths, not all paths could be used with the same frequency. We visited the three main types of habitats: (1) 48% of time surveying primary forest; (2) 30.4% of time in secondary forest; and (3) 21.6% in eucalyptus forest.

We conducted 195 d of field work, 158 during the summer and 37 during winter, spread across 2023 and 2024. Specifically, we conducted summer fieldwork from 12 January to 14 April 2023 (92 d) and 26 February to 2 May 2024 (66 d), and winter fieldwork 13–25 July 2023 (12 d) and 9 July to 3 August 2024 (25 d). Because the detectability of the chameleons is much higher during the night, we conducted 80% of searches then.

We photographed all individuals from the side to clarify or confirm species identification and recorded the GPS point with a Garmin 64S unit (Garmin Ltd., Schaffhausen, Switzerland). The stage of development was estimated by eye between newborn (e.g., several days after eclosion), juvenile (e.g., intermediate size between newborn and adult), and adult. To minimize disturbance to the animals, we did not handle or capture animals. We used a Kestrel 5000 (Nielsen-Kellerman, Boothwyn, Pennsylvania, USA) to record air temperature and relative humidity at the location of the animal. During daytime, we also recorded ultraviolet B dose by the sun at the exact position of the animal by measuring the Ultraviolet index (UVI) at which the animal was exposed at the time of its observation with a UVI radiometer Solarmeter® 6.5 (Solar Light Company, LLC, Glenside, Pennsylvania, USA). To complete the delimitation of the major habitat types established by the reserve (primary forest, secondary forest, and Eucalyptus forest), we used the NDVI (Normalized Difference Vegetation Index) to estimate plant productivity of the areas where we found chameleons. We derived NDVI data from Sentinel-2 surface reflectance imagery (Level-2A) provided by the Copernicus Program and processed on the Google Earth Engine platform (Gorelick et al. 2017). We used the December 2024 COPERNICUS/S2_SR_HARMONIZED dataset filtered for cloud coverage (< 20%) over the Andasibe–Beforona region (eastern Madagascar).

Data analysis.—We used R software (R 4.3.3; R Core Team 2024) for descriptive statistics, graphs, and statistical tests. We statistically analyzed comparisons among species of the mean climatic values (i.e., temperature, relative humidity, and UV index) and of the NDVI value only on species with the highest number of observations (> 20). Prior to applying statistical tests of comparisons, normality of the distribution of data was confirmed by a Shapiro-Wilk Test and the homogeneity of the variances was verified by a Levene's Test. For climatic values, we used a Factorial Analysis of Variance to account for the season (winter versus summer) and the time of the day (day versus night). Pairwise comparisons between species were done with a corrected *post-hoc* Tukey test. Given the non-normality of some distributions of the NDVI, we used a Kruskal-Wallis Test followed by a Dunn's *post-hoc* Test.

To assess whether the number of chameleon observations differed between seasons for the most abundant species (> 20 records), we used Generalized Linear Models (GLMs) with a Poisson error distribution. The number of observation days per season was included as a log-transformed offset to correct for unequal sampling effort between summer and winter. We checked for overdispersion by comparing the residual deviance to the residual degrees of freedom; when overdispersion was detected, negative binomial models were fitted instead. For the global analysis, we included species identity as a fixed factor to account for interspecific differences in observation rates. For species-specific analyses, we fitted separate GLMs for each abundant species to estimate seasonal differences in observation rates and their confidence intervals. For all tests, $\alpha = 0.05$.

RESULTS

We made 577 observations of chameleons of three genera: 152 observations of *Brookesia* chameleons; 403 of *Calumma* chameleons; and 22 *Furcifer* chameleons (Table 1). Four species of the genus *Brookesia* (Supplemental Information Fig. S1), three species of the genus *Furcifer* (Supplemental Information Fig. S2), and four species of the genus *Calumma* (Supplemental Information Fig. S3) were formally identified by at least one individual with expertise with these species. Despite the identifying characteristics described in the literature for the *C. nasutum* group (Glaw et al. 2025; Prötzel et al. 2020), we had too much doubt about the identification of the different species because of divergent identification based on our photographs. Conservatively, we did not attempt to distinguish the species that remain within the *C. nasutum* group (Supplemental Information Figs. S4, S5). Further studies will need to be conducted to clarify the diversity of *C. nasutum* species present in the Vohimana Reserve.

Of the 12 species of chameleons identified during the previous inventory, we were able to confirm 11. Unless it was mentioned in the previous inventory, *Calumma gastrotaenia* was not found during our field surveys, while numerous *C. furcifer* were identified, suggesting that the mention of *C. gastrotaenia* in the previous inventory was probably the result of an identification error. Finally, the presence of *Furcifer pardalis* was confirmed for the first time in Vohimana Reserve.

The number of observations varied significantly among species. The most frequently observed species (i.e., over 100) were those in the *B. superciliaris* group

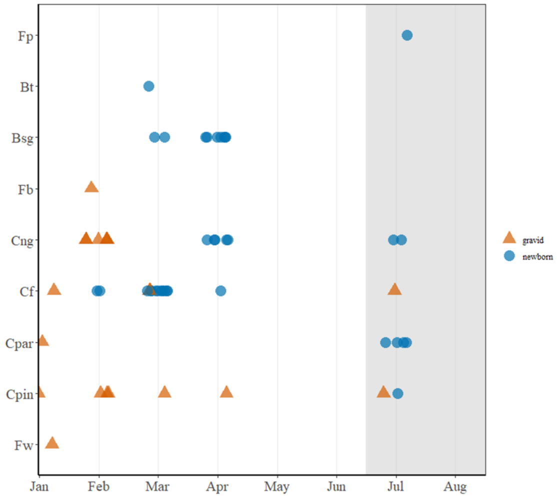

Figure 3. Chronology of observations of pregnant females (orange triangles) and newborns (blue dots) observed during the study in the Vohimana Reserve in eastern Madagascar. Grey area represents the winter field survey period. No observations were made between April and July because no field surveys were carried-out during this period. Species are Fp = Panther Chameleon (*Furcifer pardalis*), Bt = Domergue's Leaf Chameleon (*Brookesia thieli*), Bsg = Brown Leaf Chameleon group (*Brookesia superciliaris* group), Fb = Fork-nosed Chameleon (*Furcifer bifidus*), Cng = Nose-horned Chameleon group (*Calumma nasutum* group), Cf = Forked Chameleon (*Calumma furcifer*), Cpar = Parson's Chameleon (*Calumma parsonii*), Cpin = Pinocchio Chameleon (*Calumma pinocchio*), and Fw = Canopy Chameleon (*Furcifer willsii*).

and the *C. nasutum* group, and *C. pinocchio* (Table 1). After these three taxa, *C. furcifer* and *C. parsonii* are two species seen with moderate frequency. Finally, all other species were observed only sporadically (Table 1). We mainly observed adult individuals but also some animals of various growth stage and even some gravid females. Newborns and gravid females were observed in varying numbers depending on the species and at different seasons (Fig. 3, Table 1). For *B. superciliaris* group and *C. furcifer*, we found newborns only in summer, whereas *F. pardalis*, *C. parsonii* and *C. pinocchio* we found only in winter, and we found the *C. nasutum* group in both seasons. Gravid females were mainly observed in summer except for *C. furcifer* and *C. pinocchio* for which we found gravid females in both seasons.

***Habitats characteristics and species distribution*.**—Our data show that the different species do not all have identical distributions, some being relatively localized and others more widespread (Fig. 4). Animals from the *B. superciliaris* group and *C. furcifer* were very rarely found outside primary forest (Fig. 5). Despite several sparse observations, the majority of the *C. pinocchio* were found in a small patch of vegetation in the north-east of the reserve. All the other species seem less specifically linked to the primary forest and were found extensively or exclusively in secondary habitats. NDVI index ranged from 0.15 to 0.84 with a mean value at 0.69. The mean NDVI is 0.68 ± (standard error) 0.11 for *C. parsonii* (n = 24), 0.63 ± 0.13 for *C. nasutum* group (n = 207), 0.73 ± 0.07 for *C. pinocchio* (n = 118), 0.75 ± 0.03 for *B. superciliaris* group (n = 143), and 0.77 ± 0.03 for *C. furcifer* (n = 53; Fig. 6). *Calumma furcifer* was found significantly more often in areas with the highest NDVI compared to other species (Table 2). Individuals of the *B. superciliaris* group live in areas with NDVI similar to *C. pinocchio* but higher than the *C. nasutum* group and *C. parsonii*, but the differences are not significant (Table 2).

***Climatic and microclimatic data*.**—Independently of the season, microclimatic data recorded directly next to the chameleons ranged from 12° C to 31° C (mean = 22.3° C), 38% to 100% (mean = 91.7%) relative humidity, and a UVI of 0 to 13.8 (mean = 0.3). During winter, animals were exposed to relatively low temperature (mean = 18.3° C ± 2.4° C) compared to summer (24.2° C ± 1.8° C) and to a higher UVI exposure level in summer (mean = 0.5 ± 1.5) compared to winter (mean = 0.1 ± 0.2). The mean atmospheric humidity remained relatively high all year (93.3% ± 7.4% in winter, 90.9% ± 7.8°C in summer).

Variation in microclimatic variables among species were relatively low (Fig.7, Table 3). The highest daytime and night-time temperatures during the summer were recorded for *F. pardalis* (29° C during the day and 25° C at night) and *F. willsii* (27.5° C during the day and 25.2° C at night). Temperatures were also associated with the highest UV index values during the day with 8.2 for *F. pardalis* and 7.7 for *F. willsii* (Table 3), but low number of observations for these two species (Table 1) precluded statistical analysis. Microclimatic parameters differed significantly for where *B. superciliaris* group, *C. nasutum* group, *C. furcifer*, *C. parsonii* and *C. pinocchio* were found (Table 4), although the differences among species often represented relatively minor climatic variations among species with a maximum difference observed of 2.3°C, 19.97% relative humidity and 1.15 units of UV index. The *C. nasutum* group was involved in the most significant differences, which is exposed to higher temperatures and UV indices compared to other species. Conversely, *C. furcifer* and individuals of the *B. superciliaris* group are generally exposed to

Table 1. Cumulative observations made for each species of chameleon found in Vohimana Reserve, eastern Madagascar, according to the season and stage of development in the over 195 d of surveys during 2023–2024. Note 1 = not directly observed by our team but confirmed by photographs, note 2 = including *B. superciliaris* or *B. therezieni*, note 3 = possibly including *C. radamanus*, *C. fallax*, and *C. hofreiteri*, and note 4 = first observation in the reserve.

		Stage			
Species	Season	adult	juvenile	newborn	Total
Short-horned Chameleon *Calumma brevicorne*	summer	0	0	0	1
	winter	1	0	0	
Canopy Chameleon *Furcifer willsii*	summer	3	4	0	7
	winter	0	0	0	
Ramanantsoa's Leaf Chameleon *Brookesia ramanantsoai*[1]	summer	0	0	0	2
	winter	2	0	0	
Domergue's Leaf Chameleon *B. thieli*	summer	6	1	0	7
	winter	0	0	0	
Brown Leaf Chameleon group *B. superciliaris group*[2]	summer	136	1	0	143
	winter	3	3	0	
Forked Chameleon *Calumma furcifer*	summer	16	0	11	53
	winter	10	16	0	
Nose-horned Chameleon group *C. nasutum group*[3]	summer	124	5	0	207
	winter	61	15	2	
Parson's Chameleon *C. parsonii*	summer	4	7	0	24
	winter	9	0	4	
Pinocchio Chameleon *C. pinocchio*	summer	55	4	0	118
	winter	47	11	1	
Fork-nosed Chameleon *Furcifer bifidus*	summer	2	1	0	11
	winter	0	8	0	
Panther Chameleon *F. pardalis*[4]	summer	3	0	0	4
	winter	0	0	1	

lower temperatures and UV indices (Fig. 7, Tables 3 and 4).

***Seasonal detectability variations*.—**Our data show important variations in the number of observations made between winter and summer in the different habitats among species (Fig. 5, Table 1). Among the most frequently observed species (total observations > 20), seasonal differences in chameleon observation rates were significantly different for five species after accounting for unequal sampling effort. We observed four species of *Calumma* more frequently in winter than in summer. *Calumma furcifer* was observed 4.11 times more frequently in winter than summer ($Z = 5.11$, df = 1, $P < 0.005$), *C. nasutum group* 2.58 times ($Z = 6.76$, df = 1, $P < 0.005$), *C. parsonii* 5.05 times ($Z = 4.03$, df = 1, $P < 0.005$), and *C. pinocchio* 4.27 ($Z = 8.05$, df = 1, $P < 0.005$). On the other hand, *Brookesia superciliaris group* was the only taxa observed less frequently in winter than in summer with a ratio of 5.26 ($Z = 4.0$, df = 1, $P < 0.005$).

DISCUSSION

Despite clear technical and methodological limitations of this study (i.e., species identification difficulties, absence of individual marking and imbalance in the frequency of visits to the different

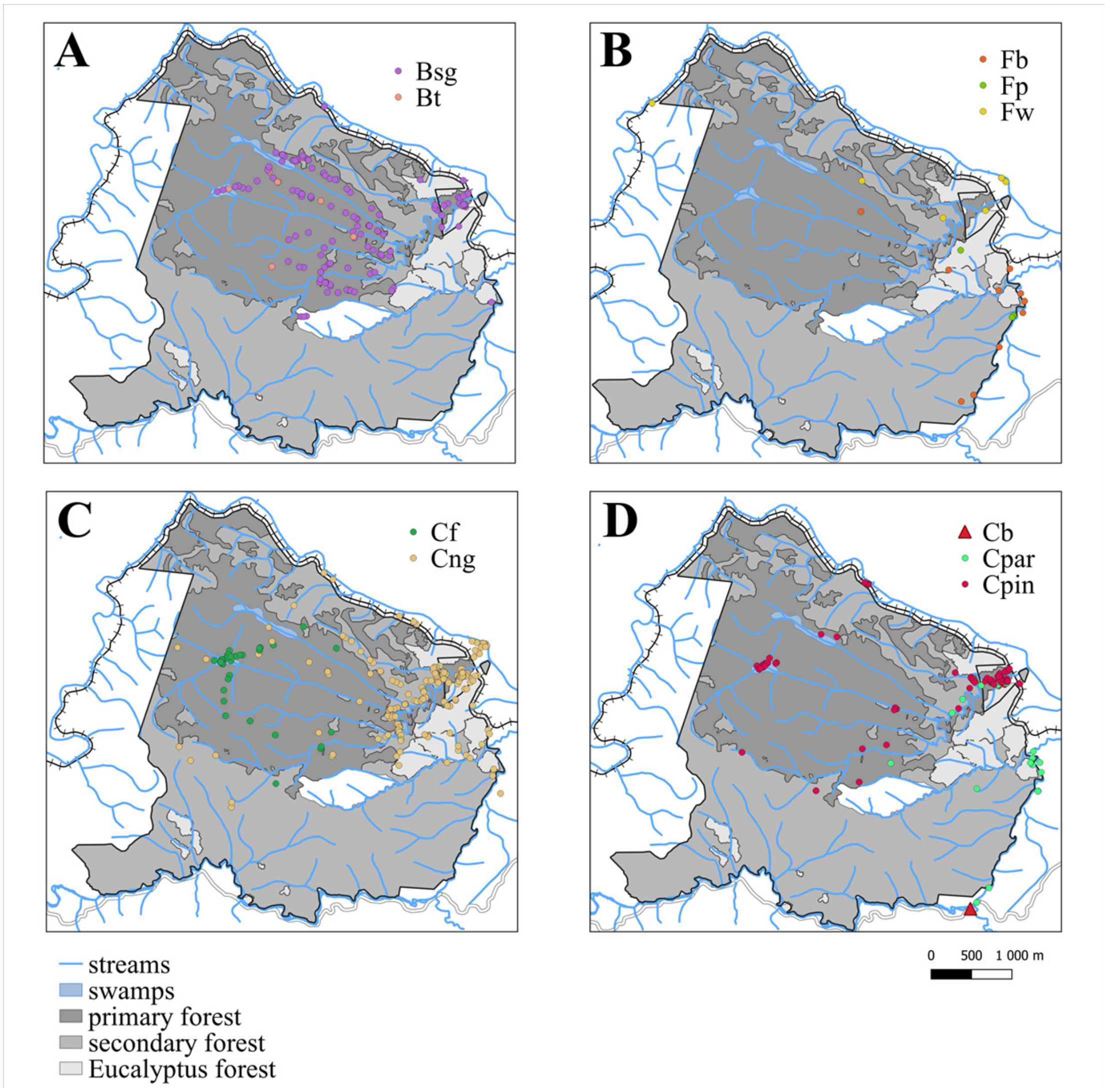

Figure 4. Geographic distribution of chameleon observations in Vohimana Reserve, eastern Madagascar, plotted by genus: (A) *Brookesia* and (B) *Furcifer*. For greater legibility, species of the *Calumma* genus have been divided on maps C and D. Species are Bsg = Brown Leaf Chameleon group (*Brookesia superciliaris* group), Bt = Domergue's Leaf Chameleon (*Brookesia thieli*), Fp = Panther Chameleon (*Furcifer pardalis*), Fb = Fork-nosed Chameleon (*Furcifer bifidus*), Fw = Canopy Chameleon (*Furcifer willsii*), Cng = Nose-horned Chameleon group (*Calumma nasutum* group), Cf = Forked Chameleon (*Calumma furcifer*), Cpar = Parson's Chameleon (*Calumma parsonii*), Cpin = Pinocchio Chameleon (*Calumma pinocchio*), Cb = Short-horned Chameleon (*Calumma brevicorne*). Each point corresponds to one observation. (Maps were drawn with Qgis software, version 3.16 Hannover).

environments), our study has yielded unprecedented data on the species diversity and distribution of the chameleons of the Vohimana reserve, habitat characterization and microclimatic conditions to which the animals are subjected. During the study, 12 species were confidently identified. Within the *C. nasutum* group, we suspect the presence of different species, but a clear identification of the species would need a specific study. The suspected species within the *C. nasutum* group are the Ambatond'Radama Nosed Chameleon (*C. radamanus*), the Angozongahy Nosed Chameleon (*C. emelinae*), the Hofreiter's Chameleon (*C. hofreiteri*), and possibly the Deceptive Chameleon (*C. fallax*), although this would require specific study to confirm. Furthermore, in addition to identifying the species within the *C. nasutum* group, it appears that these species are morphologically very similar and live in sympatry, and perhaps even syntopy. This raises the question of which ecological niche parameters differ sufficiently between these species to maintain reproductive isolation and limit competition. Specific studies seem necessary to provide answers. Finally, our observation of *F. pardalis* represents the first confirmed record of this species for the reserve.

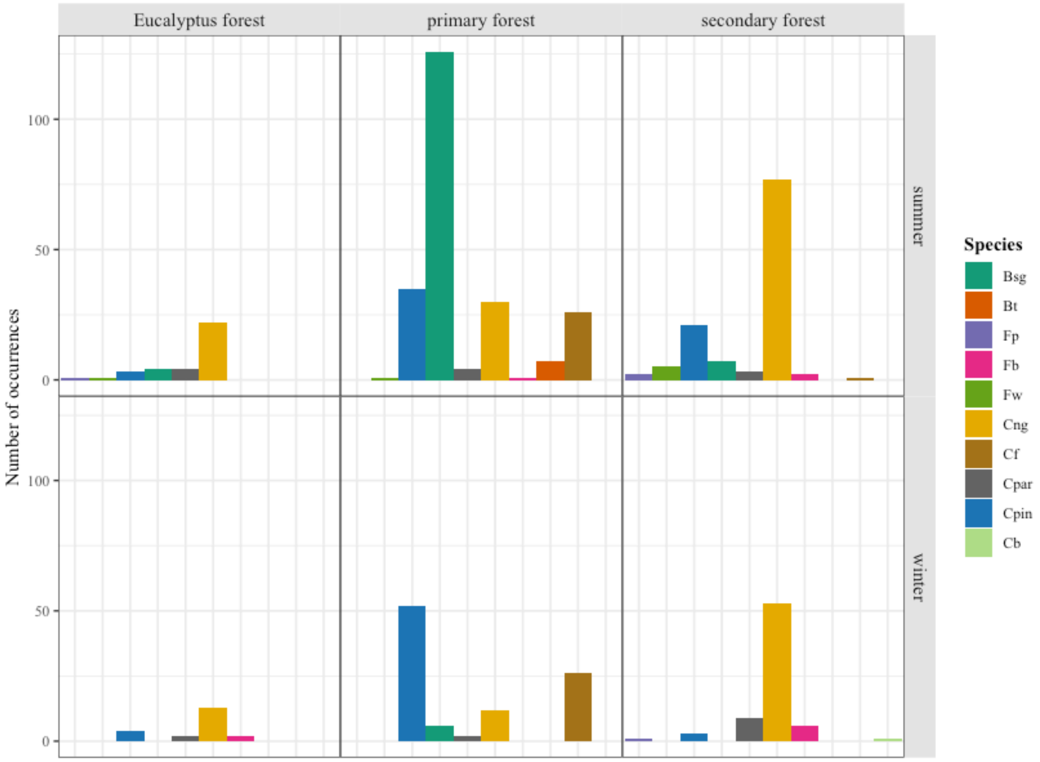

Figure 5. Number of occurrences of the different species of chameleons observed according to the season (summer vs. winter) and to the habitat type (Eucalyptus forest, primary forest, secondary forest) in Vohimana Reserve, eastern Madagascar. Species are Bsg = Brown Leaf Chameleon group (*Brookesia superciliaris* group), Bt = Domergue's Leaf Chameleon (*Brookesia thieli*), Fp = Panther Chameleon (*Furcifer pardalis*), Fb = Fork-nosed Chameleon (*Furcifer bifidus*), Fw = Canopy Chameleon (*Furcifer willsii*), Cng = Nose-horned Chameleon group (*Calumma nasutum* group), Cf = Forked Chameleon (*Calumma furcifer*), Cpar = Parson's Chameleon (*Calumma parsonii*), Cpin = Pinocchio Chameleon (*Calumma pinocchio*), and Cb = Short-horned Chameleon (*Calumma brevicorne*).

***Habitat characterization*.—**Our data reveal pronounced interspecific differences in habitat use across the three main habitat types (primary forest, secondary forest, and *Eucalyptus* forest). *Brookesia* species, *C. furcifer*, and, to a lesser extent, *C. pinocchio* were found exclusively in undisturbed, dense forest environments. This pattern was expected at least for the *B. superciliaris* group (Rabearivony et al. 2007). These habitat preferences are further supported by NDVI values, which were consistently higher in areas occupied by these three species compared with those inhabited by other species. The lower variability of NDVI observed in the habitats of the *B. superciliaris* group, *C. furcifer*, and, to a lesser extent, *C. pinocchio* suggests a pronounced preference for undisturbed forest environments, consistent with their more localized spatial distributions.

This strong habitat specificity implies that these species may be particularly vulnerable to forest degradation. A comparative study conducted before and after exploitation of the An'Ala Forest patch (area currently occupied by the Vohimana Reserve) highlighted significant impacts of forest disturbance on species richness and amphibian population density (Vallan et al. 2004). The study showed that changes in vegetation structure and microclimate caused by tree felling severely affected terrestrial understory amphibians, leading to decreased densities and, in some cases, local extinctions, whereas arboreal canopy species remained largely unaffected. In light of these findings, and considering the strong habitat associations revealed in our study, it is likely that forest degradation could have similarly deleterious effects on primary forest chameleons inhabiting the ground or lower vegetation strata, such as the *B. superciliaris* group, *C. furcifer*, and *C. pinocchio*.

More broadly, land conversion and habitat degradation are predicted to drive substantial future losses of suitable habitat for chameleons of Madagascar, with land-use change posing a greater threat than climate change according to modeling studies (Mondanaro et al. 2024). Surveys in fragmented littoral forests have shown that several chameleon species occur almost exclusively in

Table 2. Comparison of differences in mean Normalized Difference Vegetation Index (NDVI) calculated in the zone of observation between species of chameleons found in Vohimana Reserve, eastern Madagascar, after Kruskal-Wallis mean comparison test followed by a Dunn *post-hoc* test. See Table 1 for common names of species.

Pairwise comparisons	NVDI difference	*Z*-value	Adjusted *P*-value
B. superciliaris group - *C. furcifer*	-0.02	-2.398	0.021
B. superciliaris group - *C. nasutum* group	0.09	10.129	< 0.001
C. furcifer - *C. nasutum* group	0.11	9.660	< 0.001
B. superciliaris group - *C. parsonii*	0.06	3.658	< 0.001
C. furcifer - *C. parsonii*	0.08	4.847	< 0.001
C. nasutum group - *C. parsonii*	-0.03	- 1.366	0.191
B. superciliaris group - *C. pinocchio*	0.005	1.300	0.194
C. furcifer - *C. pinocchio*	0.02	3.309	0.002
C. nasutum group - *C. pinocchio*	-0.09	- 8.149	< 0.001
C. parsonii - *C.pinocchio*	-0.05	- 2.882	0.002

intact forest patches, highlighting their sensitivity to degradation and the conservation value of protected forest blocks (Hyde Roberts et al. 2025). Habitat quality and structural integrity, maintained through effective forest protection, support higher chameleon densities and promote broader community persistence compared with degraded or highly disturbed fragments (Rakotoarimalala et al. 2025). The patchy distribution of suitable microhabitats within the reserve may limit dispersal, however, particularly for species with low vagility. Conservation strategies should therefore prioritize the maintenance of habitat connectivity, especially within primary forest areas.

All the other species were found a majority of time in secondary habitat. This seems to be confirmed at least for *C. nasutum* group and *C. parsonii*, by the NDVI being preferentially lower than for other species in the areas where these two species are found confirmed by the spatial distribution of these species in the Vohimana reserve. This confirms that there is strong different habitat specificities between species, as shown for example by Brady and Griffiths (1999), Jenkins et al. (2003) and Rabearivony et al. (2007), which should be considered for habitat restoration.

Various studies have shown marked preferences for certain habitats and microhabitats, such as the use of vegetation to protect against predators and solar radiations and selection of habitats according to ground composition suitable for nesting (Hódar et al. 2000). Moreover, the Dwarf Chameleon (*Brookesia exarmata*) seems to prefer habitats with little understory and high leaf litter depth (Randrianantoandro et al. 2008), and an active avoidance of certain plant species by *B. superciliaris* in Vohimana (Colin Ruffieux, unpubl. data). In general, a preference for certain specific types of roosting sites is a factor that can influence the preference for certain types of habitats. For example, difference in perch height have been shown between the Brygoo's Chameleon (*Brookesia brygooi*), *B. exarmata*, and the Antsingy Leaf Chameleon (*B. perarmata*; Randrianantoandro et al. 2007), and the Nosy Hara Leaf Chameleon (*B. micra*) show a strong preference for dead twigs (Villeneuve 2017). Finally, Tolley (2023) was able to demonstrate that for the Cape Dwarf Chameleon (*Bradypodion pumilum*) the selection of the resting site is linked to the correlation between the size of the chameleon and the diameter of the perch.

Overall, habitat characteristics can act as major evolutionary force leading to strong inter and intraspecific local adaptations in chameleons (Barends and Petford 2025). Nevertheless, factors influencing habitat preference in chameleons remain poorly understood and merit further study, especially in a species conservation point of view considering how chameleons have limited dispersal capacities and can be sensitive to habitat change. *Calumma parsonii*, *C. pinocchio*, and animals from the *C. nasutum* group were preferentially seen in riparian environments or on the edge of the forest, which is a good illustration of how edge habitat can be important for some species (Jenkins et al. 2003; Rabearivony et al. 2015; Edmonds 2024). For example, *C. parsonii* can sometimes be described as a strictly primary forest species benefiting from dense, cool, and humid forest (Brady and Griffiths 1999); however, our observations corroborate those of Glaw and Vences (2007), as well as those of Brady and Griffiths (1999), indicating that *C. parsonii* is rather confined to edge habitats (forest edge or along watercourses) and rarely seen in the primary forest. Edge habitats (i.e., forest edge, watercourse edge, village edge) have already been noticed to be frequented by several chameleon species by Brady and Griffiths (1999): *Calumma brevicorne*, *C. nasutum* (named *C. nasuta* in Brady and Griffiths 1999), *C. parsonii*, the Antimena Chameleon (*Furcifer antimena*), the Campan's Chameleon (*F. campani*), the Lesser Chameleon (*F. minor*), and *F. willsii*. Andreone et al. (2005) also

Table 3. Mean temperature (°C ± standard error), hygrometry (% ± standard error), and UVI level (± standard error) recorded for each chameleon species or group of species encountered during the summer and winter study periods in Vohimana Reserve, eastern Madagascar. The number of observations (n) per species/group during daytime and nighttime is also given. The abbreviation UVI indicates the UV index value. See Table 1 for common names of species.

	Temperature		Hygrometry			
	day	night	day	night	UVI	n (day/night)
			Summer			
Brookesia superciliaris group	25.9 ± 2.1	23.6 ± 1.3	83.5 ± 13.5	93.5 ± 4.6	0.8 ± 1.6	21/116
Brookesia thieli	–	23.6 ± 1.3	–	94.2 ± 4.1	–	0/7
Calumma furcifer	24.5 ± 0.6	22.9 ± 1.7	87.5 ± 8.7	92.6 ± 6.4	0.1 ± 0.0	4/23
Calumma pinocchio	24.4 ± 2.2	23.8 ± 1.4	90.7 ± 6.3	92.8 ± 5.2	1.6 ± 2.2	10/49
Calumma parsonii	26.4 ± 2.1	24.6 ± 0.5	78.2 ± 11.4	91.8 ± 2.9	2.6 ± 2.2	5/6
Calumma nasutum group	25.9 ± 2.6	24.1 ± 1.4	87.4 ± 12.0	90.5 ± 5.4	2.7 ± 2.7	39/90
Calumma brevicorne	–	–	–	–	–	0/0
Furcifer pardalis	29.0	25.0	93.0	98.0 ± 0.0	8.2	1/2
Furcifer willsii	27.5 ± 0.7	25.2 ± 2.6	67.0 ± 4.2	86.0 ± 7.7	7.7 ± 2.1	2/5
Furcifer bifidus	–	23.5 ± 0.8	–	89.0 ± 12.8	–	0/3
			Winter			
Brookesia superciliaris group	20.8 ± 1.1	19.2 ± 3.5	79.5 ± 1.6	91.0 ± 10.6	0.0	3/3
Brookesia thieli	–	–	–	–	–	0/0
Calumma furcifer	–	17.3 ± 2.0	–	91.8 ± 7.5	–	0/26
Calumma pinocchio	20.2 ± 1.4	17.0 ± 2.3	93.5 ± 6.5	93.5 ± 5.2	0.08 ± 0.1	5/54
Calumma parsonii	20.9 ± 3.4	19.3 ± 1.8	90.1 ± 14.3	100.0 ± 0.0	0.3 ± 0.4	11/2
Calumma nasutum group	18.6 ± 1.8	18.9 ± 1.7	97.5 ± 3.9	94.2 ± 5.3	0.3 ± 0.5	13/65
Calumma brevicorne	26.9	–	47.5	–	0.4	1/0
Furcifer pardalis	–	16.1	–	87.8	–	0/1
Furcifer willsii	–	–	–	96.2 ± 3.2	–	0/0
Furcifer bifidus	21.4	18.1 ± 1.2	95.0	97.1 ± 2.8	1.2	1/7

mentioned in their article that the Panther Chameleon is less abundant in close forests than in open areas and anthropogenic habitats, such as forest borders, river edge, or road vegetation.

***Temperature, relative humidity, and ultraviolet B exposure*.—**Despite the marked different habitat characteristics among species, the differences in climatic conditions closest to the animals remained relatively small and overall close to the average values for the Vohimana Reserve, at least for the most abundant species. Nevertheless, it is interesting to note that more extreme climatic values were reached for certain species observed only sporadically, such as *F. willsii*, *F. pardalis*, and *C. brevicorne*. Our general observations seem to indicate that habitat selection may not be based solely on microclimatic conditions, but on other environmental factors that have yet to be identified (see previous paragraph). Microclimate is often interdependent with the plant community or the geology of the site for example, making it difficult to identify the primary cause of habitat choice as, for example, the presence of a specific vegetation linked to the proximity of rivers (see Jenkins et al. 2003). This necessitates independently testing each biotic and abiotic characteristic of the habitat.

Nevertheless, this seems to rule out a strong preference for a microclimatic niche specific to certain chameleons. That said, considering that the number of observations per species we made between summer and winter and day and night is not balanced, it is possible that we were not able to detect certain differences. It is important to distinguish here between the climatic conditions to which animals

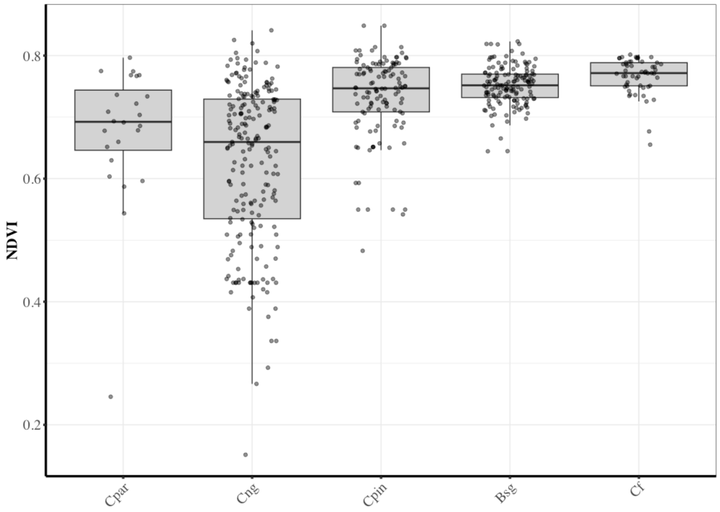

Figure 6. Boxplots of the Normalized Difference Vegetation Index (NDVI) measured in the observation area of each chameleon observed for the most abundant species (i.e., > 20 observations) in the Vohimana Reserve, eastern Madagascar. Species are Bsg = Brown Leaf Chameleon group (*Brookesia superciliaris* group), Cng = Nose-horned Chameleon group (*Calumma nasutum* group), Cf = Forked Chameleon (*Calumma furcifer*), Cpar = Parson's Chameleon (*Calumma parsonii*), and Cpin = Pinocchio Chameleon (*Calumma pinocchio*). Each point corresponds to one observation.

are subjected and the preferred climatic conditions. Indeed, determining species preferences would have involved, for each climatic parameter, measuring not only the microclimatic conditions at the animal level, but also the maximum values available in the environment at the time of observation, as in the study by Edmonds et al. (2018).

The apparent preference for dense forest observed for the *B. superciliaris* group and *C. furcifer* suggests that these species are naturally exposed to very low levels of UV-B radiation, which is what we found. Exposure to UV-B radiation in insectivorous reptile species is essential for vitamin D3 photoconversion but the dose needed for each species to fulfil their needs is poorly known and certainly highly variable and linked to species ecology (Ferguson et al. 2005, 2009; Baines et al. 2016). Edmonds et al. (2018) found that *C. nasutum* and *C. brevicorne* are both exposed to a lower dose than naturally available in the habitat and show different median UVI values. We found values of 2.2 in summer and 0.1 in winter of median UVI for *C. nasutum* group. It seems that during the summer, the UVI exposure received by *C. nasutum* group in the Vohimana Reserve is substantially higher than what has been measured for the same species by Edmonds et al. (2018), who found a median value of 0.4 for males and 0.25 for females. Data collection by Edmonds et al. (2018) have been done at the end of the austral summer (May-June), however, and it seems from our data that there is much variation in Ultraviolet B exposure between winter and summer.

***Seasonal detectability variation*.—**We observed seasonal differences in detectability that varied among species. Rabearivony et al. (2015) reported species-specific variability in seasonal abundance, with the Elongate Leaf Chameleon (*Paleon nasus*) showing higher abundance in summer, whereas *C. gastrotaenia*, the Glaw's Chameleon (*Calumma glawi*), and *C. nasutum* displayed the opposite pattern. In our study, the most striking example is the *B. superciliaris* group, which was most abundant in summer but among the rarest in winter, a pattern not observed in other species. Similar seasonal fluctuations in abundance have been reported for several *Brookesia* species in Ranomafana, with lower abundances in winter (Rabearivony 1999; Rabearivony et al. 2007). Given their small size, *Brookesia* are likely to have limited seasonal dispersal ability, leading us to hypothesize a shift in microhabitat during winter that renders them less detectable, as suggested for several species by Prötzel et al. (2016). No direct observations in our study allowed us to confirm where *Brookesia* disappear during winter, however, and this should be the focus of future research, as documenting such seasonal microhabitat shifts could have important conservation implications. In contrast, four out of five *Calumma* species exhibited an increased detectability in winter, consistent with observations for *C. nasutum* at three different sites in Madagascar (Brady and Griffiths 1999). Brady and Griffiths (1999) attribute this increase to an influx of new recruits into the winter population.

Table 4. Pairwise comparisons of mean microclimatic data values (e.g. temperature, relative humidity, and UV index) between species after ANOVA and Tukey's post-hoc test according to season (i.e. summer, winter) and time of observation (i.e. day, night) for chameleons from Vohimana Reserve, eastern Madagascar. Only significant differences are presented. See Table 1 for common names of species.

Pairwise comparisons		Estimate	*t*-value	*P*-value
	UV Index - Summer			
Brookesia superciliaris group - *Calumma nasutum* group		-0.69	-5.06	< 0.001
B. superciliaris group - *Calumma parsonii*		-1.04	-2.99	0.024
Calumma furcifer - *Calumma nasutum* group		-0.80	-3.41	0.006
Calumma furcifer - *Calumma parsonii*		-1.15	-2.90	0.031
Calumma nasutum group - *Calumma pinocchio*		0.55	3.14	0.015
	Relative Humidity - Summer			
day	*Calumma nasutum* group - *Calumma parsonii*	9.21	2.82	0.040
	Calumma parsonii - *Calumma pinocchio*	-12.50	-3.32	0.008
night	*B. superciliaris* group - *Calumma nasutum* group	2.94	3.05	0.020
	Relative Humidity - Winter			
day	*B. superciliaris* group - *Calumma nasutum* group	-17.97	-3.44	0.003
	Calumma nasutum group - *Calumma parsonii*	7.46	2.65	0.041
	Temperature – Summer			
night	*Calumma furcifer* - *Calumma nasutum* group	-1.20	-2.88	0.034
	Temperature - Winter			
day	*Calumma nasutum group - Calumma parsonii*	-2.30	-3.14	0.010
night	*Calumma furcifer* - *Calumma nasutum* group	-1.62	-3.92	0.001
	Calumma nasutum group - *Calumma pinocchio*	1.90	5.70	< 0.001

Our data show a higher number of juvenile observations in winter than in summer for the *C. nasutum* group, *C. pinocchio*, and *C. bifidus*, whereas *C. parsonii* and *C. furcifer* exhibited similar numbers of juveniles across seasons. Although the precise age of individuals cannot be determined, these observations provide insight into potential seasonal patterns of reproduction, albeit with caution due to the small sample size. While our data do not allow us to fully confirm the hypothesis of Brady and Griffiths (1999), the higher number of juvenile observations in the *C. nasutum* group may partially explain its increased detectability in winter. Despite this, the mechanisms underlying the increased detectability of certain species in winter remain unclear. The marked seasonal variation in detectability across species emphasizes the need for long-term, seasonally stratified monitoring protocols. Relying on short-term or single-season surveys may severely underestimate species presence and abundance, particularly for taxa such as the *B. superciliaris* group, which may undergo seasonal microhabitat shifts.

***Conclusion*.—**In the context of ongoing habitat fragmentation and climate change, conservation strategies should aim not only to maintain forest cover but also to preserve the fine-scale environmental conditions essential for species persistence. Protecting areas with stable microclimates, securing habitat corridors, and implementing multi-season monitoring are critical measures. Our findings also provide valuable baseline data to inform microhabitat suitability models and support *ex-situ* conservation programs. Given that chameleons are particularly sensitive to artificial conditions in captivity (Aduriz et al. 2024), and that most of the species studied here are rarely or never kept in captivity, particular attention should be paid to the specific microclimatic conditions and their seasonal variations documented in this study, such as temperature, atmospheric humidity, and UV index when planning *ex-situ* conservation efforts. It is also important to consider potential local geographic variations in environmental conditions for widely distributed species, which may result in local adaptations differing from those recorded in Vohimana.

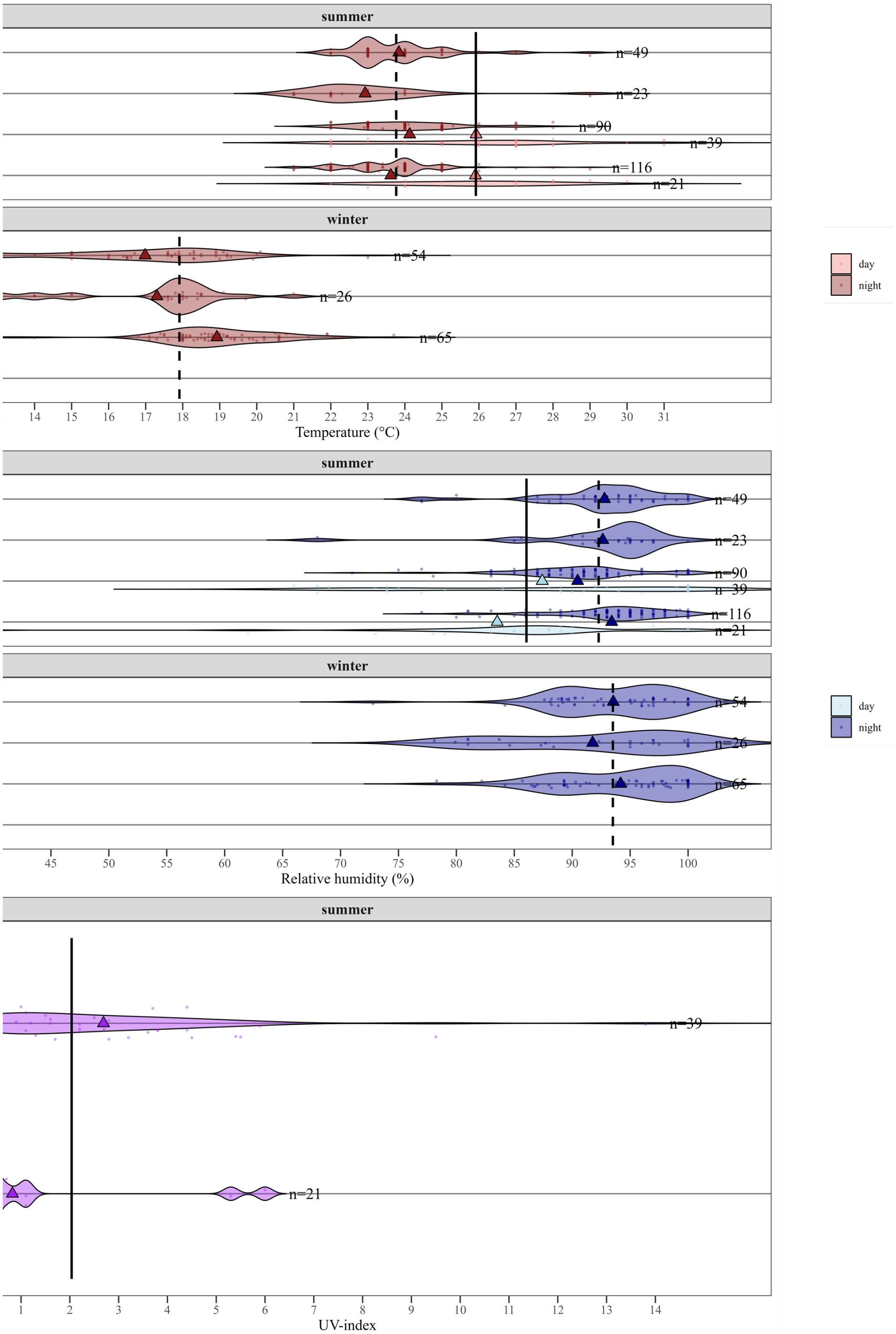

Figure 7. Violin plot showing (A) temperatures, (B) relative humidity, and (C) UV index measured in the immediate vicinity of each chameleon observed in Vohimana Reserve, eastern Madagascar. Violin plots show the distribution and variability of the measured variable in each group, with width representing data density and the central line indicating the median. Only values for the most abundant species (n > 20) are presented. Data are presented by season (i.e., summer, winter) and by time of day (i.e., day, night). The triangles indicate the average temperatures per species (day and night). The continuous and discontinuous vertical lines indicate the average value for all observations during the day and night, respectively. Missing data indicate that no observations were made for this species during this season or at this time of day. Species are Bsg = Brown Leaf Chameleon group (*Brookesia superciliaris* group), Cng = Nose-horned Chameleon group (*Calumma nasutum* group), Cf = Forked Chameleon (*Calumma furcifer*), and Cpin = Pinocchio Chameleon (*Calumma pinocchio*).

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Olivier Marquis is a naturalist with a lifelong passion for reptiles and amphibian. He obtained his Ph.D. at the University of Savoie (France) in 2006 after studying local adaptations in Brown Frog (*Rana temporaria*) along environmental gradients in the French Alps. He is a Herpetologist at the National Museum of Natural History in Paris and curator of ectotherms at the Paris Zoo. At the zoo, Olivier is in charge of the welfare of the reptiles, amphibians, and invertebrates, and he is also responsible for developing *in-situ* and *ex-situ* research and conservation projects on reptiles and amphibians. His main research interests are reptile and amphibian behavior and ecology in the framework of conservation biology, with fieldwork having been conducted in Europe, Madagascar, and French Guiana. Olivier is the Vice-chair of the Amphibian Taxon Advisory Group of the European Association of Zoos and Aquariums, and also member of several International Union for Conservation of Nature (IUCN) specialist groups (i.e., Crocodile, Chameleon, and the Animal Biobanking for Conservation). Finally, since 2023, he has been the Scientific Advisor of the Caméléon Center Conservation NGO dedicated to the study and conservation of the chameleons. (Photographed by Ghislain Balemboy).

Marc Gansuana is an internationally renowned crocodile expert and a member of the International Union for Conservation of Nature Species Survival Commission (IUCN SSC) Crocodile Specialist Group (CSG). He left his native France to dedicate his life to wildlife conservation, working first in Tunisia and later around the world as a designer and director of zoological institutions, a consultant, and a specialist in audiovisual productions for wildlife organizations. Inspired by Madagascar, where he has lived for over 20 y, Marc broadened his field expertise through a wide range of natural science approaches, driven by a deep need to learn, share knowledge, and remain closely connected to nature. A self-taught and passionate naturalist, he founded EWE, a specialized company developing innovative tools for Madagascar, including large-scale international scientific missions, bush logistics and film production management, photography, astronomy, entomology, and related disciplines. Long involved in the management and conservation of biodiversity hotspots of Madagascar, Marc is now expanding this work through Langaha Be. In parallel, he oversees ecological monitoring and research development for Man and the Environment, the NGO managing the Vohimana Reserve. (Photographed by Isabelle Coulon).

Sébastien Métrailler is an independent Herpetologist specializing in the ecology, conservation, and management of reptiles, with particular expertise in chameleons and tortoises. He is the Founder and President of Chameleon Center Conservation, a Swiss NGO dedicated to the scientific study and *in situ* and *ex situ* conservation of chameleons. In this capacity, Sébastien designs and coordinates long-term research programs in collaboration with scientific institutions, local NGOs, and conservation stakeholders. His career is distinguished by strong project management skills, including protocol development, coordination of multidisciplinary teams, budget management, and operational monitoring of field projects. He is a member of the Tortoise and Freshwater Turtle Specialist Group of the International Union for Conservation of Nature (IUCN) and is the Vice-president of the Swiss Association Protection and Recovery of Turtles (Centre Emys). Sébastien also contributes to the conservation and management of turtle populations. In parallel, he develops training and conservation breeding activities through Zoo-Conseil, in connection with the welfare of reptiles and the interactions between responsible captivity and conservation. (Photographed by Véronique Piouceau).