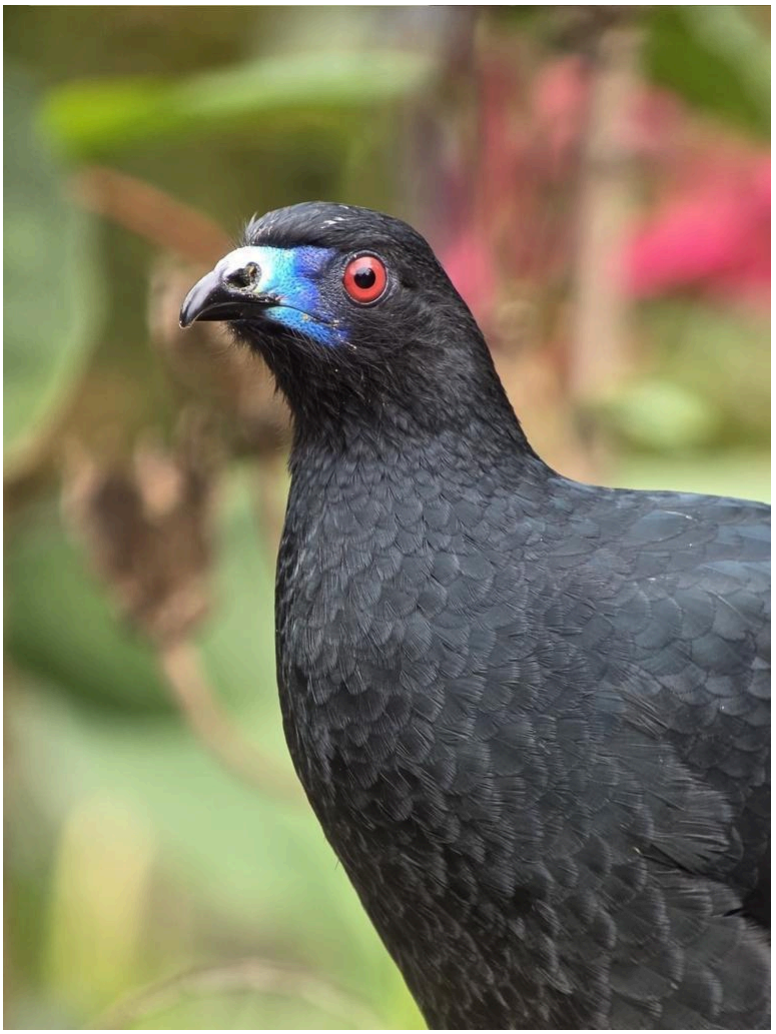
Evaluation of the ground behaviour of *Chamaepetes unicolor* (black guan*)* inside the cloud forest of Cloudbridge Nature Reserve



Black Guan *(Chamaepetes unicolor),* picture by Henry Sandi Amador (INaturalist)

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Abstract

Chamaepetes unicolor, the Black Guan, is a frugivorous cracid species endemic to Costa Rica and Western Panama. Because of his ecological requirement, he's seen as an indicator of cloud forest integrity, even if its ecology remains poorly documented. This study aims to identify the distribution, abundance and behaviour of *C. unicolor* in Cloudbridge Nature Reserve, a private cloud forest reserve in the Talamanca mountains of Costa Rica, by using camera trapping and line transect survey. With King's density model, the global population density was estimated at 4.05 individuals/km², this characterization is close to a previous estimation from Tapantí National Park (3.82 individuals/km²). By taking with caution the following values because of the low detection counts, the monthly estimations varied considerably, from 1.6 to 9.1 individuals/km², constantly in augmentation as the rainy season sets in. The detection rates did not differ significantly among the three forest types present in the reserve (old growth, natural regrowth and planted; Kruskal-Wallis, $p = 0.577$). Ecological gradients such as canopy cover and elevations drive to the same conclusion; the detection rates did not differ significantly. That translates to a lack of habitat effect supported by multivariate model selection, in which the null model was selected against environmental predictors. However, the marked seasonal pattern in reproduction was the most robust finding, juvenile detections associated with parental behaviour appeared exclusively during the rainy season (Wilcoxon, $W = 8$, $p = 0.005$). Parental behaviour was observed in 100% juvenile detections. Three behaviours dominated the observations (84% combined), walking, rest and running. It reflects a detection bias inherent to ground-level camera trapping which is not allowed to identify the arboreal behaviour. Some isolated observations of possible insectivorous foraging ($n = 2$) and territorial defense ($n=1$), even if anecdotal, may provide directions for future research. Taken together, these results provide an ecological baseline for *C. unicolor* in Cloudbridge Nature Reserve, confirming the rainy season as a critical period for reproduction and Cloudbridge Nature Reserve as a reproduction site. This study permits us to offer guidance for conservation planning within Cloudbridge Nature Reserve and comparable cloud forest habitats.

Acknowledgments

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On the same occasion, I want to thank all the volunteers and research interns I could meet during my time in Cloudbridge, with a special thought for Jade Delahaije and Selina Ziegler, who were the people I spent most of my time with, working with the camera trap grid. They all helped me during my research, especially during the afternoon survey and sometimes in very roughs' conditions. Furthermore, they all supported me when I needed help, for personal or professional reasons, which I am very grateful for.

To finish, I also want to thank Manon Hess, internship tutor, and Olivier Rodrigues, responsible for the research path. Both researchers work in "Ecole d'ingénieur de Purpan". Manon has always made sure to find out how I was going, if I needed any help and was always voluntary to respond to me at any moment If I encountered any problems. Olivier made sure the project reflection was going well and was also voluntary to read the project before my arrival in Cloudbridge to help me if I had any questions.

Without all these people, this project wouldn't be done properly and my time passed in this reserve wouldn't be that good.

Thanks to all of you for your positive attitude, your time, the delicious food in potluck, the help and the incredible memories.

Introduction

A lot of tropical forests have been felled and burned in order to be replaced by grazing lands, coffee and some other crops like rice, sugar cane or pineapple (Jadin et al. 2016). During the 20th century, some expansionist politics of development in Costa Rica have encouraged the colonization of forest lands (Zahawi et al. 2015). These politics have led to the creation of "isolated biodiversity islets", in some places, reduced to just a few trees in the middle of a meadow (Newcomer et al. 2022). This fragmentation has caused a population decline for many emblematic species like *Procnias tricarunculatus,* a bird which struggles to cross large open zones (Harvey et Haber 1998).

Since the middle of the 1990s, after being known as one of the countries with the highest rate of deforestation which comes with a biodiversity decrease (Giam 2017), Costa Rica has begun a trend towards reforestation, supported by the national Payment for Environmental Services (PES) program (Arriagada et al. 2012). Some pastures have also reverted to secondary forests (Newcomer et al. 2022) with replanting action, as we can see in Cloudbridge Nature Reserve.

Cloudbridge is a private nature reserve that stretches from 1550m to 2600m in the Talamanca mountains of Costa Rica. Since 2002, just under 200 hectares of land have formed this important research site and conservation area. Most of this land was cattle pasture or cultivated land at that time, though there is some old-growth forest as well. Since its beginning, Cloudbridge has been dedicated to the conservation and reforestation of the Cloudforest (« Welcome to Cloudbridge! » 2024).

The forest management is not the only threat against the cloudforest species. Global warming pushes the species to a higher altitude to find their optimal temperature. In fact, the species that already live close to the summit find nowhere to migrate, which exposes them to local extinction (Colwell et al. 2008).

That is the case of *Chamaepetes unicolor*, an endemic bird species from Costa Rica and the western Panama (Menacho-Odio et al. 2019). It is usually seen in forests between 600m and 3100m (Bonilla Sánchez 2023). *C. unicolor* is more often seen in high altitude between March and June for its breeding season. That makes it a partial altitudinal migrant (Barçante et al. 2017; Chaves-Campos 2023). Despite the UICN characterization as a "Least concern" species related to its mature individual's population, the population is decreasing (Adsett et al. 2020). Although this conservation classification by the IUCN, the Avian Conservation Assessment gave a population score of 4 for the *C. unicolor*, and a score of 5 for both breeding and non-breeding areas of distribution (Panjabi et al. 2024). All these scores are ranged from 1 to 5, knowing that 1 is the best score and 5 the worst. Population scores indicate vulnerability due to the total number of breeding-aged adult individuals in the global population. . Breeding and non-breeding areas, scores indicate a species' vulnerability due to the geographic extent of its range in either the breeding or non-breeding seasons separately.

(Panjabi et al. 2024). In this situation, the Avian Conservation Assessment shows us that *C. unicolor's* population is fragile and needs conservation actions.

C. unicolor is a frugivorous species essential for the seed dispersal of many species like *Thibaudia costaricensis* or other plants from the *Cecropia* and *Ocotea* genera (Thel et al. 2015; Bonilla Sánchez 2023). Its ecological requirements link this species with the minimally disturbed ecosystems that make it an indicator species to assess the integrity of forest ecosystems (Bonilla Sánchez 2023). In addition, *C. unicolor* prefers cloudforest ecosystems, and particularly for rugged terrain with slopes and streams (Bonilla Sánchez 2023) that suits Cloudbridge's ecosystem. Moreover, its breeding season starts in March until July (Chaves-Campos 2023) especially in high altitude areas, as we can find in Cloudbridge (Chaves-Campos 2023). However, it is very difficult to see this species without video equipment. In fact, *C. unicolor* is a skittish bird, 61% of individuals emit an alarm call between 0 and 8 meters from a human presence (Bonilla Sánchez 2023).

Objectives

Because of this indicator quality, the stay period (between April to July), and the affinity this species has with the ecosystem, it could be of interest to conduct a monitoring project with the objective of identifying the type of behaviour *Chamaepetes unicolor* has inside the reserve. In addition, understanding the species' habitat use would provide valuable context for interpreting its role within the ecosystem.

General objective

To determine the behaviour of *C. unicolor* within the cloud forest of Cloudbridge Nature Reserve during its stay period (April–July).

Secondary objectives

- To identify the spatial distribution and habitat use of *C. unicolor* within the reserve.
- To estimate the abundance of *C. unicolor* at the study site.
- To characterise the activity patterns of *C. unicolor* within the reserve.

Materials and Methods

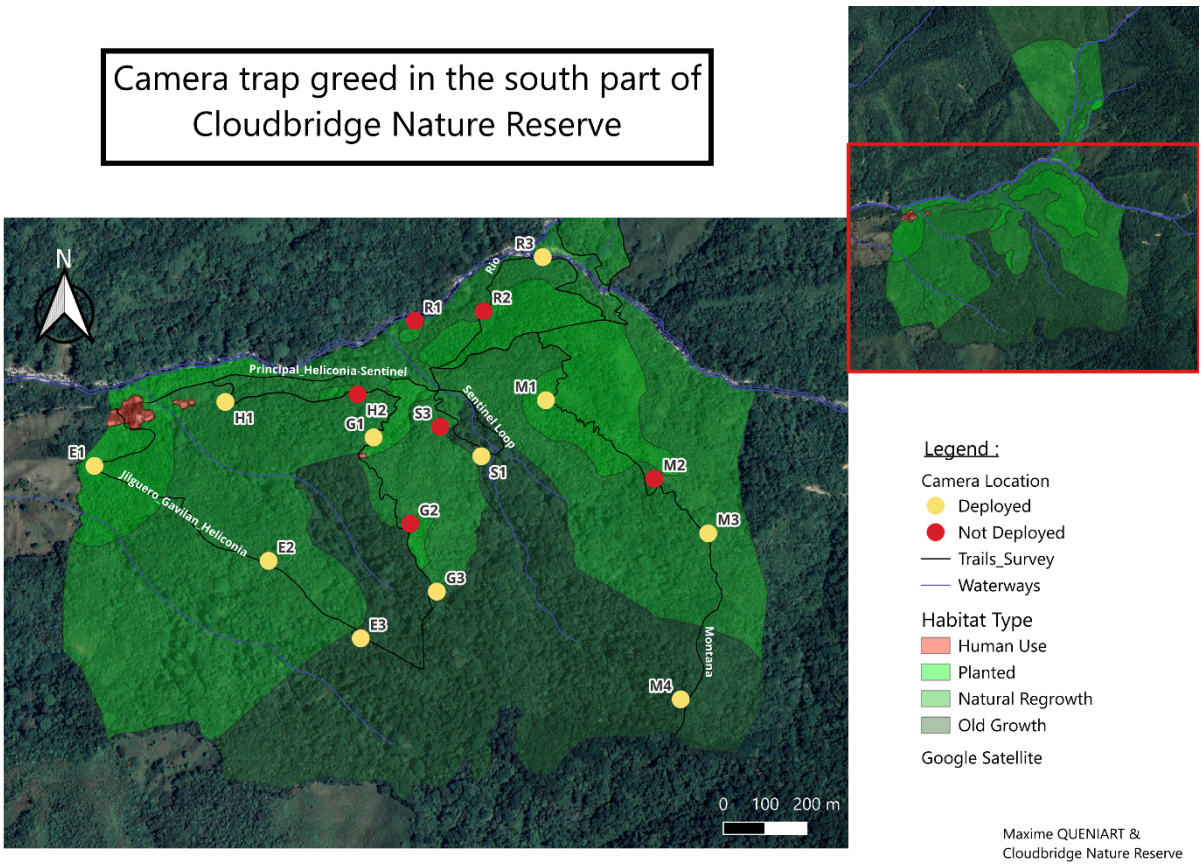
1) Study site

Cloudbridge Nature Reserve is an ecological conservation place inside the Tamalanca mountain, and adjacent to Chirripó National Park. It iss dedicated to the protection and the restoration of the cloud forest

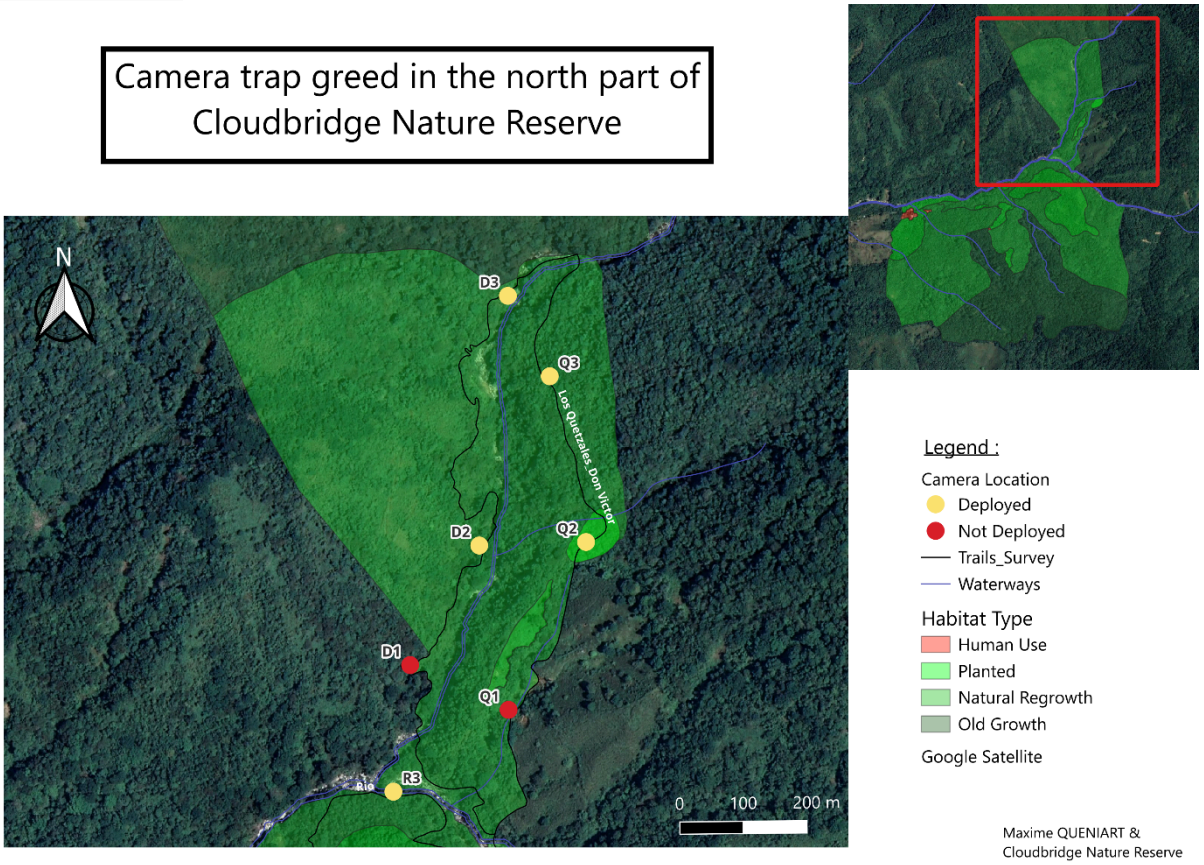
This place is characterized by three different t habitats types : old growth, natural regrowth and planted forest with a wide range of elevation from 1550 to 2600 m a.s.l . Public and private trails pass inside each of these habitat types. Some trails such as El Jilguero, Gavilán, Heliconia, Río, Sentinel, Montaña, Don Víctor and Los Quetzales have some camera traps deployed in.

The camera trap grid is from the Wild Cat Imaging Project (WCIP) in collaboration with Cloudbridge Nature Reserve. They decided to deploy it to conduct monitoring of the wild felids present in the reserve. As an intern or independent researcher, the WCIP allowed us to use the data to develop our own project in exchange for taking care of them.

Camera trap greed in the south part of Cloudbridge Nature Reserve



Camera trap greed in the north part of Cloudbridge Nature Reserve



2) Data collection

Two types of data collection were applied: camera trapping and surveys.

a) Camera trapping :

This protocol outlined the standardized procedure for checking camera traps, collecting data, and managing video files within The Wild Cat Imaging Project (WCIP) at Cloudbridge Nature Reserve. It was made by Ben Luke, founder of the WCIP and adapted by Jade Delahaije, intern at Cloudbridge.

Camera Trap Checks: Camera traps were checked every two weeks following the project monitoring schedule.

When checking camera stations:

- Brought the SD card holder with all the SD cards and new AA batteries for each camera to be checked.
- Replaced the SD card with the corresponding replacement card and formatted the new card.
- Checked the battery level. If battery charge is above 25%, batteries may remain in the camera for the next two-week cycle. If the charge was below 25% (or one bar),we replaced all batteries. Recorded all information in the Epicollect5 app.

- Before leaving the site, it was verified that the camera was functioning correctly, confirmed all settings were properly configured, and cleared any debris that could cause false triggers.

Uploading Camera Trap Data : All files were uploaded to the external project hard drive immediately upon returning from the field.

- Inserted the SD card and the project hard drive into the WCIP laptop.
- On the project hard drive, we opened the folder titled "Camera Data" and navigated to "Cloudbridge_Camera_Locations". Opened the "Location_ID" folder and selected the location corresponding to the camera station from which the SD card was collected.
- Created a new folder named with the collection date of the SD card (pick-up date).
- Transferred all files from the SD card into this folder. Once the transfer was completed, formatted the SD card to exFAT and ejected it.
- Entered the name of the newly created folder in the "Datatrack" sheet on the Google Drive and marked it was uploaded.

Data Entry : Once files were uploaded to the external hard drive, each folder was imported into Timelapse and all videos were reviewed and logged.

- Imported the folder into Timelapse and viewed each video.
- Entered the correct information for each video and marked any bird videos and false triggers accordingly.
- When it was done, marked the folder as entered in the “Datatrack” sheet on the Google Drive.
- Proceeded to the next folder

Data Checks: After data entry was completed for all videos, a quality check was performed before exporting the dataset.

- Reviewed all entered information for each video and corrected any errors.
- For videos flagged for deletion, verified that no relevant content is present before permanently deleting them.
- Once all checks were completed, marked the folder as checked in the "Datatrack" sheet on Google Drive. And exported the final dataset to the Google Drive.

Guan observation: For each occurrence of the guan, the date, time, weather, numbers of individuals, numbers of adults or juveniles, the camera location, the habitat type, altitude, canopy cover and the behaviours were taken.

In relation to the behaviours observed:

- Walking: Action of walking on the ground in front of the camera.
- Running: Action of running on the ground in front of the camera.
- Feeding: Action of eating in front of the camera.
- Foraging: Action of looking for food in front of the camera.

- Parental: Take as parental behaviour any time an adult is seen followed by a juvenile, feeding a juvenile, foraging with juvenile.
- Flying: Action of flying, landing or flying away in front of the camera.
- Rest: Take as a rest behaviour any time the bird stops and looks around or resting in front of the camera.
- Breeding: Action of reproduction in front of the camera.

b) **Visual encounter surveys :**

We used the line transect method as Bonilla -Sánchez and Chaves-Campos (2023) did during their studies. This method allowed us to rapidly cover an important study area and it was also appropriate for large species that fly easily in the presence of humans (Gregory et al. 2004). Moreover, line transects had a higher tolerance for the misestimation of distance between the bird and the transect because the increase is linear rather than the geometric increase of the point transect (Gregory et al. 2004). In this case, we did the same trails used by the camera data collection of Cloudbridge. Every week we did two different trails, one in the morning (starting at 7 a.m.) and the other during the afternoon (starting at 2 p.m.) both at a slow pace. Because of the difficulty it could represent in detecting birds, we were always at least 2 people when applying the method even if it is also possible to do it alone. For which *C. unicolor* seen, the date, the coordinates - taken with the smartphone app "Gaia GPS"- , the distance between the transect and the bird, the weather, the canopy cover, the altitude and the behaviours were taken.

The same behavioural classification was for both camera-trap video observation and visual encounter survey. Only the position of the ground (ground or tree) was added.

c) **For each part of the methodology :**

The canopy cover was measured thanks to Sentinel-2 images from the European Union's Copernicus program, processed by CNES for the Theia cluster.

Altitude as each sample location was determined using QGIS, and the raster layer provided by Cloudbridge.

Data Analysis

Sampling effort: The active trap-days per camera were the base to quantify the camera effort. The active trap-days were calculated with the sum of daily intervals between each deployment start and date. To account for unequal sampling effort across cameras and seasons, all detection metrics were standardized to the number of events per 100 trap-days. Hereafter this is referred to as e detection rate. For the season comparisons, traps-days were grouped by season at the camera level. Thanks to this methodology, each day was assigned to a season, dry season (December to April) or rainy season (May-November). Only the months with, at least, 100 traps-days were retained for all the season analyses to avoid rate estimates based on negligible effort.

Density estimation: The population density was calculated with the King model used with line transect (Bonilla Sánchez 2023; Gregory et al. 2004). For the global or the monthly density, the detections were grouped into 2m distances classes. The threshold of detection (w) was determined as the first distance class at which the detection number of detection dropped by more than 50% relative to the previous class. This methodology represents the distance beyond which the detection probability is considered insufficient. Only the individuals detected before were taken for analysis. If no distance class drops by more than 50% relative to the previous one, the maximum observed detection class distance was used as a w. This fallback solution could slightly overestimate the surveyed strip width and, by consequence, underestimate density for those periods. The monthly density estimate calculated with this fallback solution should be interpreted with caution. The Density (D, individuals/km²) was estimated thanks to the formula $D = \frac{n}{2 \times w \times L}$, where n is the number of individuals detected before the threshold and L the total transect length surveyed during the corresponding period. This methodology was applied to estimate the global density during all the time of the study, but also to estimate the density for each monthly period to track the temporal variation of density.

Daily activity patterns: The distribution of the detection across each day (24h cycle) was visualized thanks to the kernel density estimation applied to the hour of each detection. The activity peaks of *C. unicolor* were identified as local maximums of the density curve. The seasonal differences were examined by separate and overlaying the density curves for the dry and the rainy seasons.

Behaviour analysis: For each camera-trap event, the presence, note 1, and the absence, note 0, of eight behaviours were recorded (feeding, foraging, walking, running, rest, flying, parental and breeding). The behavioural analysis was defined as the relative frequency of each behaviour across all detections, expressed as a percentage of total behavioural observations.

Detection rate by habitat type: The detection rate was compared among the three habitat types of forest present in Cloudbridge (Old Growth, Natural Regrowth and planted). The comparison was made using Kruskal-Wallis test, chosen over ANOVA because of the small

sample size (n = 15 cameras) and non-normal distribution rates. If the Kruskal-Wallis test was significant, pairwise comparisons were conducted using Dunn's post-hoc test with Holm correction for multiple comparisons.

Season variation in detection, group size, and juvenile presence: The monthly detection rate, juvenile detection rates and mean group sizes were compared between seasons thanks to the Wilcoxon ran-sum test. The descriptive statistics information (mean, median, standard deviation and 95% confidence intervals) were calculated for each season.

Behavioural rate by season: The behaviour event rates (made per 100 trap-days) were calculated at the camera and season level. Since several behaviours were only recorded in one season (feeding, flying, parental in the rainy season), a Wilcoxon rank-sum test was applied only on the behaviours recorded in each season (foraging, resting, running, walking)

Behavioural rates along environmental gradients: The relationship between the behaviours rate and two continuous environmental variables, elevation in meters and canopy cover with the NDVI index, were calculated with the Spearman rank correlations. To avoid excluding the cameras with zero detections for a given behaviour and biasing the correlation, all the cameras were retained for each behaviour. This was done by creating a complete camera and behaviour grid and filling unobserved behaviour with a zero before calculation.

Behavioural rates by habitat type: The behaviour events rates were compared across each type of forest using a Kruskal-Wallis test. Then, a Dunn post-hoc test with Holm correction was also done where a significant difference ($p < 0.05$) was detected.

Assoication between juveniles and parental behaviour: The simultaneous presence of juveniles and parental behaviour was examined thanks to a contingency table with the juvenile presence (nbr_juv > 0) against the parental behaviour occurrence (parental = 1)

Multivariate modelling: To see the common contributions of habitat type, elevation, and canopy cover to variation in detections rates, a set of negative binomials generalized linear models (GLM-NB) was adjusted to the camera detections counts (per 100 days-trap), using the log of traps days to take in account the sampling effort. The model selection was performed thanks to the Akaike's Information Criterion (AIC; the models with a $\Delta AIC < 2$ of the best models were considered equivalent). The collinearity among predictors was evaluated thanks to the variance inflation factors (VIF). For the behaviour data, when each camera has an observation for all eight behaviours, a negative binomial generalized linear mixed models (GLMM, package glmmTMB on R) were adjusted thanks to the camera identity (name of the camera) as a random intercept. Only three candidate models were compared (behaviour and habitat type, behaviour and elevation, behaviour and canopy cover). The best model was identified by AIC. All the residuals' diagnostics were performed thanks to the simulated quantile residuals (package DHARMa)

All analyses were conducted in R (version ≥ 4.3). Statistical significance was set at $\alpha = 0.05$ throughout.

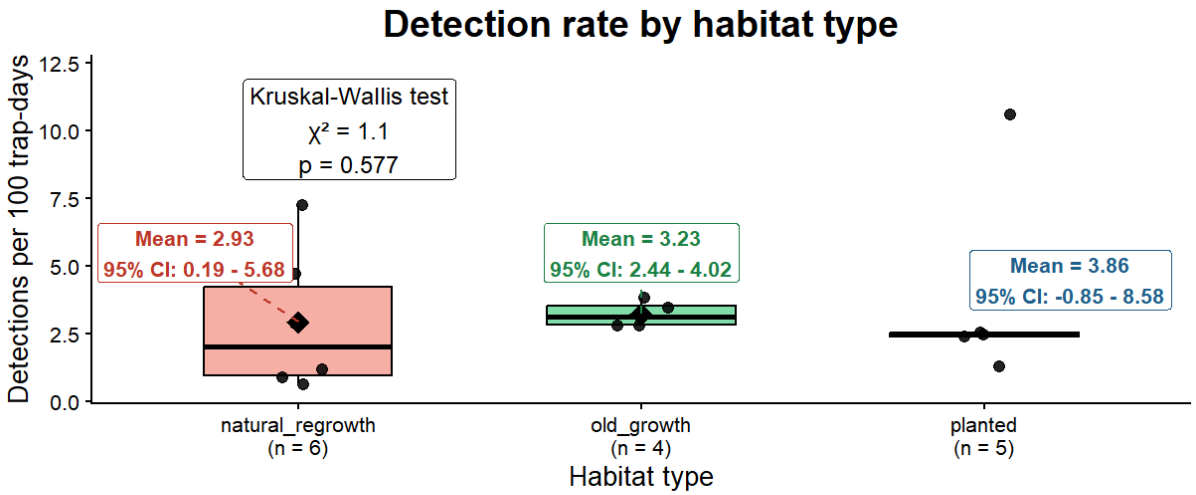
Results

Sampling effort: The camera trap grid worked for 617 days in total. Across the 18 camera traps deployed, the cumulative effort is 4,279 trap days, ranging from 8 traps-day corresponding to the camera G2, with an effort of 1.3% to 471 trap days corresponding to the camera G3 with an effort of 76.3%. G2 was only operational during a single deployment period, because of that the result from this camera is treated with caution in all per-camera analyses. In total, eleven cameras accumulated more than 150 trap-days corresponding to a ratio-effort superior to 24%.

Population density: A total of 21 observations were recorded during the line transect with a total amount of 24 *C. unicolor*. The cumulative distance was 138.7km. At the global scale, the detection threshold was reached at w = 8m (Fig. A1). The global surveyed strop area was calculated to 2,22 km² with a number of detection n = 9 within the threshold. The global density was estimated to be **4.05 individuals/km²**. The monthly density have a big variation between April 2026: **1.62 individuals/km** (w = 20m, n = 3, L = 46.2km) to **9.09 individuals/km²** in June 2026 (w = 10 m, n = 7, L = 38.5 km) passing through May 2026 with a density of **3.47 individuals/km²** (w = 8 m, n = 3, L = 54 km) (Fig. A2, A3). The detection threshold of 20m applied to April reflects the fallback procedure corresponding to the maximum observed distance, as the low number of detections in April prevents a clear identification of a 50% drop of detection between two class distances; the April density estimate should be interpreted with caution.

Camera trap detection: A total of 149 detection events were recorded across all the camera traps between October 2024 and June 2026. Monthly detection counts ranged from 6 (April and August) to 21 (October), without an obvious single-month peak. Most of the detection were on E1, El Jilguero trail and Q3 and D3, Don Victor and Los Quetzales.

Detection rate by habitat type: The mean detection rates per 100 trap-days were, for the natural regrowth, 2.93 ± 2.61 and a median of 2.04 with n = 6 cameras. For the old growth forest, the mean is 3.23 ± 0.50 and a median of 3.14 with n = 4. The planted forest has a mean of 3.86 ± 3.80 and a median of 2.47 with n = 5 cameras (Fig.1). Even if the detection rates tended to be slightly higher in planted forest, this difference was not statistically significant (Kruskal-Wallis: $\chi^2 = 1.10$, df = 2, p = 0.577). And none of the pairwise comparisons reached significance after a Holm correction (all P.adj > 0.77; Dunn's test). The standard deviations characterized to be large in planted and natural regrowth habitat reflect a high inter-camera variability inside these habitat types.



Habitat	n	Mean	Median	SD
natural_regrowth	6	2.93	2.04	2.61
old_growth	4	3.23	3.14	0.50
planted	5	3.86	2.47	3.80

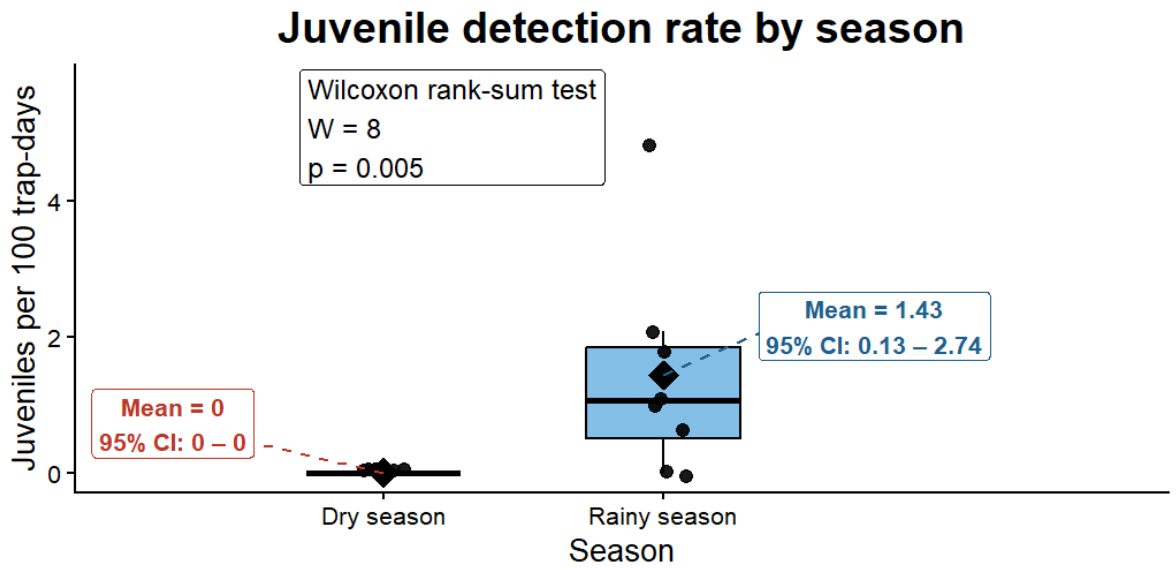
Horizontal lines = medians; black diamonds = means; boxes = interquartile ranges.

Figure 1 : Detection rate by habitat type

Environmental characteristics by habitat type: The mean elevation differed among all the three habitat types: 1729 m for planted, 1808 m for natural regrowth and 1910 m for old growth. But the difference observed between the habitat type and the elevation was not statistically significant (Kruskal-Wallis: $\chi^2 = 4.08$, df = 2, p = 0.130). Even if the closest comparison by pair was between old growth and planted forest (Dunn Z = 2.02, P.adj = 0.131). The mean canopy cover, evaluated with the NDVI index, was homogeneous across each habitat type: 0.783 ± 0.044 for the natural regrowth, 0.758 ± 0.039 for the old-growth and 0.790 ± 0.018 for the planted. This homogeneous characteristic was confirmed by a Kruskal-Wallis test: $\chi^2 = 2.23$, df = 2, p = 0.328.

Detection rate among the environmental gradients: The overall detection rates showed no significant relationship with elevation which showed a Spearman test with ρ = 0.093 and p = 0.744 or the canopy cover. However, canopy cover showed a stronger positive association with detection rates than elevation, although this relationship was not statistically significant (Spearman test with ρ = 0.264, p = 0.340. (Fig A4), (Fig A5)

Seasonal variation: Monthly detection rates did not differ significantly between seasons (Wilcoxon rank-sum test: W = 15, p = 0.083), although the results showed a tendency toward seasonal variation, (Fig A6). In opposition, the juvenile detection rate was significantly higher in the rainy season than in the rainy season with W = 8, p = 0.005,Figure 2 : Juvenile detection rate by season. The mean group size did not differ significantly between seasons with W = 18, p = 0.153, Figure A 7 : Group size by season.



Season	n (months)	Mean	Median	SD
Dry season	8	0.00	0.00	0.00
Rainy season	8	1.43	1.06	1.56

Horizontal lines = medians; black diamonds = means; boxes = interquartile ranges.

Figure 2 : Juvenile detection rate by season

Daily activity pattern: The camera trap detection was concentrated during the day. Two distinct activity peaks were identified from kernel density estimation of detection times, (Fig 3). Also, two different patterns could be identified between the seasons: the dry season showed a bigger peak in the morning and the rainy season in the afternoon, (Fig A8). *C. unicolor* activity was largely reduced during the nighttime hours (18h-5h).

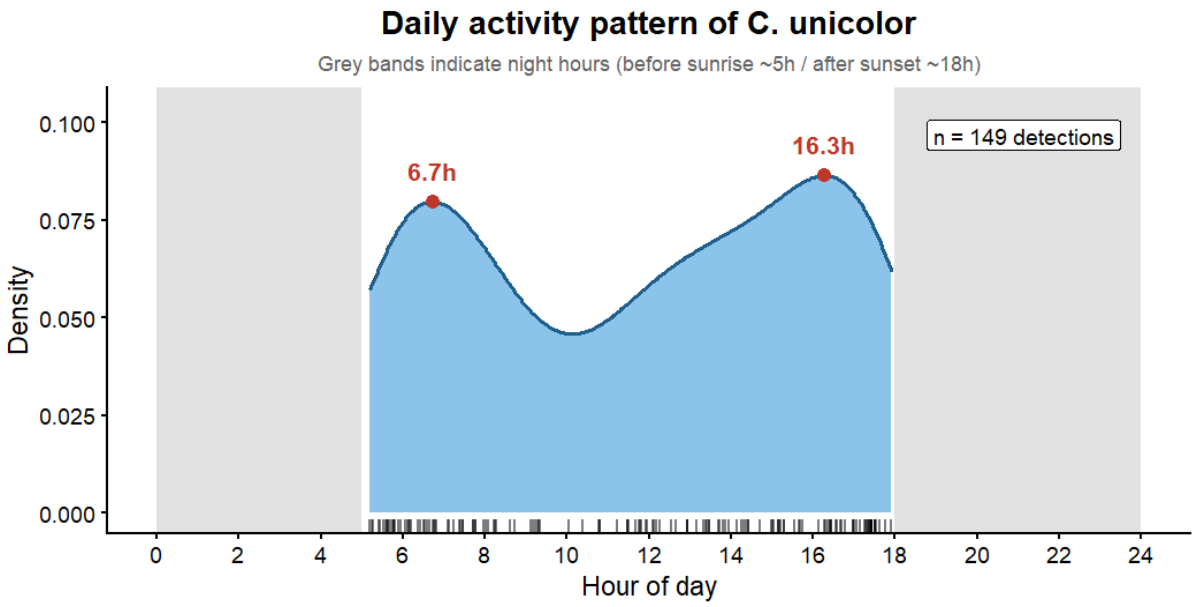


Figure 3 : Daily activity pattern of Chamaepetes unicolor

Behavioural analysis: In total, 224 behavioural events were recorded with 149 detection events. Of the eight behaviours, walking was the most frequently observed, n = 91 representing 40.6% of the observations, followed by resting (n = 49, 21.9%), and running (n = 48, 21.4%). Parental behaviour represents 9.4% of the observations (n = 21). Feeding, foraging and flying were recorded in 2.2% of the observations each n = 5. No breeding behaviour was recorded, n = 0.

Incidental behavioural observations: In addition to the behaviours coded in the ethogram, two independent camera trap events recorded showed an apparent insectivorous foraging, in which individuals were running into vegetation. One of the two events showed one individual coming back from the vegetation with a dark object in the beak, which did not seem to be some fruit. For the second event, the individuals ran into vegetation, looked for something in it and got nothing, it seemed that it was foraging invertebrates. One other event recorded apparent territorial defense behaviour between conspecifics, characterized by aggressive postures, chasing, and wing movements. As these behaviours fell outside the ethogram and were recorded on only two and one occasions; they were not included in the quantitative analyses presented above and are reported here as incidental observations.

Association between juveniles and parental behaviour: Juveniles were detected in 21 camera-trap events. In addition, parental behaviour was recorded in all these 21 events, representing 100% of the observations. No juvenile was recorded or observed without an adult demonstrating parental behaviour.

Behavioural rates by habitat type: After a correction for the camera effort, none of the behaviour showed a significant difference in event rate among the habitat types. That was shown thanks to Kruskal-Wallis tests, all p > 0.32; (Fig 4). Dunn's post-hoc tests were not necessary as no Kruskal-Wallis test reached p < 0.05.

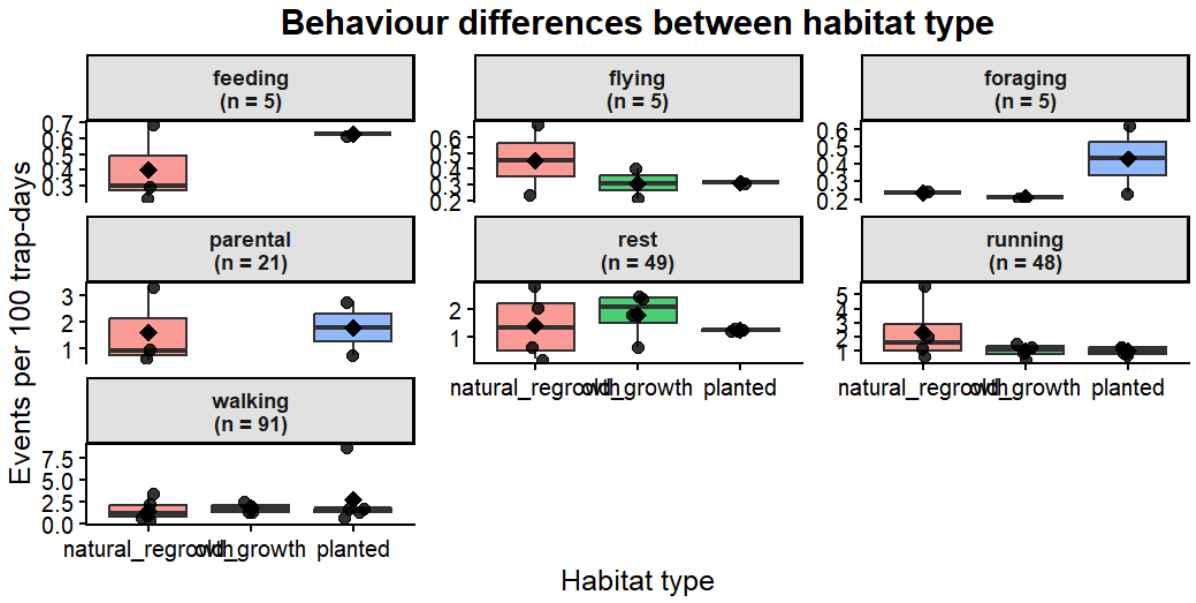


Figure 4 : Behaviour differences between habitat type

Behavioural rates by season: In all the recorded behaviour, feeding (n = 5), flying (n = 5) and parental behaviour (n = 21) were recorded exclusively during the rainy season, (Fig 5). With all the other four behaviours recorded in both seasons (foraging, rest, running, walking), none of them showed a statistically significant difference in event rate between seasons. That was shown with Wilcoxon rank-sum tests: all p > 0.29)

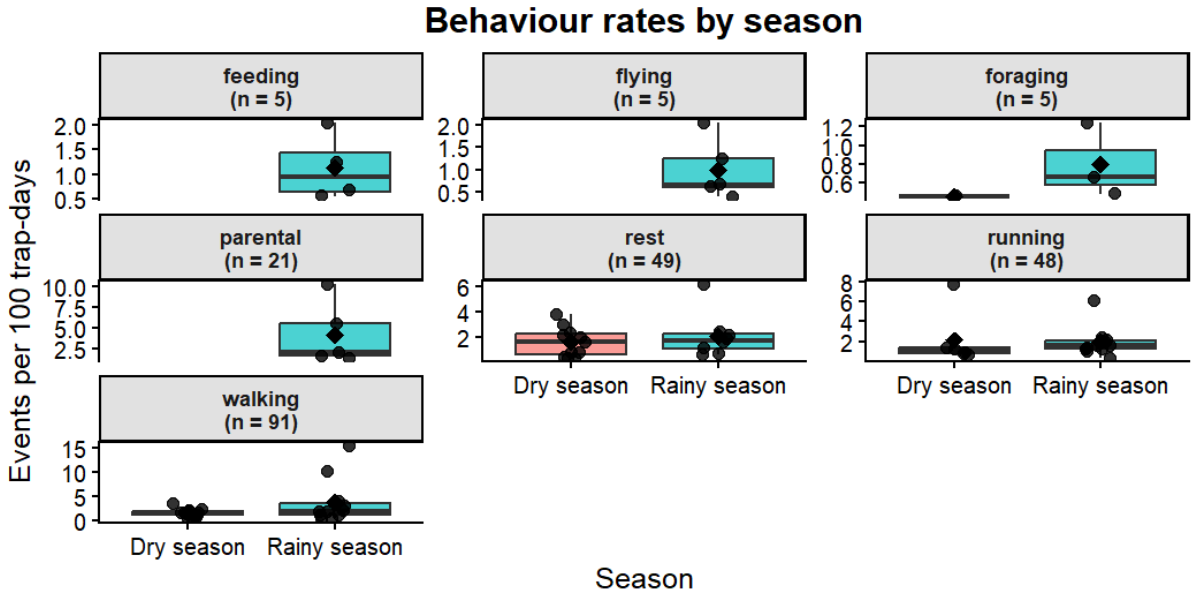


Figure 5 : Behaviour rates by season

Behavioural rates along environmental gradients: None of all the behaviours showed a significant Spearman correlation between event rate and elevation, all p > 0.17, (Fig A9). Otherwise, parental behaviour (ρ = 0.447, p = 0.095) and feeding (ρ = 0.440, p = 0.101) showed a positive trend with the canopy cover approaching the significance threshold, (Fig A10). That suggests a potential association between denser canopy and higher rate of these two behaviours, even when it is not confirmed statistically with the current sample size (n = 15 cameras).

Results - Multivariate models

Collinearity assessment: Before every model fitting, the overlap between the two variables habitat type and elevation was evaluated by regressing elevation on habitat type. The regression obtained a R^2 = 0.29 which signifies a moderate but acceptable association. That suggests that the two predictors capture partially two overlapping gradients without causing a big collinearity problem. The variance inflation factors (VIF) confirmed it calculated on the full model with the three variables: habitat types, elevation and canopy cover at the same time, obtaining a low result corresponding to GVIF^(1/2df) ≤ 1.19, which is below than the conventional threshold of 2.5. But the three variables (habitat types, canopy cover and elevation) were tested in separate models as a precaution because of the small sample size (n = 15 cameras)

Part A – Drivers of overall detection rate: In total, five candidates negative binomial GLMs were compared by AIC to explain the detection counts per camera. A log(trap-days) was included to account for sampling effort. Overall, the null model (intercept only) was the best supported model with an AIC = 97.10. But the canopy cover with a ΔAIC = 0.21 and the elevation model with a ΔAIC = 0.50 are statistically equivalent (ΔAIC < 2). Otherwise, the models including habitat type, with or without canopy cover showed less support with the data (ΔAIC > 2.86) (Table 1). The selection on the null model showed that none of the environmental predictors, which are habitat type, elevation or canopy cover, significantly improved the prediction of detection rate. The residuals diagnostics confirmed an adequate model fit. It showed no significant over- or underdispersion detected with a DHARMa dispersion test: dispersion ratio = 1.19, p = 0.544.

Model	df	AIC	Delta AIC
Null	2	97,09595	0
Canopy	3	97,3026	0,206651
Elevation	3	97,59682	0,500868
Habitat	4	100,28749	3,19154

Table 1 : AIC detection rates multivariate models

Part B – Driver of behavioural event rates: The behavioural dataset comprised 105 observations (corresponding to 15 cameras × 7 behaviours). The camera identity was included as a random intercept in all the models to consider the non-independence of multiple behaviours recorded at the same location. Overall, three candidates of negative binomial GLMMs were compared: one including behaviour type and habitat type as fixed effects, one with behaviour type and elevation and the last one with the behaviour type and the canopy cover.

The canopy cover model was the best supported with an AIC = 344.42. The model with the elevation was statistically equivalent with a ΔAIC = 0.49 < 2. The habitat type model received less support with a ΔAIC = 3.51, (Tab 2). Moreover, an interaction model between behaviour type and habitat type was realized but showed a severe instability for old-growth interactions (standard errors > 7,000). This standard error is the reflection of an overparametrized model relative to the current data, because of that, it was not retained.

Model	df	AIC	Delta AIC
Canopy	10	344,4222	0
Elevation	10	344,9087	0,4865007
Simple	11	347,9304	3,5081685

Table 2 : AIC behaviours multivariate models

Inside the best supported model, corresponding to behaviour + canopy cover, the behaviour type was the dominant driver of event rate variation, especially walking ($\beta = 2.90$, $z = 5.51$, $p < 0.001$), rest ($\beta = 2.46$, $z = 4.55$, $p < 0.001$), running ($\beta = 2.35$, $z = 4.38$, $p < 0.001$) and parental behaviour care ($\beta = 1.38$, $z = 2.45$, $p = 0.014$). They are all occurring at significantly higher rates than feeding, which is the reference behaviour. The other behaviours, flying and foraging, did not differ from feeding, both $p > 0.97$. The canopy cover effect was marked positive but not statistically significant ($\beta = 7.42$, $SE = 5.53$, $z = 1.34$, $p = 0.180$) which is consistent with the Spearman correlation reported above. The elevation model showed identical results, where the elevation had no significant effect on event rates ($\beta = -0.0016$, $z = -1.04$, $p = 0.296$). The residual diagnostics confirmed an adequate fit for the best model, with no significant dispersion issues with DHARMa dispersion test (dispersion ratio = 1.09, $p = 0.588$).

Together, these models confirm that the behavioural composition, and not the habitat type, elevation or canopy cover, was the first source of variation in event rate across cameras. None of the environmental predictors reached a statistical significance in explaining the detection or the behavioural rates when the sampling effort was taken in account. It is also important to mention that these results should be interpreted as exploratory because of the limited sample size ($n = 15$ cameras), which restrained the statistical power to detect moderate effect sizes.

Discussion

This study shows the activity pattern, behavioural analysis, habitat use and population density of *C. unicolor* using a combination of camera trapping and surveys in the cloud forest of Cloudbridge Nature Reserve. Despite the limitations associated with a limited number of cameras and a relatively short study period, the results offer valuable baseline data on this species.

Population density: The global density estimate inside the reserve (4.05 individuals/km²) was similar to the that found in 2023 in the Tapantí sector of the Tapantí-Macizo de la Muerte in the Talamanca (3.82 individuals/km²;Bonilla Sánchez 2023). The augmentation of the density throughout the month reported in this study has been documented before (Bonilla Sánchez 2023), and it is expected because of the seasonal altitudinal migration behaviour showed by *C. unicolor* (Chaves-Campos 2023; Newcomer et al. 2022). However, the value of the monthly density has to be interpreted with caution because they rest in very few individuals' detection (respectively 3,3 and 7). Importantly, the April estimate was calculated on the fallback detection threshold (maximum observed distance replacing the 50% drop criterion). Which could have as consequence to overestimate strip width and underestimate the density. The April value should be treated as a lower bound rather than a point estimate. Overall, the futures surveys should be effectuated with a greater transect effort distributed more evenly across months could be essential to dissociate the true seasonal density fluctuations from the methodological noise.

Habitat uses: One of the principal questions of this study was to find if *C. unicolor* showed differential use of the three different forest types present in Cloudbridge : planted forest, natural regrowth or old growth. Even if some studies showed that *C. unicolor* is most likely seen in the planted forest (Schut 2025) or in contradiction, in the habitat similar to the old growth (Wilms et Kappelle 2006); The detection rates did not differ significantly across habitat type. Two interpretations can be proposed. The first one is that *C. unicolor* even if it has a preference to mature forest corresponding to the old growth could also be relatively habitat generalist and can exploit secondary forest as the mature forest if it showed a certain structural requirements required (Schut 2025; Wilms et Kappelle 2006). This kind of behaviour can match with other cracids observations which can persist in degraded habitat if the hunting pressure is low and some forest connectivity is maintained (Chaves-Campos 2023). The second hypothesis is about statistical power. It could be feasible that the statistical power to detect a real difference in habitat use was limited by the small number of cameras in each one of the different types of forest (n = 4 to 6), making an impossibility to exclude any biological rule which cannot be detected with these data.

Environmental gradients: None of the environmental gradients evaluated showed a significant correlation. The relatively small range of canopy cover recorded across all the cameras , likely constrained the ability to detect a gradient effect because of the low environmental variation which could be insufficient for analysis to detect any gradient effect

on the behaviour or the detection rate. In the same way, even if the elevation gradient varied across cameras by approximately 180m (1,729 m to 1.910m, after normalization), this range may not span the ecological threshold above or below which habitat quality changes meaningfully for this species. Other studies conducted about cracids have demonstrated the elevational preferences links to food availability and thermal conditions (Chaves-Campos 2004; Colwell et al. 2008). That could suggest that the patterns could be observed over larger spatial scales than those sampled in Cloudbridge. Moreover, the positive but non-significant trend between canopy cover and parental behaviour rates could be noticed and worth particular attention in future studies with expanded sample size, as it could reflect an association between denser canopy and greater representation of the feeding and parental behaviours, which, for the second one, would be represent a better representation of the nesting area.

Seasonal patterns: The most robust biological finding concerned the seasonality characters of the juvenile detection, which were significantly more frequent, and only observed during the rainy season than during the dry season. This pattern confirms that the reproduction of *C. unicolor* is temporally synchronized with the rainy season (Chaves-Campos 2004), which is also a common strategy observed in with the tropical forest birds which synchronize the chick-rearing peak demands with the periods of maximum food availability (GWINNER 1996). The rainy season in tropical montane forests can provide an elevated fruiting activity and increases invertebrate abundance, both of which are critical food sources for growing cracid chicks (Poulin et al. 1992). This interpretation is supported by the observations that parental behaviour was recorded exclusively during the rainy season in our camera-trap dataset, suggesting that ground-level activity associated with reproduction and chick rearing is concentrated within this period. Moreover, the overall detection rates showed a tendency to be higher in the rainy season which may reflect an increased ground-level movements during the breeding period in Cloudbridge during the breeding season, confirmation would require a larger dataset. The absence of signifiable season variation in mean group size is consistent with the generally solitary or pair-based social structure reported for *C. uncilor* (Stiles et al. 1989), with no evidence of seasonal aggregation behaviour as seen in some other cracid species.

Daily activity patterns: The most of the camera detections were concentrated during the daylight hours, with a drop during the nighttime, consistent with the strictly diurnal habitats reported for most cracids (Vaurie 1968). The two activity patterns peaks identified likely correspond to the classic bimodal pattern observed in many tropical Galliformes, with a morning peak followed by a decrease in activity and an afternoon peak before a night roosting period (Santos et al. 2022; Pardo et al. 2017). The comparison of activity patterns between dry and rainy seasons suggested broadly similar temporal distributions, even if the limited number of completed season (1) precluded formal statistical comparison

Behavioural analysis and parental behaviour: In all of the observations, walking, resting and running were the most frequently recorded behaviour while feeding and foraging together were not observed often. This abnormal distribution likely reflects a detection bias inherent to ground-level camera trapping than the true behaviour of the species. *C. unicolor*¸ like other

cracids, is primarily an arboreal frugivore that feeds in the forest canopy (Wenny 2000). It means that the ground level camera captures exclusively the ground behaviour of *C. unicolor* avoiding all capture about tree canopy behaviour. The apparent overrepresentation of locomotion behaviour is a methodological artefact that should be taken in account during the interpretation. Knowing this limitation, the exclusive occurrence of parental behaviour in association with juvenile detection (100% of the occurrences), provides a strong signal of parental investment during the chick-rearing period. This pattern is consistent with the life history strategy of cracids, which are characterized by low reproductive rates, large eggs, and extended parental care that reflects a K-selected strategy (Cassill 2019) well documented across the family Cracidae (Brooks 2006).

Multivariate models: The model selection confirmed the patterns described above. None of the environmental predictors considered explained the variation of detection rates between the cameras once the sampling effort was considered. The non-significant positive signal of a potential canopy effect on behaviour reminds the correlations described earlier and need cautionary attention. The random effects link to the cameras was non-negligible across all models). That confirms an among-camera heterogeneity in baseline event rates that was not explained by the predictors included, justifying the use of mixed models over simpler fixed-approaches.

The camera-level random effect was non-negligible across all models, confirming substantial among-camera heterogeneity in baseline event rates that was not explained by the predictors included, and justifying the use of mixed models over simpler fixed-effect approaches.

Incidental observations: Beyond the quantified behaviours, two anecdotal but noteworthy observations were observed during video review. First, apparent insectivorous foraging suggests that *C. unicolor* diet may not be exclusively composed of fruits and vegetations, as it's known for cracids, but could include an animal protein component. This behaviour could be not surprising when it's compared with dietary shifts documented in other frugivorous birds during the breeding period, when protein demands for chick growth typically increase (Poulin et al. 1992). Furthermore, the two observations of apparent insects foraging were observed with chicks' presence. The second event with one occurrence which suggest territorial defense behaviours between conspecifics point to a potential dimension of intraspecific spacing or aggression not previously described for this species, which could relate not to mate guarding or nest-site defense during the breeding season (Brooks 2006). Given the extremely small number of observations, these patterns should be treated as hypothesis-generating rather than conclusive, but they highlight two promising directions, dietary flexibly and territorial behaviour.

Methodological considerations and limitations: Some methodological constraints limit the conclusions that can be taken from this study. Primarily, the number of camera traps (n = 15) is at the limits sample size recommended for robust habitat modelling in ecological studies (Fearer et al. 2007), and the highly unequal effort between cameras (ranging from 8 to 471 trap-days) introduces variability that the standardization only partially corrects. The line transect dataset was, in the same way, constrained. Only 21 detections recorded over three

months and density estimates resting on a low individual count in two of three months. However, the king density model was chosen to compensate for this kind of situation (Bonilla Sánchez 2023), an incertitude can remain. These limitations mean that all quantitative results, including density estimations, correlations, coefficients and model parameters, should be interpreted as preliminary and exploratory rather than a definition population level conclusion. On the side; the effort correction, zero retention in environmental gradient analyses, mixed-model structure for repeated camera-level measurements, and model selection by AIC; represents an approach that can be directly extended with additional data.

Conservation implications: Despite the preliminary nature of this study, it provides a useful baseline information for the *C. unciolor* conservation's management in montane forest landscape. The apparent tolerance of the species for different forest types; old growth, planted and natural regeneration; suggests that all the conservation strategies do not need to focus exclusively on old-growth forests as primary forests appear to remain likely important as a source population. Also, the identification of the rainy season as the critical period for juvenile presence and parental behaviour highlights the importance of reducing human disturbance and management activities, such as forest clearing, during this period. Finally, the estimated density of individuals/km², even if uncertain, provides a first reference point in Cloudbridge for population monitoring and can serve as a baseline for future estimates to compare the assessed population trends.

Conclusion

This study provides a quantitative baseline on the density, activity patterns, habitat use and ground behavioural ecology of *C. unicolor* in the cloud forest of Cloudbridge Nature Reserve. It combines camera trapping and line transect distance sampling. Three findings are shown to be robust and biologically significant despite the constraints imposed by a modest sampling effort. First, juvenile presence and parental behaviours were only present during the rainy season, with parental care recorded in 100% of events with juveniles, showing a synchronized reproductive strategy timed to seasonal resource availability. In second, the behaviour type; more than habitat, elevation or canopy cover, was the dominant driver of variations in event rate across cameras, a pattern confirmed by univariate test and multivariate model selection. Third, detection rates and behavioural rates showed no significant relationship with any habitat type or environment gradient. That suggests that, within the range of conditions sampled, the species may tolerate a degree of habitat heterogeneity, including natural regrowth and planted forest.

At the same time, some results, like the monthly fluctuations for the estimated density and the incidental observations of potential insectivorous foraging and territorial behaviours, should be taken as preliminary signals rather than affirmative conclusions. The small number of cameras, the short duration of the survey and the unequal distribution of sampling effort across all cameras and months constrain the statistical power of this study and lead with caution to the exploration of these findings to the broader population. Even if this work has some valuable results, these limitations show an improvement for future studies: expanding the camera trap network, extending the line transect surveys across a full annual cycle, and implementing to the ethogram the new potential behaviours as territorial interactions and insectivorous diet. These changes could considerably improve the future studies about this species.

Altogether, this study represents an initial ecological profile of *C.unicolor* that can directly inform conservation planning of this species in Cloudbridge Nature Reserve. The apparent flexibility in terms of habitat use suggests that conservation strategies don't need to be strictly restricted to old-growth forests. At the same time, the confirmation of the rainy season as a critical period for reproduction and the identification of Cloudbridge Nature Reserve as a reproduction site, highlight a specific temporal window in which human disturbance should be minimized. If the camera trap monitoring and the transect monitoring continue, the analytic pipeline developed here: as the effort-corrected detection rates, mixed-effects modelling of behavioural data, and multi-model AIC comparison; provides a reproducible baseline for tracking population and behavioural tendencies across time, and to improve our knowledge of this rarely studied species.

Appendix

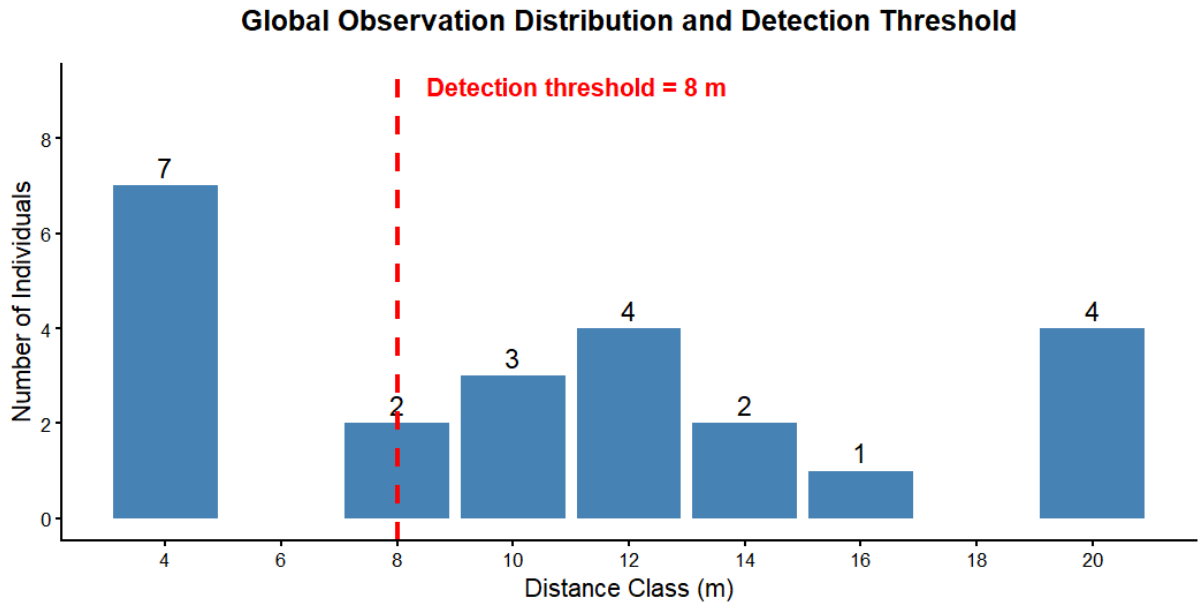


Figure A 1 : Global observation distribution and detection threshold

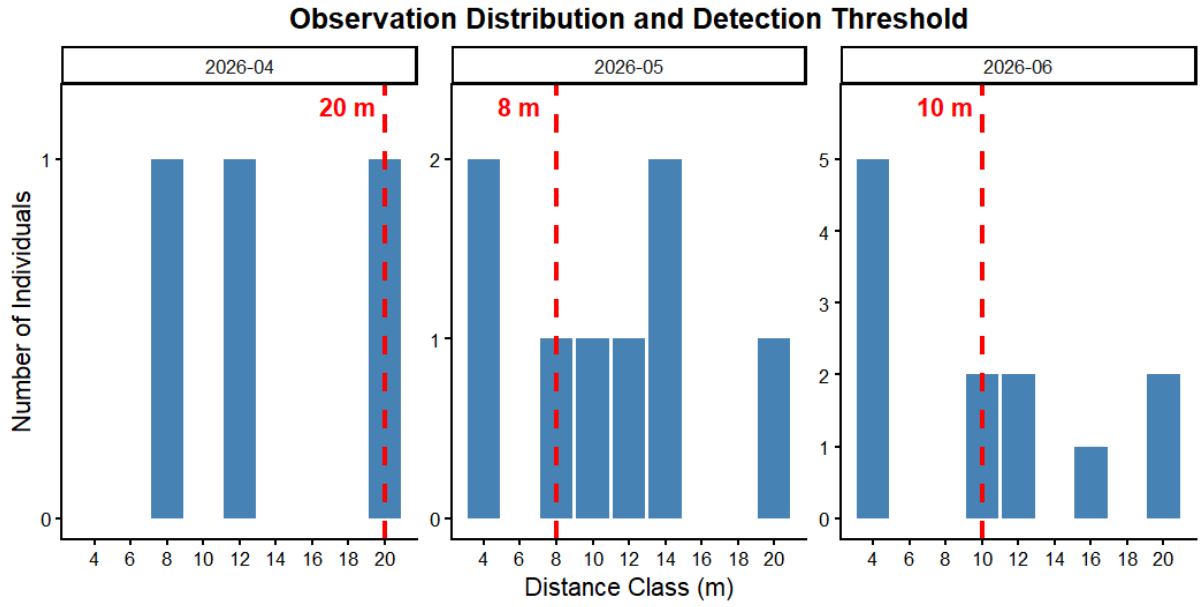


Figure A 2 : Observation distribution and detection threshold

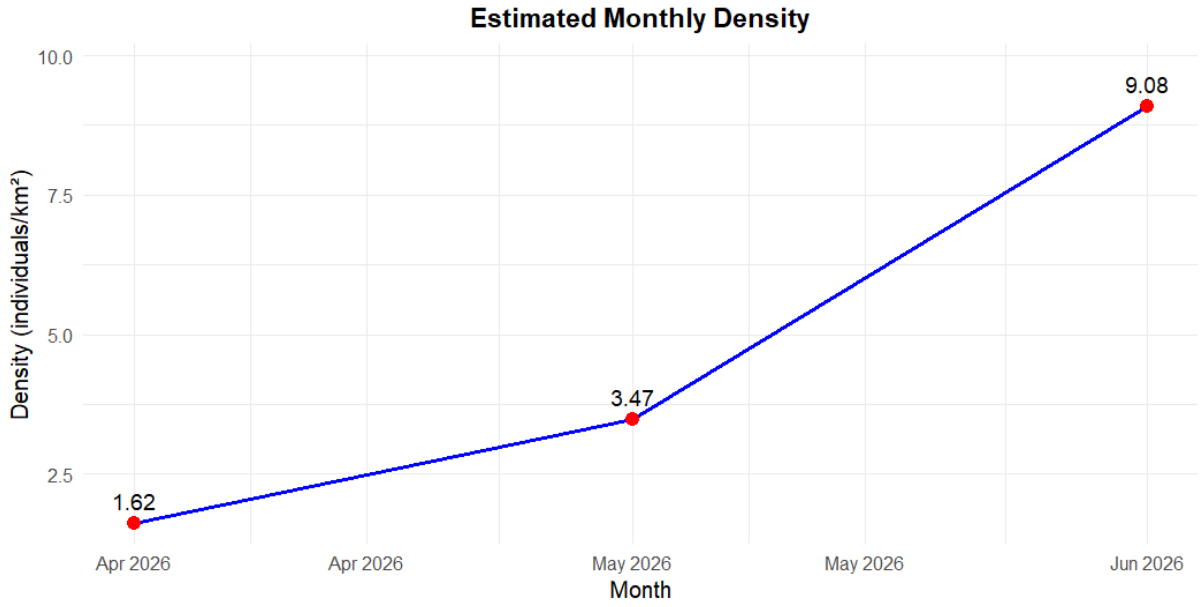


Figure A 3 : Estimated monthly density

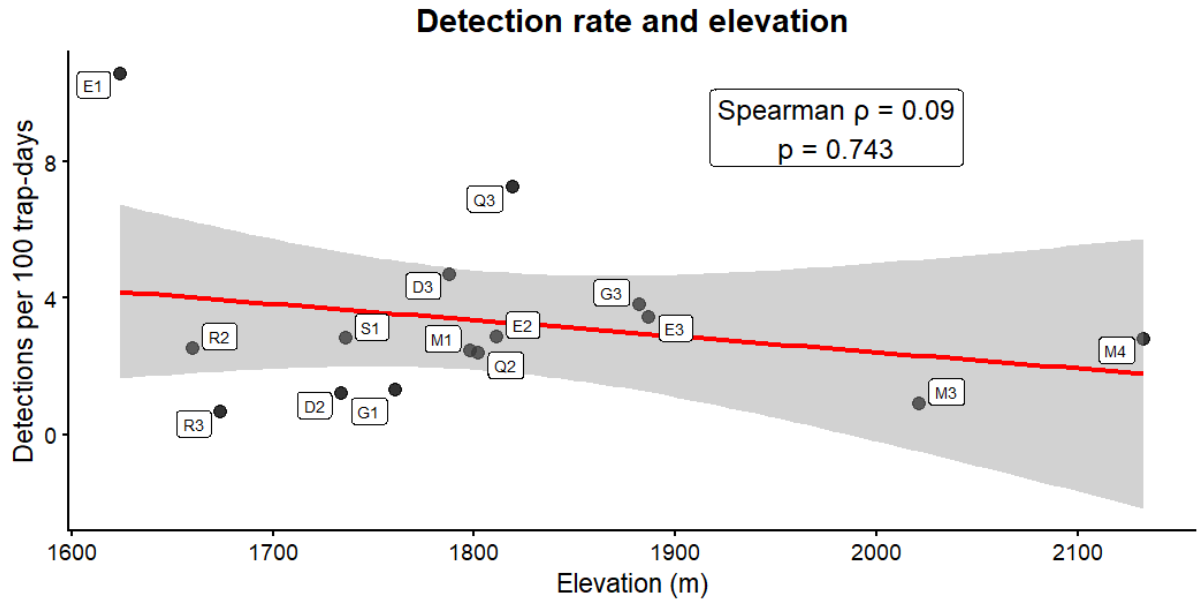


Figure A 4 : Detection rate and elevation

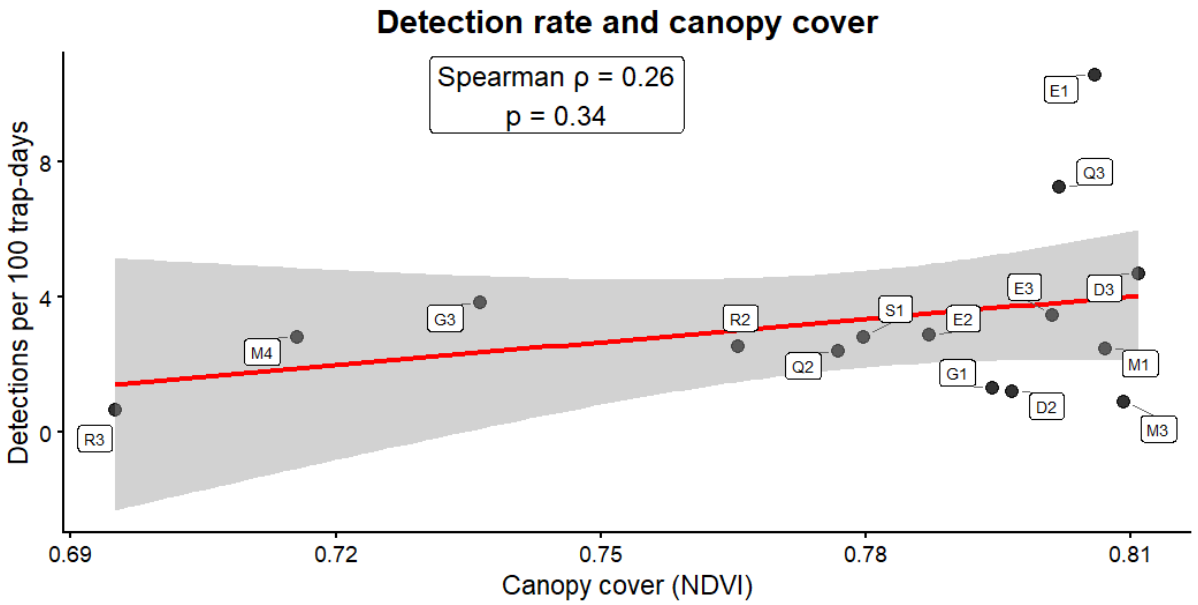
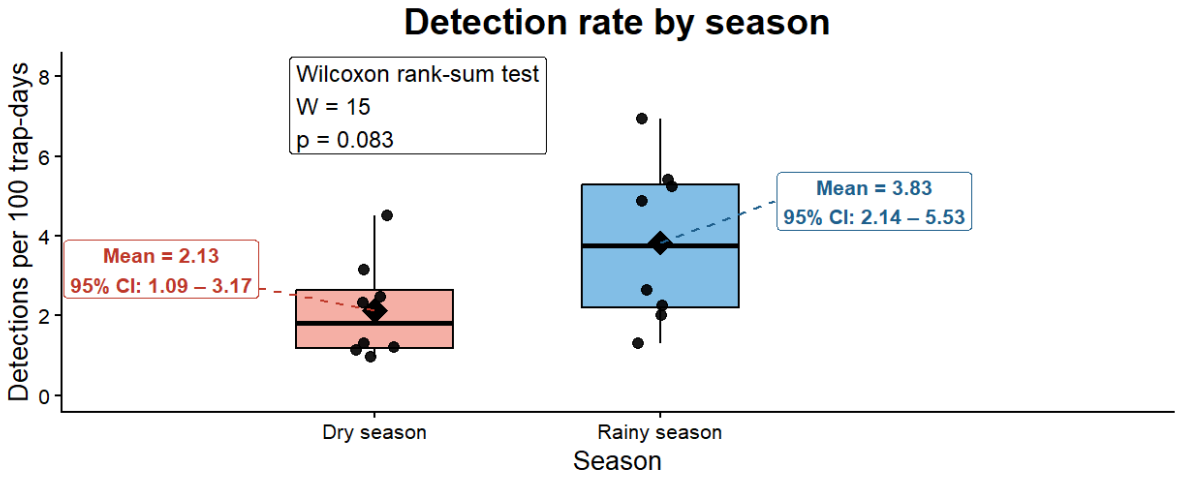


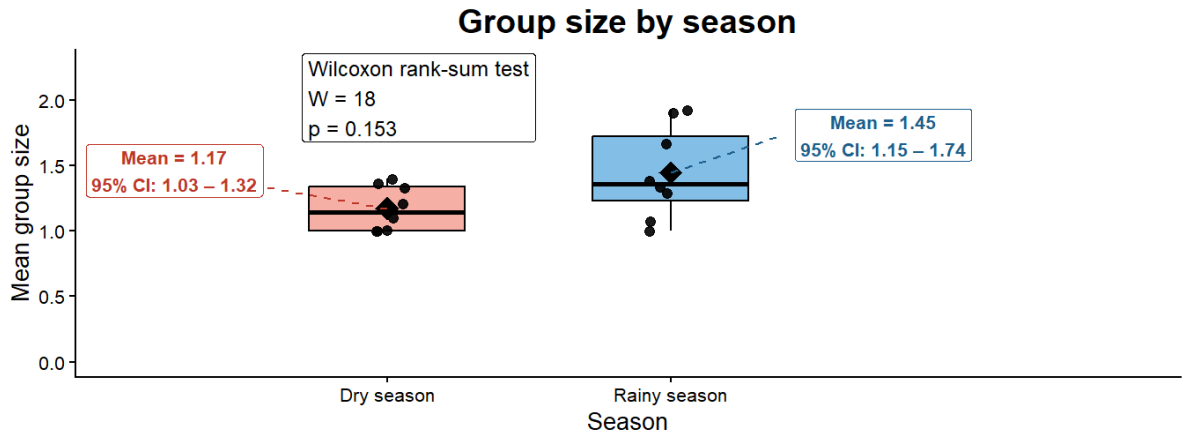
Figure A 5 : Detection rate and canopy cover



Season	n (months)	Mean	Median	SD
Dry season	8	2.13	1.82	1.24
Rainy season	8	3.83	3.76	2.03

Horizontal lines = medians; black diamonds = means; boxes = interquartile ranges.

Figure A 6 : Detection rates by season



Season	n (months)	Mean	Median	SD
Dry season	8	1.17	1.15	0.17
Rainy season	8	1.45	1.36	0.35

Horizontal lines = medians; black diamonds = means; boxes = interquartile ranges.

Figure A 7 : Group size by season

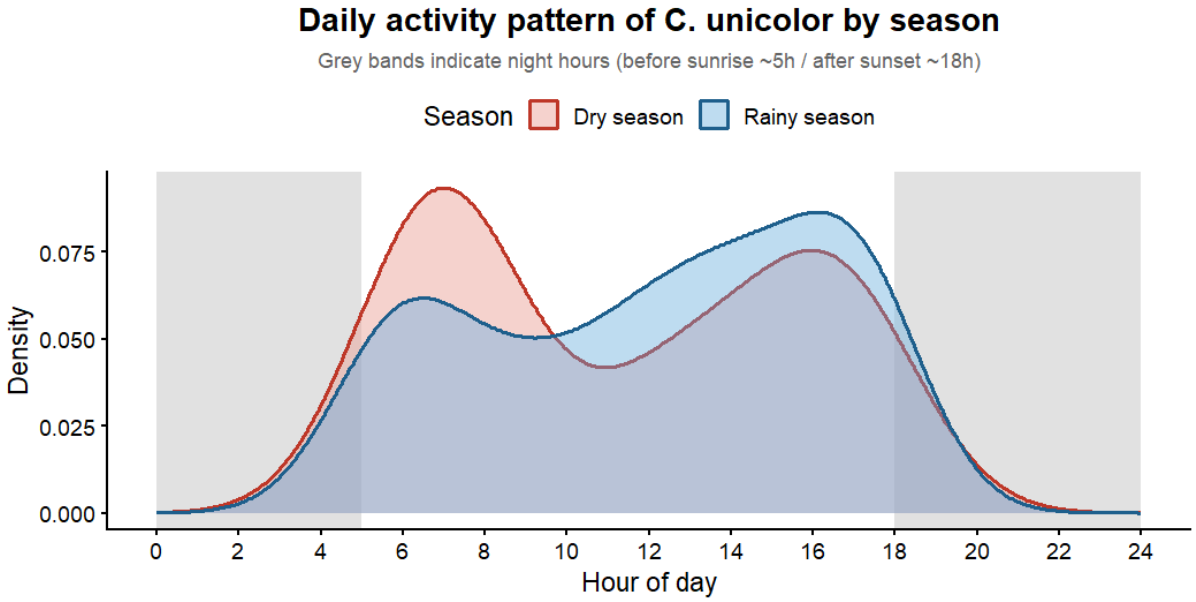


Figure A 8 : Daily activity pattern of Chamaepetes unicolor by season

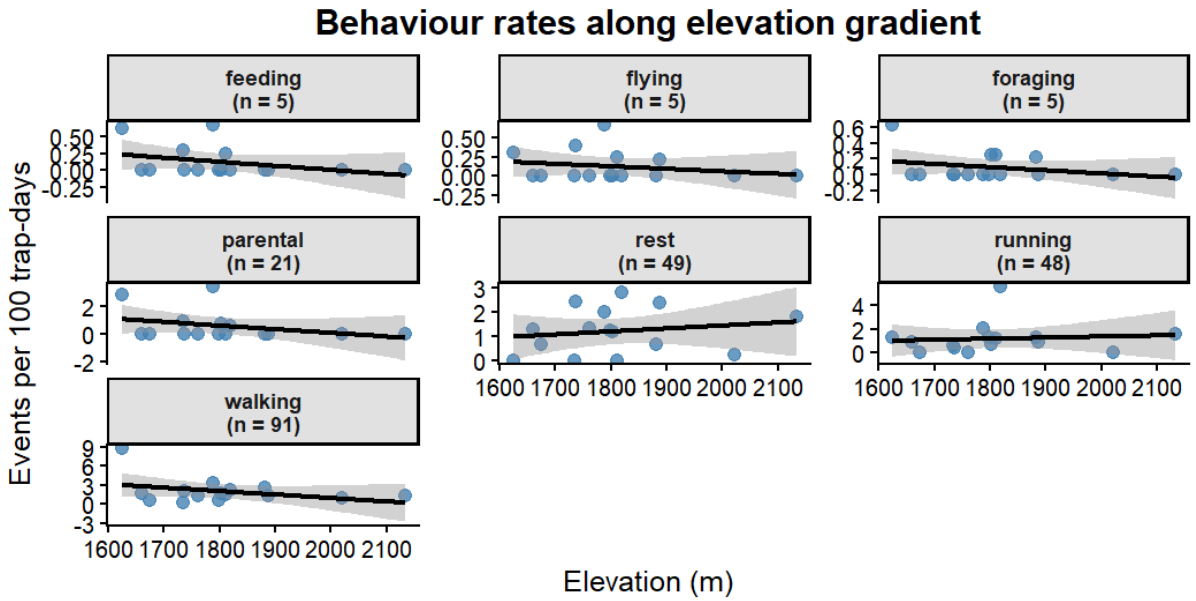


Figure A 9 : Behaviour rates along elevation gradient

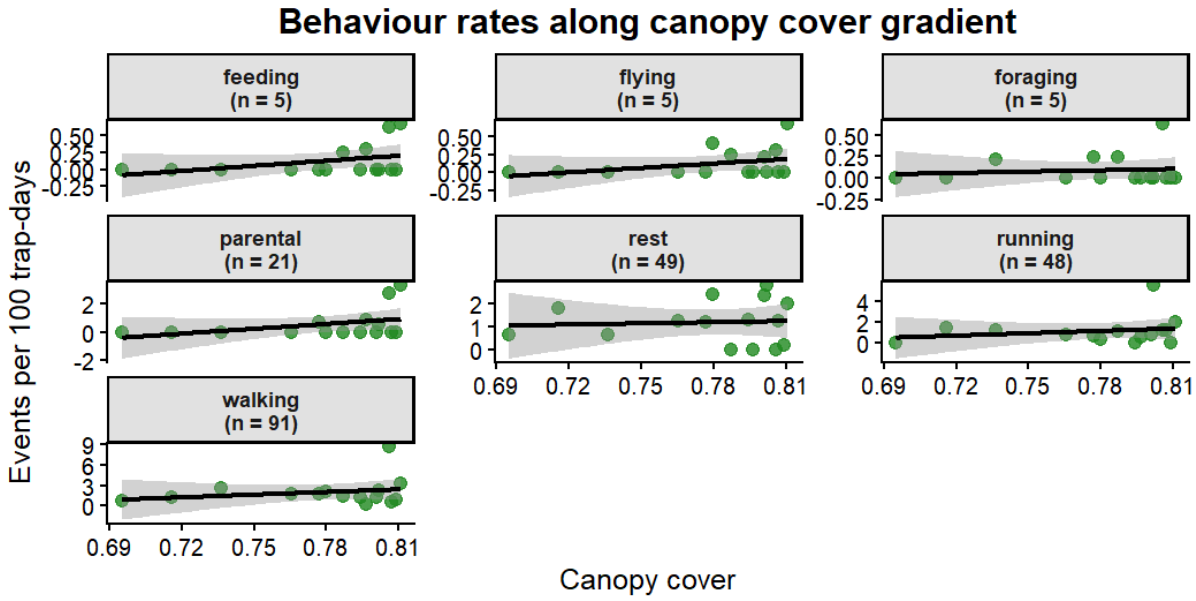


Figure A 10 : Behaviour rates along canopy cover gradient

Table of Illustrations

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