Shaped by the Forest

Research report about the behavioural differences of the white-nosed coati *(Nasua narica)* across the three forest types in Cloudbridge Nature Reserve.

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“Shaped by the Forest”

This research report focuses on the question of whether the behavioural patterns of the white-nosed coati (*Nasua narica*) differ between successional forest stages in Cloudbridge Nature Reserve. This study therefore aims to identify if behavioural patterns vary across the three forest types, assess whether solitary adult males, females and family bands differ in detection rates across these forest types and determine whether temporal activity patterns and seasonal detection rates are different in these forest types.

Cover image: Cloudbridge Nature Reserve (2023).

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Acknowledgements

This research report presents a study on the behaviour of the white-nosed coati (*Nasua narica*) across different forest successional stages in a montane cloud forest at Cloudbridge Nature Reserve. This report is written as a part of a research internship during the third year of the BSc Applied Biology programme at HAS green academy in Venlo. I would like to thank the team at Cloudbridge Nature Reserve for the opportunities and trust to conduct this research, as well as for their guidance, expertise and support in making this project possible. I would also like to thank my supervisor from HAS green academy, Sam Mulders for his guidance and support throughout the preparation and duration of this internship. With this research I hope to contribute to a better understanding of the ecosystem and the way in which forest succession influences animal behaviour and gain valuable insights into how conservation works on mammal communities.

Costa Rica, July 2026
Jade Delahaije

Abstract

Animal behaviour provides valuable insights into ecosystem functioning and can be used to evaluate the effects of habitat restoration. This study investigated whether forest type influenced the behaviour of the white-nosed coati (*Nasua narica*) within Cloudbridge Nature Reserve, Costa Rica. Because common species can provide insight into broader ecological processes that may also apply to more elusive mammal species. Data were collected during a 20-week field study period using motion-activated camera traps that are part of an ongoing long-term monitoring programme. Historical camera-trap data were incorporated to increase the temporal coverage of the study. Camera-trap observations were used to analyse behavioural patterns, detection rates of different social groupings (family bands, solitary males and solitary females), temporal activity patterns and seasonal detection rates across forest types. Forest type did not significantly influence behaviour patterns, social grouping, temporal activity patterns and seasonal detection rates. Instead, forest type primarily affected the overall number of detections, with planted forest showing higher detection rates than natural regrowth and old growth forest. Additional analyses revealed that behavioural patterns and seasonal detection rates differed significantly among social groupings, indicating that social organisation explained behavioural variation more strongly than forest type. These findings suggest that behavioural variation in *N. narica* is more strongly associated with intrinsic biological factors, such as social organisation and species-specific characteristics, than with differences in forest succession. The results further indicate that the forest types within Cloudbridge Nature Reserve provide ecological conditions suitable for *N. narica* to maintain its natural behavioural repertoire despite differences in successional stage. As behaviour reflects how animals interact with their environment, these findings provide encouraging evidence that restoration efforts are supporting functional habitat conditions for a habitat generalist species like *N. narica.* Continued monitoring of both common and rarer mammal species is recommended to improve understanding of ecological processes and to evaluate the long-term effectiveness of forest restoration for conserving mammal communities.

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1. Introduction

Since 1970 wildlife populations have declined by an average of 73% (WWF, 2024). Right now, the loss of biodiversity is happening 10 to 100 times faster than the natural baseline. The loss is progressing at a concerning pace (IPBES, 2019). This accelerated decline is largely driven by increased human pressure on natural ecosystems, which has substantially reduced global biodiversity over the past five decades (Foley et al., 2005; Millennium Ecosystem Assessment, 2005). Habitat fragmentation, deforestation and climate change have contributed substantially to biodiversity decline (Foley et al., 2005; IPBES, 2019). All life on Earth, including humans, relies on biodiversity, as it is responsible for various ecosystem services, resources and products (IPBES, 2019).

Restoring biodiversity is therefore essential (Fisher et al., 2012). Conservation efforts have played an important role in mitigating biodiversity loss and remain crucial for preventing further declines (Pimm et al., 1995). By protecting ecosystems and maintaining key ecological processes, conservation strategies help safeguard species and ecosystem functioning. In addition, actively restoring degraded ecosystems is vital to reverse biodiversity loss. This can be achieved through habitat rehabilitation to enable the recovery of functional ecosystems, replanting native vegetation and the removal of invasive species (Roux, 2025). One of the leaders in biodiversity conservation is Costa Rica (Jiménez et al., 2015). It is recognized as one of the world's 36 biodiversity hotspots (Myers et al., 2000). Despite covering only approximately 0.03% of the Earth's total land surface, the country houses an estimated 5% of the global biodiversity (Wainwright, 2007). This richness is reflected in high species density, defined as the number of species per unit of area (Valerio, 1999; Acuña, 2002). Costa Rica actively protects its nature by restoring habitats and promoting wildlife recovery (Tafoya et al., 2020). These conservation efforts range from government-supported national parks to smaller, privately managed initiatives that contribute to nature protection through diverse approaches (Fabiano & Ahmed, 2019).

One of these privately managed initiatives is Cloudbridge. Cloudbridge is a private nature reserve located on the Pacific slope of the Talamanca mountain range in Costa Rica. Established in 2002, the reserve covers nearly 200 hectares and has four mission points: conservation, reforestation, education and research (Cloudbridge Nature Reserve, 2025). In the past, the area was dominated by agriculture and cattle pasture. Due to restoration and replanting of native vegetation, it is now a montane cloud forest. Which supports high vertebrate diversity, including multiple threatened species such as the jaguar, oncilla, central American spider monkey and dice's cottontail (Cloudbridge Nature Reserve, n.d.-a). Cloud forests are a rare and fragile ecosystem, making up approximately 2.5 percent of tropical forests worldwide (Bubb et al., 2004). They play a crucial role in regulating water cycles due to their high capacity for moisture retention (Oliveira et al., 2014). The reserve functions as a research and educational platform supported by local staff and international researchers (Cloudbridge Nature Reserve, n.d.-b). Successional forests are known to vary considerably in their abiotic and biotic characteristics as a result of age and historical land use (Guariguata & Ostertag, 2001). This is reflected within Cloudbridge, where reforestation and conservation efforts have resulted in three distinct forest types: old growth forest, natural regrowth forest and planted forest (Fleer, 2017).

Successional forest stages can strongly influence how species use their habitat (Suchomel et al., 2020). Habitat selection is not random, but is driven by resource availability (Prevedello et al., 2010). As a result, mammalian behaviour can provide valuable insights into ecosystem

structure and functioning. Understanding habitat use is fundamental for identifying the environmental factors that determine species distribution and abundance, as animals tend to occupy areas that offer suitable resources rather than using areas randomly (Garshelis, 2000).

Behavioural research plays an important role in conservation, as it helps to understand how animals interact with their environment and respond to management and restoration actions, thereby influencing conservation outcomes (Greggor et al., 2019; Sutherland, 1998). Due to practical considerations such as detectability and sample size, behavioural studies are often conducted on relatively common species, which allow the collection of sufficient data for robust ecological analyses (McGill et al., 2007). Common species may provide insight into broader ecological processes shaping mammal communities (Siddig et al., 2016). Patterns observed in common species can help identify habitat features that are likely important for rarer species, although such extrapolations should be made cautiously (Gaston, 2011). As rare species are often more specialised and less behaviourally flexible, meaning their responses may differ (Lindenmayer & Likens, 2011)

One of the most common species in Cloudbridge Nature Reserve is the white-nosed coati (*Nasua narica*). They are part of the family *Procyonidae*, same as kinkajous and raccoons. *N. narica* is the most social species of this family and their social structure is known to influence behavioural patterns (Gompper, 1996). They are diurnal and display a complex social structure: adult males are solitary, and females live in family bands with juveniles of both sexes. However, an unusual feature occurs: three to four weeks before parturition, females leave the family bands to give birth and nurse their young up to 35 – 40 days postpartum (Russell, 1982). Males disperse and become solitary at around two years of age (Gaston, 2022; Kaufmann, 1962). Neotropical mammals play a key role in tropical ecosystems, as they interact within food chains (Cuarón, 2000). *N. narica* is an omnivore and a generalist feeder, mainly eating insects and fruits (Gompper, 1995).

Previous studies have examined the behaviour of *N. narica,* including differences in social and asocial behaviour across altitudinal gradients and microhabitat preference. Although altitude did not affect distribution, it did influence behaviour: individuals at lower elevations displayed more social behaviour, whereas those at higher elevations showed a higher proportion of asocial behaviour (Gaston, 2022). *N. narica* were mainly observed in natural regrowth forest, however, none of the measured microhabitat variables were significantly associated with sightings (Nicolau, 2022).

Despite these findings, it remains unclear whether behavioural patterns differ across successional forest stages. Investigating behavioural differences among forest types may provide valuable insight into how *N. narica* responds to variation in forest structure, successional dynamics and restoration efforts. Such knowledge may contribute to a broader understanding of ecosystem functioning and animal responses to restoration, while providing important guidance for conservation and ecosystem management strategies, ultimately supporting more effective conservation outcomes. Therefore, this study aimed to (1) determine if forest type influences behavioural patterns, (2) investigate whether solitary adult males, females and family bands differ in detection rates across forest types, (3) evaluate whether daily temporal activity patterns differ among forest types and (4) determine if seasonal detection rates differ among the three forest types. By using cameras already deployed in the reserve across the three forest types for a period of 18 weeks, complemented by historical data.

Objectives

General objective:

To investigate how the behaviour of the white-nosed coatis (*Nasua narica*) varies across the three forest types in Cloudbridge Nature Reserve, in order to better understand how habitat differences influence behavioural patterns.

Secondary objectives

1. To investigate whether forest type influences behavioural patterns.
2. To evaluate whether solitary adult males, females and family bands differ in detection rates across forest types.
3. To assess whether daily temporal activity patterns differ among the three forest types.
4. To determine if seasonal detection rates differ among the three forest types.

2. Methodology

2.1 Study Area

This study was conducted within Cloudbridge Nature Reserve, located in the Talamanca mountain range. The reserve spans an elevational gradient of 1,500–2,200m and is characterized by steep mountainous terrain. It consists of tropical montane cloud forest, with daytime temperatures typically ranging from 25–30°C, while nighttime temperatures drop to 10–20°C. The reserve comprises three distinct forest types: planted forest, natural regrowth forest and old growth forest. Maps illustrating the different forest types and camera trap locations are presented in Figure 1 and Figure 2. Some of the stations shown on the map are no longer active, but have been in the past and provided historical data. Additional details on the stations are shown in Appendix 1.

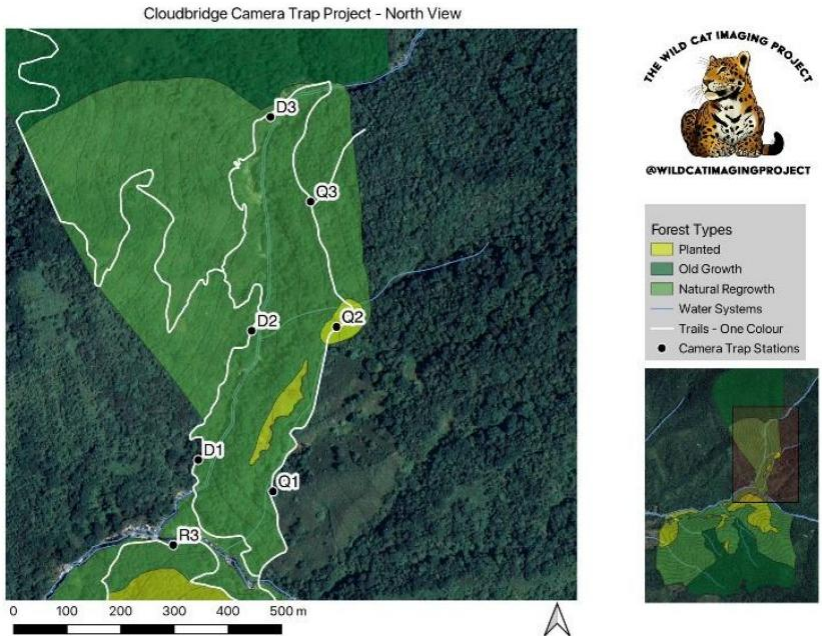

Figure 1: Map of the northern section of the study area within Cloudbridge Nature Reserve, showing the different forest types (color-coded) and the location of camera traps labelled by camera name.

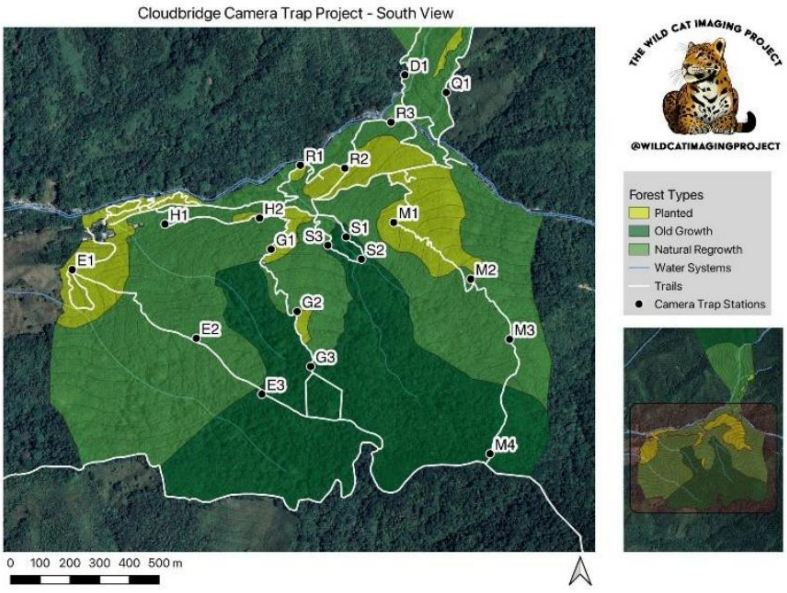

Figure 2: Map of the southern section of the study area within Cloudbridge Nature Reserve, showing the different forest types (color-coded) and the location of camera traps labelled by camera name.

2.2 Camera trap setup

Camera traps used in this study were predominantly Browning Trail Cameras (BTC-7E-HP5). All cameras were mounted approximately 40–50 cm above ground level and positioned to maximize visibility of the trail surface, thereby increasing the likelihood of detections. The cameras were configured using the following settings: video mode, 1-second trigger delay, 10-second recording length, ultra video quality, high sensitivity, smart IR enabled, HDR enabled, Image data strip enabled and temperature displayed in Fahrenheit. Each time a new SD card was inserted, the card was formatted by selecting the "delete all" option on the camera. All camera traps operated continuously, remaining active 24 hours per day throughout the sampling period.

2.3 Data collection and processing

Fieldwork and data collection for this study took place between 23 February and 26 June. During this period, motion-activated camera traps were used to collect wildlife data. These camera traps had already been deployed as part of an ongoing long-term research project at Cloudbridge Nature Reserve. Since deployment, the cameras had continuously collected data and remained active 24 hours per day. In addition to data collected during the fieldwork period, all available historical camera trap data stored on the external project hard drive were included in the analysis. Because the duration of camera deployment differed among stations, the active sampling period varied between camera trap locations. The total amount of active camera trap nights per camera can be found in Appendix 1.

Each camera trap station was checked every two weeks according to a fixed rotation schedule. During these checks, SD cards were replaced and collected and batteries were replaced when necessary. Once collected, the camera trap videos were reviewed, organised and processed using a protocol originally developed by Benjamin Luke, founder of The Wild Cat Imaging Project, and subsequently adapted for this study (Appendix 2). The camera trap videos were used to assess the behaviour of *N. narica* and to analyse social grouping.

Behaviour was classified using an ethogram adapted from the classification developed by Gaston (2022), shown in Appendix 3. The original ethogram was modified to better suit the present study and the characteristics of camera trap footage. Behaviours that were considered ambiguous, difficult to distinguish or not biologically relevant were removed. In addition, new behaviours were added to account for behaviours that were observed in the camera trap videos but were not included in the original ethogram. Social grouping classification was based on visible sex characteristics and the number of individuals. Date and time were also recorded to analyse temporal activity patterns and seasonal detection rates. For each observation the date, time, camera ID, forest type, social grouping and behaviour were recorded. To reduce pseudo-replication, consecutive camera trap videos recorded within a five-minute interval were treated as a single detection event, unless clear morphological differences indicated the presence of different individuals. For social groups, all individuals passing a camera within the same five-minute interval were considered part of a single event and recorded as one detection. Videos were excluded from behavioural analyses when species identification was uncertain or when behaviour could not be reliably classified when only part of the animal was visible.

2.4 Statistical analysis

For all the objectives the collected data were stored in Microsoft Excel (version 2511) and analysed using R-Studio (version 2026.01.0+ 392). The statistical analysis focused on the four objectives and statistical significance was assessed at $\alpha = 0.05$.

2.4.1 Behavioural patterns

To investigate whether forest type influenced behavioural patterns of *N. narica*, count-based generalized linear models (GLM) were fitted. Behavioural observations were analysed as count data, with the number of observations per behaviour type per camera station used as the response variable. Data were visualised using a grouped bar plot to explore differences in behavioural frequencies among forest types. A negative binomial generalized linear model was used, because the data showed substantial overdispersion. Sampling effort was standardised by calculating the number of active trap nights per camera. These active trap nights were included as a log-transformed offset term to account for unequal sampling effort among camera stations. A negative binomial model was fitted with forest type and behaviour as fixed explanatory variables. Type III likelihood ratio chi-square tests were used to assess the overall significance of forest type and behaviour. Pairwise comparisons among forest types were performed using estimated marginal means with Tukey-adjusted post-hoc tests. To assess whether forest type influenced behavioural patterns, an interaction term between forest type and behaviour was added to the model. Models with and without the interaction term were compared using a likelihood ratio chi-square test.

2.4.2 Social grouping

To assess whether forest type influenced differences in detection rates of solitary adult males, solitary females and family bands, a generalized linear model (GLM) with a negative binomial error distribution was fitted, as the response variable consisted of count data and showed overdispersion. There were also detections where it was unclear which social grouping was involved, because no genitals were visible. For those detections, 'unknown' was entered and they were not included in the statistical analyses. The social grouping was visualized using a grouped bar plot to explore the difference in detection rates among forest types. Detection counts were modelled as a function of forest type, social grouping and their interaction. The number of active camera trap nights was included as a log-transformed offset to make up for variation in sampling effort. First the main effects of social grouping and forest type were tested separately, followed by an interaction model including both predictors. Significance of main effects and interaction was assessed using likelihood ratio chi-square tests based on analysis of deviance. Post-hoc pairwise comparisons were conducted using estimated marginal means with Tukey adjustment for multiple testing.

2.4.3 Temporal activity patterns

To determine whether forest type influences the temporal activity patterns of *N. narica*, activity patterns were visualised using kernel density estimation (KDE) plots, based on the camera trap detection times. These plots were used to compare diel activity patterns among the three forest types. Differences in temporal activity distributions were statistically assessed using the Watson-Wheeler test for homogeneity of circular data. In addition, pairwise overlap coefficients (Δ) were calculated to quantify the similarity of activity patterns between forest types. The values were categorized as $\Delta \leq 0.25$ indicating low overlap, $0.25 > \Delta < 0.5$ mid-low, $0.5 < \Delta < 0.75$ mid-high, and $\Delta > 0.75$ high overlap.

2.4.4 Seasonal detection rates

To analyse whether forest type influences the seasonal detection rates of N. narica, camera trap detections were aggregated per month and camera station. To account for unequal sampling effort among camera trap stations and months, active camera trap nights were included as an offset in the model. Seasonal detection rates were visualized using line plots of monthly detection rates across forest types. Detection counts were analysed using a negative binomial generalized linear model (GLM) with a log link to account for overdispersion in the count data. Monthly detections were modelled as a function of month, forest type and their interaction. Main effects of month and forest type were evaluated first, after which an interaction term was included to test whether seasonal detection patterns differed among forest types. Model significance was assessed using likelihood ratio chi-square test based on analysis of deviance, where the models with and without the interaction term were compared. Post-hoc pairwise comparisons were performed using estimated marginal means with Tukey adjustment to account for multiple comparisons.

3. Results

This study focused on multiple objectives to investigate behavioural differences of *N. narica* and the influence of forest type within Cloudbridge Nature Reserve. First, the results regarding behavioural patterns across forest types are presented. Second, differences in social grouping detections among forest types are described. Third, temporal activity patterns are analysed to assess whether activity timing differs in the three forest types. Finally, seasonal detection rates are presented to evaluate whether seasonal activity patterns vary across forest types.

3.1 Behavioural patterns

A total of 752 independent detections were recorded across the three forest types, representing a range of behavioural categories. Behavioural observations appeared to be most frequent in planted forest (Figure 3). Behavioural counts differed significantly among forest types (χ^2 = 30.95, df = 2, $p < 0.001$). Post-hoc comparisons showed significantly higher detection rates in planted forest compared with natural regrowth ($p = 0.0003$) and old growth forest ($p < 0.0001$), whereas no significant difference was found between natural regrowth and old growth forest ($p = 0.226$). The frequency also differed significantly among behaviour categories ($\chi^2 = 68.93$, df = 12, $p < 0.001$), with walking, foraging and running among the most frequently observed behaviours. However, the interaction between forest type and behaviour showed no significant effect (Ratio $\chi^2 = 12.70$, df = 14, $p = 0.55$).

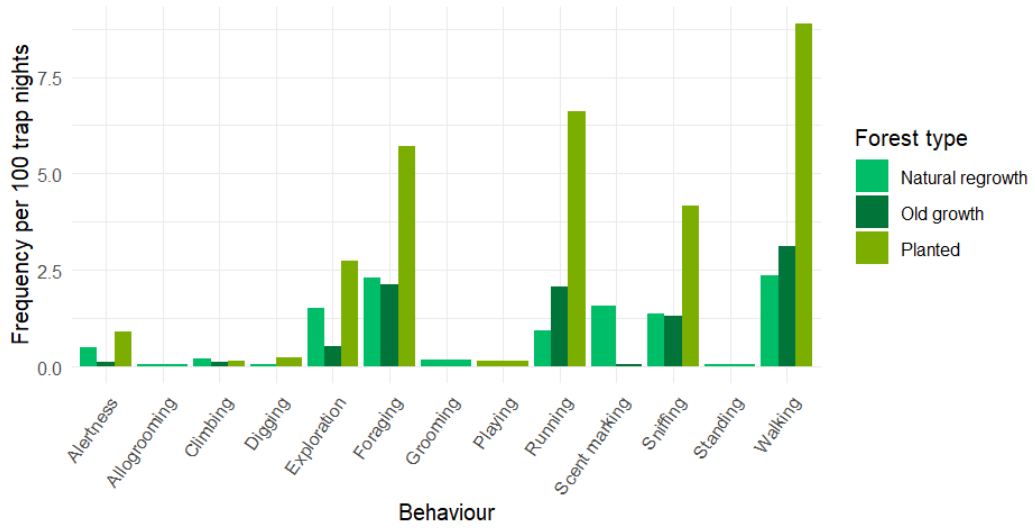

Figure 3: Grouped bar plot showing the frequency of behavioural categories of N. narica across the three forest types, standardized by 100 trap nights. Behaviour categories are displayed on the x-axis, behavioural frequency on the y-axis, and colours represent the three different forest types.

3.2 Social grouping

A total of 522 independent detections of *N. narica* were included in the analysis across 17 camera trap locations, spanning the three forest types: natural regrowth, old growth and planted forest. The three social groupings: solitary male, female and family bands were recorded in all forest types (Figure 4). Detections differed significantly among forest types ($\chi^2 = 15.29$, df = 2, $p < 0.001$). Post-hoc comparisons showed significantly higher detection rates in planted forest compared with natural regrowth ($p = 0.0044$) and old growth forest ($p = 0.0032$), whereas no significant difference was found between natural regrowth and old growth forest ($p = 0.9232$). Social grouping also showed a significant effect between the different categories ($\chi^2 = 8.34$, df = 2, $p = 0.015$). Post-hoc comparisons revealed that females had significantly lower detection rates than family bands ($p = 0.011$, while solitary males did not differ significantly from family bands ($p = 0.824$) and showed a trend compared to females ($p = 0.058$). An interaction between forest type and social grouping showed no significant interaction effect ($\chi^2 = 1.34$, df = 4, $p = 0.86$). But post-hoc comparisons indicated a significant difference between females and family bands in planted forest ($p = 0.0380$), however this pattern was not consistent across other forest types. Although one pairwise comparison was significant, the overall interaction between forest type and social grouping was not significant.

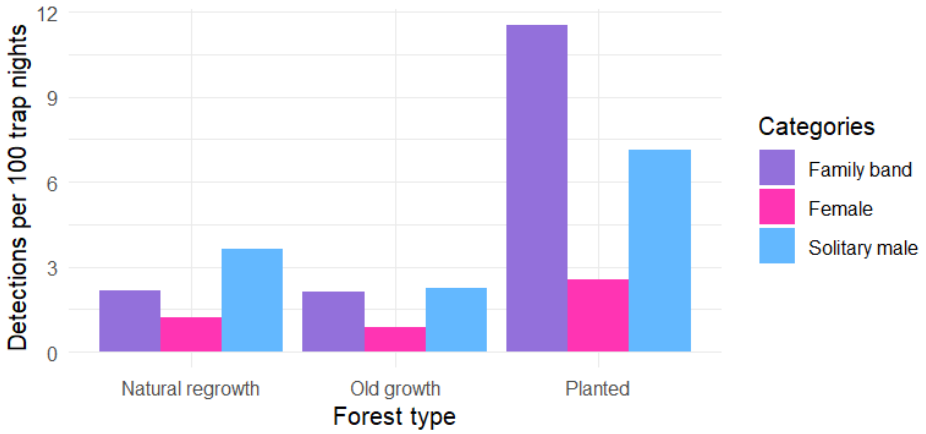

Figure 4: Grouped bar plot showing the detections of the different social groupings of N. narica across the three different forest types, standardized by 100 trap nights. The forest types are displayed on the x-axis, the frequency of detections on the y-axis and the different colours represent the different social groupings.

3.3 Temporal activity patterns

Figure 5 illustrates the temporal activity patterns of *N. narica* across the three forest types. *N. narica* exhibited a predominantly diurnal activity pattern, with most detections occurring between 5 a.m. and 5 p.m. Kernel density estimates showed highly similar activity distributions among the forest types. Pairwise overlap coefficients were high ($\Delta = 0.90–0.93$) across all forest-type comparisons. Mean activity times were also similar among forest types, ranging from 11.4–11.7 hours. The Watson-Wheeler test also showed that there were no significant differences in temporal activity patterns between the forest types ($W = 4.73$, df = 4, $p = 0.32$).

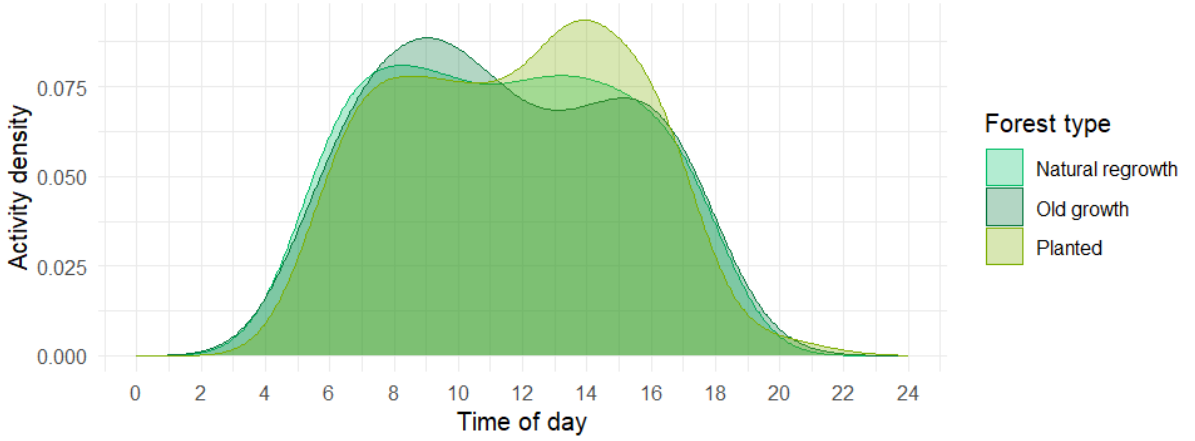

Figure 5: Temporal activity pattern of N. narica in the three different forest types based on kernel density estimates. The time of day is displayed on the x-axis, activity density on the y-axis, colours indicate the different forest types and the curves represent the relative activity distribution over a 24-hour period.

3.4 Seasonal detection rates

A line plot shows the seasonal detection rates of *N. narica* across the three different forest types. Month as a predictor had no significant effect on detection rates ($\chi^2 = 11.11$, df = 11, p = 0.434). In contrast, forest type had a significant effect on detection rates ($\chi^2 = 12.57$, df = 2, p = 0.0019), with planted forest exhibiting higher detection rates than natural regrowth and old growth forest (Figure 6). However, the interaction between month and forest type was not significant ($\chi^2 = 11.52$, df = 22, p = 0.967). Post-hoc comparisons revealed no significant differences between months within forest types or between forest types within individual months.

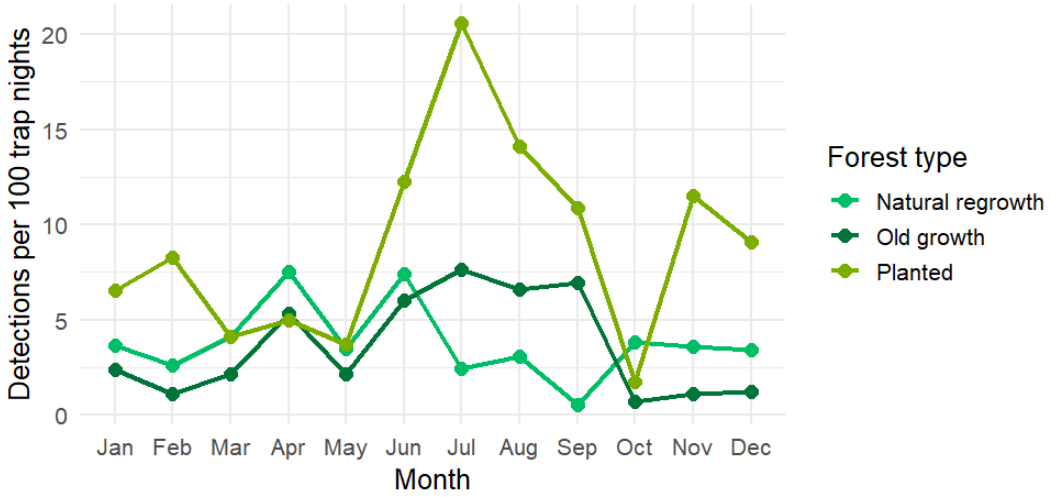

Figure 6: Line plots showing the seasonal detection rates of N. narica across the three forest types, standardized per 100 trap nights. The months are displayed on the x-axis, the frequency of detections on the y-axis and the colours indicate the three different forest types.

3.5 Additional analyses

Because forest type showed no influence on the behavioural patterns, temporal activity patterns and seasonal detection rates of *N. narica*, additional exploratory analyses were conducted. These analyses were conducted to investigate whether another explanatory variable could be found. These analyses were not part of the original objectives, but were included to provide further ecological interpretation of the observed patterns

3.5.1 Behavioural patterns across social groupings

Behaviour composition differed significantly among social groups ($\chi^2 = 128$, $p < 0.001$). Family bands showed higher frequencies of foraging and running behaviour, whereas solitary males exhibited relatively more scent marking. Solitary females showed relatively higher frequencies of alertness and walking behaviour as shown in Figure 7.

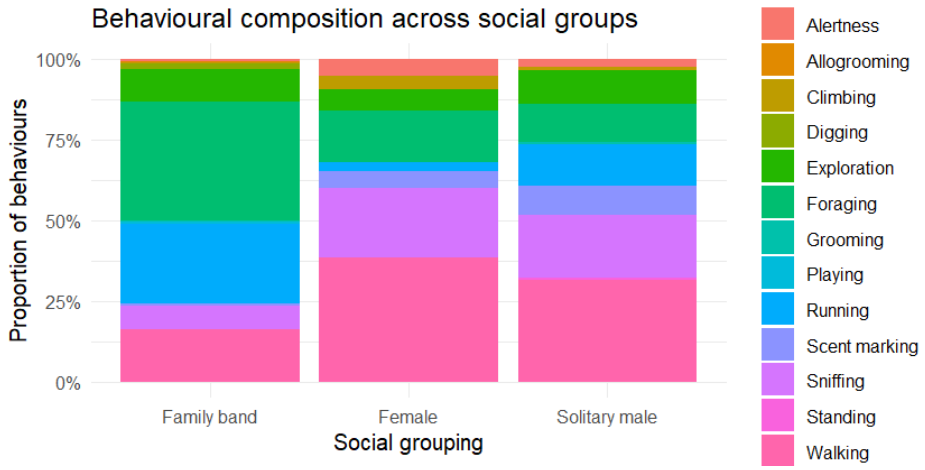

Figure 7: Stacked bar plot showing the proportion of behavioural categories across different social groupings. The social groupings are displayed on the x-axis, the proportion of behaviours on the y-axis and the colours indicate the different types of behaviour.

3.5.2 Temporal activity patterns among social groups

A Watson–Wheeler test showed no significant differences in temporal activity patterns among social groups, as shown in Figure 8 ($W = 5.54$, $df = 4$, $p = 0.236$). Pairwise overlap coefficients were consistently high ($\Delta = 0.868–0.924$).

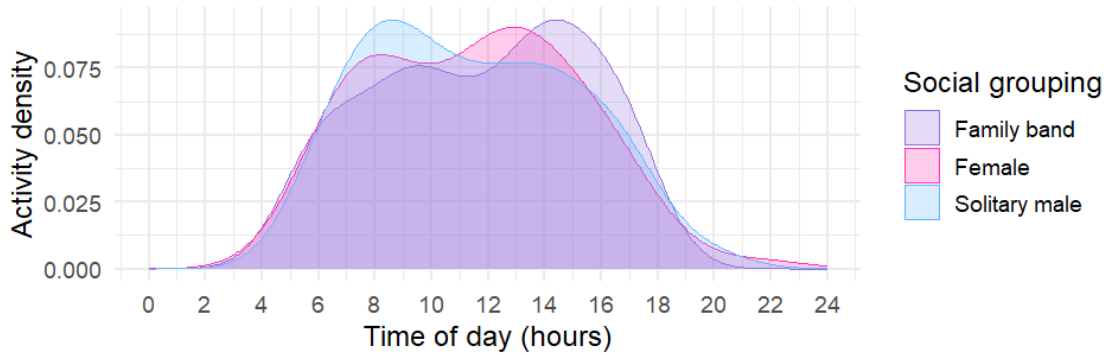

Figure 8: Temporal activity pattern of N. narica across the three social groupings based on kernel density estimates. The time of day is displayed on the x-axis, activity density on the y-axis, colours indicate the different social groupings and the curves represent the relative activity distribution over a 24-hour period

3.5.3 Seasonal detection patterns among social groups

Seasonal detection patterns differed significantly among social groups (Figure 9). A negative binomial model revealed a significant effect of the interaction between month and social grouping ($\chi^2 = 70.44$, df = 22, $p < 0.001$).

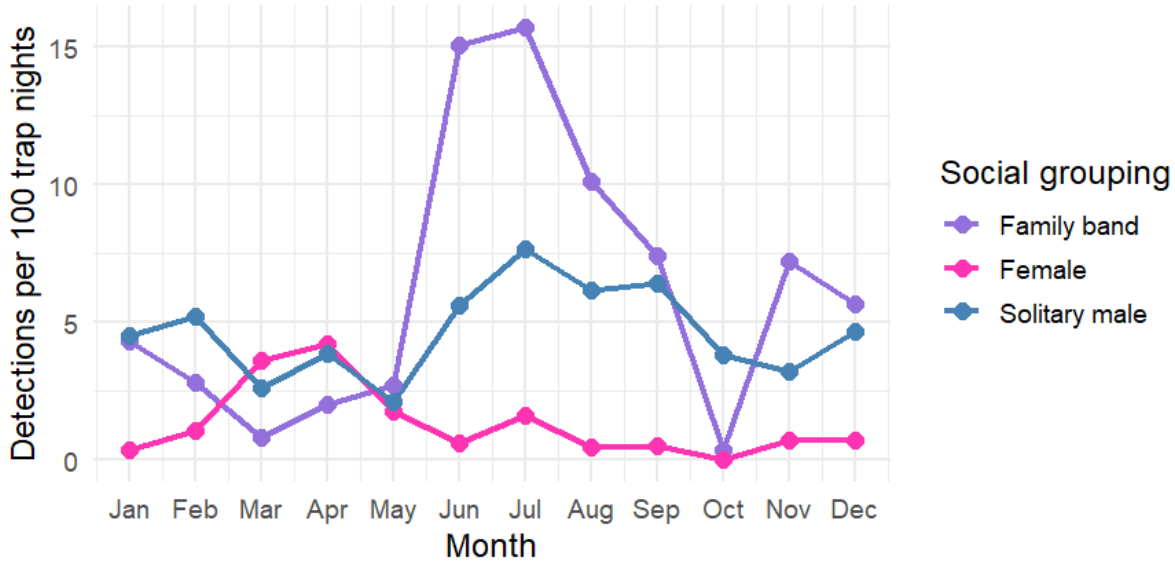

Figure 9: Line plots showing the seasonal detection rates of N. narica across the three social groups, standardized per 100 trap nights. The months are displayed on the x-axis, the frequency of detections on the y-axis and the colours indicate the three different social groups.

4. Discussion and conclusion

This study investigated whether forest type influenced the behaviour of *N. narica* within Cloudbridge Nature Reserve. Although planted forest yielded significantly higher overall detection rates than natural regrowth and old growth forest, behavioural patterns, social organisation, temporal activity patterns and seasonal detection rates remained largely consistent across forest types. While additional results showed that social organisation did influence behavioural patterns and seasonal detection rates. This indicates that behavioural differences were explained more by social organisation than by differences in forest type.

The higher detection rates in planted forest may be related to the species' preference for open forests and tropical woodlands (Cuarón et al., 2016). This is consistent with a previous camera-trap study in Costa Rica, which described *N. narica* as a habitat generalist and well adapted to human-modified landscapes, including regenerating forest (Cove et al., 2014). Cove et al. (2014) also reported that detection probability decreases with increasing forest cover, suggesting that differences in vegetation structure may partly explain the higher detection rates observed in planted forest. In contrast, Nicolau (2022) reported the highest number of detections in natural regrowth forest within Cloudbridge Nature Reserve. However, Nicolau (2022) did not account for variation in sampling effort and natural regrowth contained substantially more camera stations than planted forest. By incorporating active camera trap nights as an offset in statistical analyses, the present study provides a more reliable comparison of detection rates among forest types. Likewise, Gaston (2022) found that individuals at lower elevations displayed more social behaviour, than those at higher elevations, whereas no differences in behavioural patterns among forest types were detected in the present study.

Behavioural frequencies also differed significantly among behavioural categories, with walking, foraging and running being the most frequently recorded. These behaviours are characteristic for the species, as *N. narica* spends approximately 90% of its active time foraging on the ground (Kaufmann, 1962; Russell, 1982). Importantly, behavioural patterns did not differ among forest type, indicating that *N. narica* expressed similar behaviour repertoire regardless of forest type. This consistency suggests that the restored forest types within Cloudbridge Nature Reserve provide suitable habitat that allows the species to maintain their natural behaviour. Interestingly, the additional analyses showed that behavioural patterns were influenced by social organisation. Family bands were characterises by higher frequencies of foraging and locomotion behaviours, whereas solitary males exhibited more scent marking and females showed higher levels of vigilance and walking. These findings suggest that the behavioural pattern of *N. narica* is reflected more by species-specific social roles, than by differences in forest succession.

Social organisation also influenced detection rates. Family bands were detected significantly more often than solitary females, whereas no difference was found between family bands and solitary males. The comparison between solitary males and solitary females only showed a statistical trend. This pattern is consistent with the natural social organisation of *N. narica*, in which adult females normally live in family bands together with juveniles, while adult males are predominantly solitary outside of the breeding season (Kaufmann, 1962; Russell, 1982). Consequently, solitary females are expected to be detected less frequently than family bands. One explanation for this social organisation of *N. narica* is the anti-predator advantage associated with group living. Previous research demonstrated that solitary females experience substantially higher predation risks than females living in family bands, more than five times

higher. Also, more than 50% of adult mortality was caused by predation by felids. Primarily pumas (*Puma concolor*) and jaguars (*Panthera onca*), were identified as the main predators (Booth-Binczik, 2001; Hass & Valenzuela, 2002). Predation is considered an important ecological driver, shaping animal behaviour, with prey species modifying their behaviour, activity patterns and vigilance in response to the threat (Lima & Dill, 1990). This contributes to the stability of family bands. The behavioural differences observed among social groupings as an additional result, supports this interpretation. Family bands spent proportionally more time foraging, whereas solitary females displayed relatively more vigilance-related behaviours. This pattern is consistent with the anti-predator benefits of group living, where collective vigilance reduces the need for each individual to remain alert. Allowing more time to be allocated on foraging (Elgar, 1989; Beauchamp, 2003).

Although no significant interaction was found between forest type and social grouping, exploratory pairwise comparisons showed that family bands were detected more frequently than solitary females in planted forest. Because the overall interaction was not significant, this isolated comparison should be interpreted with caution. Nevertheless, several ecological mechanisms may explain the higher detection rates of family bands in this forest type. Planted forest is generally characterised by a more open vegetation structure, potentially increasing exposure to predators. Under these conditions, the anti-predator benefit of group living may become advantageous. As collective vigilance improves predator detection and reduces individual predation risk (Elgar, 1989; Di Blanca & Hirsch, 2006). It is therefore possible that family bands may be better able to exploit these habitats, despite the potentially greater predation risk. Particularly if these habitats provide access to food resources under lower levels of competition. Even though this should be interpreted with caution this hypothesis is biologically plausible, additional studies examining predator occurrence and habitat use would be required to confirm this.

Forest type did not influence temporal activity patterns of *N. narica*. The Watson–Wheeler test showed no significant differences among forest types, while the high overlap coefficients $\Delta = 0.90–0.93$), indicated a highly similar activity pattern. Likewise, temporal activity patterns did not differ among social groups. Together, these findings suggest that daily activity patterns are relatively conserved within the species and are influenced less by habitat characteristics or social organisation, than by intrinsic biological factors. These findings are consistent with the species being primarily diurnal (Leopold 1959) and align with a previous study reporting that *N. narica* is most active during daylight hours (Pérez-Irineo & Santos-Moreno, 2016). Although Rojas-Sánchez et al. (2026) stated that foraging behaviour and intra- and interspecific interactions contribute to shaping temporal activity patterns, the present results suggest that differences in social organisation alone are insufficient to alter the timing of daily activity. Other ecological drivers, such as predator activity or food availability may therefore play a more important role.

Seasonal detection rates of *N. narica* likewise remained consistent across forest types .
The absence of a significant interaction between month and forest type, indicates that forest succession did not alter seasonal detection patterns throughout the year. Instead, forest type primarily influenced the overall number of detections, with planted forest showing higher detection rates than natural regrowth and old growth forest. Furthermore, there was no overall monthly effect detected, suggesting that detection rates remained relatively stable throughout the year. This agrees with Pérez-Irineo & Santos-Moreno (2016), who likewise reported limited seasonal variation in *N. narica* detections. In contrast, Cambronero et al. (2023) found significant seasonal differences in detection rates in another Costa Rican forest ecosystem.

This discrepancy may be explained by differences in environmental conditions. Montane cloud forests, such as Cloudbridge Nature Reserve experience relatively stable temperatures, consistently high precipitation and lower seasonal climatic variability than many other tropical forest ecosystems (Jarvis & Mulligan, 2011). Such environmental stability may reduce seasonal fluctuations in resource availability, thereby potentially contributing to the consistent detection rates observed throughout the year.

Interestingly, the additional analyses demonstrated that seasonal patterns did differ significantly among social groups. Pairwise comparisons showed that solitary females where detected less frequently than family bands during several months. These patterns closely reflect the reproductive biology of *N. Narica*. Where adult females temporarily leave the family bands three to four weeks before parturition, with birthing season being from April to May (Gompper, 1995). Females remain solitary while nursing their offspring before rejoining the family bands with their juveniles (Kaufmann, 1962). Reproduction is highly synchronized, with most births occurring within a two-week period during the wet season (Kaufmann, 1962; Russell, 1982), at the moment when there is an increase in food and water availability (Smythe, 1970). Accordingly, the additional analyses showed the highest detections of solitary females in April, followed by a pronounced increase in family band detections from May-June. This close correspondence between the observed seasonal detection rates and the known reproductive cycle provides further support that seasonal changes are better explained by social organisation and species-specific characteristics, rather than forest type.

A limitation of this study is that a considerable proportion of detections could not be confidently assigned to a social grouping and therefore had to be classified as unknown. As a result, these observations were excluded from the social-grouping analyses, reducing the effective sample size particularly for solitary males and solitary females. This may have reduced the statistical power. In contrast, family bands were generally easier to identify, because multiple individuals were visible simultaneously. Potentially resulting in more reliable estimates for this social category. Despite this limitation, the main ecological patterns remained consistent across the different analyses, suggesting that the overall conclusions are robust.

Overall, this study demonstrates that the behavioural differences in *N. narica* are explained more strongly by intrinsic biological characteristics, such as social organisation, survival tactics and reproductive biology than by differences in forest succession. The absence of differences between forest type further suggest that other ecological factors, such as predator presence or food and water availability, may play a greater role in shaping behaviour. Forest type influenced overall detection rates, but not behavioural patterns, social grouping, temporal activity patterns or seasonal detection patterns of *N. narica.* These findings suggest that the different forest types in Cloudbridge Nature Reserve provide habitat suitable for *N. narica* to maintain its natural behavioural repertoire. As behaviour reflects how animals interact with their environment, these results show that the restored forest types are sufficient for this habitat generalist species.

Although these findings are encouraging, *N. narica* is a habitat generalist species. This research could gain valuable insights in broader ecological processes and mammal communities, but occurrence of more specialist, rare and elusive species depends on many additional factors. Therefore future research should examine behavioural responses of different mammal species, particularly habitat-specialists and elusive predators. This could determine whether ecological benefits observed for *N. narica* extend across the wider

mammal community. Continued long-term camera trap monitoring is necessary to improve understanding of how restoration and animal behaviour contribute to ecosystem functioning and conservation over time.

5. Reference list

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6. Appendices

Appendix 1
Camera trap station details.

Table 1: The camera trap stations used during this research and additional details.

Camera ID	Trial name	Forest type	GPS longitude	GPS latitude	Elevation (M)	Currently deployed	Historical data	Active camera trap nights
D2	Don Victor	Natural regrowth	9,47881	-83,5677	1734	Yes	Yes	333
D3	Don Victor	Natural regrowth	9,48238	-83,5673	1788	Yes	Yes	148
E1	El Jilguero	Planted	9,47074	-83,5787	1624	Yes	Yes	335
E2	El Jilguero	Natural regrowth	9,46867	-83,5749	1811	Yes	Yes	431
E3	El Jilguero	Old growth	9,46698	-83,5729	1887	Yes	Yes	477
G1	Gavilan	Planted	9,47136	-83,5726	1761	Yes	Yes	166
G2	Gavilan	Natural regrowth	9,46948	-83,57183	1848	No	Yes	8
G3	Gavilan	Old growth	9,468	-83,5713	1882	Yes	Yes	485
H1	Heliconia	Natural regrowth	9,47275	-83,5758	1579	Yes	Yes	122
M1	Montana	Planted	9,47217	-83,5689	1798	Yes	Yes	162
M3	Montana	Natural regrowth	9,46927	-83,5653	2021	Yes	Yes	443
M4	Montana	Old growth	9,46565	-83,5659	2133	Yes	Yes	391
Q2	Los Quetzales	Planted	9,47886	-83,5662	1802	Yes	Yes	417
Q3	Los Quetzales	Natural regrowth	9,48123	-83,5667	1819	Yes	Yes	179
R2	Rio	Planted	9,47411	-83,5702	1660	No	Yes	236
R3	Rio	Natural regrowth	9,47529	-83,5689	1674	Yes	Yes	166
S1	Sentinel	Old growth	9,47095	-83,5703	1765	Yes	Yes	262
S2	Sentinel	Old growth	9,47159	-83,5712	1744	No	Yes	77

Appendix 2

Adapted camera trap protocol (based on Benjamin Luke, founder of The Wild Cat Imaging Project).

The Wild Cat Imaging Project – Cloudbridge Nature Reserve
This protocol outlines the standardized procedure for checking camera traps, collecting data, and managing video files within The Wild Cat Imaging Project (WCIP) at Cloudbridge Nature Reserve.

Camera Trap Checks
Camera traps are checked every two weeks following the project monitoring schedule.
When checking camera stations:

- Bring the SD card holder with all the SD cards and new AA batteries for each camera to be checked.
- Replace the SD card with the corresponding replacement card and format the new card.
- Check the battery level. If battery charge is **above 25%**, batteries may remain in the camera for the next two-week cycle. If charge is **below 25%** (or one bar), replace all batteries. Record all information in the Epicollect5 app.
- Before leaving the site, verify that the camera is functioning **correctly**, confirm all settings are properly configured, and clear any debris that could cause false triggers.

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

- Insert the SD card and the project hard drive into the WCIP laptop.
- On the project hard drive, open the folder titled "**Camera Data**" and navigate to "**Cloudbridge_Camera_Locations**". Open the "**Location_ID**" folder and select the location corresponding to the camera station from which the SD card was collected.
- Create a new folder named with the collection date of the SD card (pick-up date).
- Transfer all files from the SD card into this folder. Once the transfer is complete, format the **SD card** to exFAT and eject it.
- Enter the name of the newly created folder in the "Datatrack" sheet on the Google Drive and mark it as uploaded.

Data Entry
Once files have been uploaded to the external hard drive, each folder must be imported into Timelapse and all videos must be reviewed and logged.

- Import the folder into Timelapse and view each video.
- Enter the **correct information** for each video and mark any bird videos and false triggers accordingly.
- When done, mark the folder as entered in the “Datatrack” sheet on the Google Drive.

Data Checks
After data entry is complete for all videos, a quality check must be performed before exporting the dataset.

- Review all entered information for each video and **correct any errors**.
- For videos flagged for deletion, verify that no relevant content is present before permanently deleting them..
- Once all checks are complete, mark the folder as checked in the "Datatrack" sheet on the Google Drive. And export the final dataset to the Google Drive.

Appendix 3
Adjusted ethogram of *N. narica* behaviour categories, modified from Gaston (2022).

Table 2: Adjusted ethogram of N. narica behaviour (modified from Gaston, 2022) used to classify behaviour.

Behaviour code	**Description**
Walking	Normal movement using legs from one position to another
Standing	Stationary on back legs
Foraging	Actively searching for food and eating
Sniffing	Using nose to search through environment
Sitting	Positioned in upright stance while not moving
Exploration	Looking around environment
Resting	Non-movement lying down
Digging	Using claws to dig into ground
Chirping	Displaying chirp noise
Biting	Using teeth to grip and tear an object
Scratching	Running paws through fur
Alertness	Head positioned upright, looking around
Running	Faster movement than normal
Head shaking	Head moving from side to side
Shaking	Body moving from side to side
Climbing	Moving up a tree
Crawling	Movement flat to the ground
Allogrooming	Grooming an individual of the same species using front teeth and claws to comb and nibble fur and skin (Kaufmann 1962; Smith 1977; Krinsley 1989)
Grooming	Grooming themselves using front teeth and claws to comb and nibble fur and skin (Kaufmann 1962; Smith 1977; Krinsley 1989)
Playing	Social behaviour where they wrestle, chase and mock-bite an individual of the same species (Kaufmann 1962; Smith 1977; Logan and Longino 2013)
Fighting	Asocial behaviour characterized by lunging, biting, chasing and paw striking. (Kaufmann 1962)
Scent marking	Wiping urine secretions onto trees, logs, and vines with groin or abdomen (Krinsley 1989; Gompper 1995)