

Collared Peccary
(Pecari tajacu)
Behaviour and SubHabitat Preference in
Montane Cloud Forests

An Evaluative and Comparative Study Within the Biome and Different Environments



By Adam Morrow

## **Abstract**

This study details a dry season survey of collared peccaries (*Pecari tajacu*) in a montane cloud forest environment located within Cloudbridge Nature Reserve. Results suggest that human disturbance may influence the animals' distribution and behaviour more than other variables such as elevation, temperature, sub-habitat type, etc. This is suggested primarily by an apparent avoidance of humans by *P. tajacu*, since they are observed more frequently at times when human traffic decreases, i.e. dusk and dawn. Comparing camera traps per sub-habitat appears to support this, although it remains inconclusive due to uneven sampling. *P. tajacu* also appears to prefer old growth forests over other sub-habitats; the definitive reasoning behind this remains unclear. For extra abiotic variables, the animals seem to prefer higher elevations and have no clear temperature preference. The elevation correlation remains unclear, but the temperature indifference is likely due to the mild climate of the montane cloud forest, allowing the animals to be active at all times. In comparison to other biomes and studies, some interesting observations are identified, suggesting variations between contrasting populations. This paper concludes by highlighting the importance of responsible ecotourism to balance visitor experience and animal welfare.

### Introduction

Few of the New World's mammals have been more extensively studied than collared peccaries (Pecari tajacu). The species is a member of the suborder Suiformes, which includes pigs and peccaries, but is distinct from "true pigs" found in the family Suidae. Instead, P. tajacu is grouped with other peccary species in the family *Tayassuidae*, informally referred to as "New World pigs" (Donkin, 1985, Gongora et al., 2006, Mayer and Brisbin, 2008). The species is still often subject to taxonomic debate, as some sources refer to it as Dicotyles tajacu (Marinho et al., 2019). Across scientific literature and research, P. tajacu has been studied quite comprehensively concerning many aspects of its biology. Of these, there is research on their sociality, movement, game meat viability, life history, etc., as well as the species' ecological importance, with studies showing that the species influences plant biodiversity composition as a direct consequence of its herbivory. (Bigler, 1974, Byers et al., 1981, Osorto Nuñez et al., 2024, dos Santos Morais et al., 2022,). Ecologically, P. tajacu is also an important prey species for many New World carnivores, especially those found in the neotropics, such as jaguars (*Panthera onca*), mountain lions (Puma concolor) and coyotes (Canis latrans) (dos Santos et al., 2024, Osorto Nuñez et al., 2024, O'Brien et al., 2005). The species' significance as a widespread prey species is exemplified by its remarkable adaptability, being able to survive in a plethora of different biomes, from arid deserts to humid forests, at both high and low elevations (Bigler, 1974, Bodson, 2024, Carson et al., 2013). As such, P. tajacu boasts an impressive distribution, inhabiting most of the land between Arizona and Argentina (Donkin, 1985). Consequently, P. tajacu can be found in the montane cloud forests of Costa Rica, including the high-elevation forests of the Talamanca Mountains (Bodson, 2024). Despite this fact, there is an apparent gap in scientific literature centred on P. tajacu within this environment, especially in comparison to populations in other biomes. The species has been included as part of general monitoring surveys, for example, at Cloudbridge Nature Reserve; however, they have not been the central focus of these studies (Bodson, 2024). To close this knowledge gap, this research aims to analyse the behaviour and sub-habitat preference of P. tajacu within montane cloud forests; any differences observed from previous studies in different habitats and altitudes will be compared and contrasted. Should any of the results yield a noticeable difference, it may be possible that one or several altered variables, as a consequence of the contrasting environments, caused the change. Within the cloud forest context, this study will focus on P. tajacu distribution, group sizes, sub-habitat preferences, general observed behaviour, temporal activity patterns, and reaction to human presence. Some complementary variables were collected to help explain the reasoning for behavioural factors, such as weather, temperature, forest type, human presence and predator presence. Corroborating this collection of variables will help provide a better understanding of P. tajacu ecology and behaviour within these niche habitats.

The main aims of this research are as follows.

- 1. Determine the forest type preference (if any) for *P. tajacu* within the cloud forest biome between primary/old growth, secondary/natural regrowth and planted regrowth and suggest possible reasons for said differences.
- 2. Examine *P. tajacu* within these environments to create a basic overview of their behaviour.
- 3. A basic understanding of how *P. tajacu* react to human presence, both as an immediate behavioural response and as a general disturbance.
- 4. Identify possible differences in group and litter numbers between montane cloud forests and lowland habitats.
- 5. Function as an updated general study on *P. tajacu* on factors such as temperature and temporal activity preference, impact of predator presence, etc.

It is hoped that the results of this study, concerning each research objective, can be extrapolated to contribute to related works, e.g. neotropical predator studies, habitat regeneration analysis, etc.

## **Hypotheses**

To address the aims of this study, there were five main predictions concerning its results.

- 1. *P. tajacu* will prefer old growth forest over other cloud forest sub-habitats.
- 2. Increased human presence will negatively impact *P. tajacu* presence. When confronted with human presence, *P. tajacu* will react negatively.
- 3. Increased predator presence will negatively affect *P. tajacu* presence.
- 4. Group sizes will be greater on average in lowland biomes compared to montane ones.
- 5. Juvenile/litter numbers will be lower in the montane cloud forest compared to lowland habitats.

The reasons for these hypothetical results may derive from many unaccounted variables inherent in differing environments, e.g. oxygen supply, differing flora demographics, atmospheric temperature, resource availability, etc. Such factors may alter abiotic pressure by reducing respiration rates, limiting food intake, reducing enzymatic rates, etc. These, in turn, could decrease energy availability for *P. tajacu*, negatively impacting the survivability of individuals and altering their behaviour accordingly. Lower energy reserves may also cause the animals to reduce their reproductive rate.

It is important to note that many of the speculative causes for these hypotheses, should they be accurate, could not be investigated in this study, as it exceeded the scope of the research at hand. Consequently, investigating these variables to understand their impact on *P. tajacu* presents promising and insightful future research.

## **Methodology**

As previously mentioned, this research was composed of a variety of variables, both quantitative and qualitative. Quantitative factors involved enumerating observed individuals, temperature, time of day, elevation and comparative sub-habitat distribution. All of these factors were collected using camera traps, which recorded the individuals, temperature, and time of day. Since not all cameras were of uniform brand and model, certain variables, like temperature, were missed in a small collection of samples. Null values were omitted from the particular variable's analysis. Elevation was measured by taking the camera location coordinates with a GPS and using them on an online coordinate-elevation map. Sub-habitats were identified using a map made in conjunction with the Wild Cat Imaging Project (WCIP) to evenly distribute sample sites. Qualitative variables included any inter- and intra-species behaviour from *P. tajacu*, including human presence, both positive and negative. This data was collected by reviewing the camera trap footage and cataloguing each observed behaviour.

### **Primary Method**

The primary mode for collecting data was through camera trapping, which allowed animal behaviour to be recorded whilst minimising the disruption caused by the observer effect (Appendix i). Each camera was placed along set sample points on trails found within Cloudbridge Nature Reserve; the equipment was regularly maintained through biweekly alternations of batteries and SD cards, ensuring that data recording was as continuous as possible. Cameras were placed along the trail for four reasons: ease of user accessibility, unobstructed video captures, increased the likelihood of data recording (since P. tajacu are known to travel along trails in transit to other forest locations (Harmsen et al., 2010), and being able to accurately record levels of human disturbance. Alongside recording *P. tajacu* sightings, human and predator presence were recorded, since they were likely to influence P. tajacu behaviour and distribution. When possible, camera settings were standardised to take 10-second videos, with a medium motion sensitivity, with a minimum interval of 3 seconds. These settings were chosen to reduce the number of false triggers in the data collection, as well as providing enough footage to analyse behaviour; the interval, in particular, meant that large groups of peccaries could be recorded as seamlessly as possible. Due to logistical limitations, there was a mixture of camera brands used and not all of them allowed these exact settings; however, the majority could facilitate them. Once the footage was collected, the information was tabulated and entered into a database spreadsheet, including information such as the camera location, forest type, time of observation, species, number of individuals, weather conditions, altitude, behaviour and extra notes. Observed fauna was assumed to be part of the same group/recording if the subsequent video was less than 5 minutes after the previous video; enumeration in these circumstances was completed to the best of the observer's ability to identify unique individuals. The total number of each video group was only the number that the observer could be confident in. When dealing with behaviour, each observation was broadly categorised into a general behaviour type, then specified into a subtype, which was described and identified as positive/negative. To semi-quantify the data, a simple ethogram (Table 1) was devised to categorise and group together similar behaviours to have a more regulated and standardised approach to the interpretation, reducing observer bias. Below illustrates the completed ethogram.

Table 1: Ethogram Detailing all Observed P. tajacu Behaviour

Behaviour Group Type	Behaviour Sub-Type	Description	Connotation
Traversal	Walking	Slow moving traversal usually done in a line or loose group, accompanied by other behaviours	Neutral
	Trotting	Intermediate, brisk traversal often performed when catching up to group members	Neutral
	Running	Fast traversal performed either to catch up with group members or when startled	Neutral
	Limping	Faltering, irregular gait presumably caused by sustained injury from predation or competition	Negative
Foraging	Sniffing	Olfactory behaviour to detect and investigate environmental stimuli, commonly includes the shovelling of leaf litter	Neutral
	Nutrition	Active consumption of food resources in the environment	Neutral
Social	Vocalising	Includes a collection of grunts and squeals commonly used to signal to group members about stimuli or intraspecies behaviour	Neutral
	Reciprocal Head-to-Rear Rubbing	Two individuals align antiparallel to each other and reciprocally rub the side of their snout to the side of the other's rear	Positive
	Parental correction	Somewhat aggressive grunting and corrective biting to bring juvenile's behaviour back in line e.g. positional correction to be risk averse	Positive/Negative
Other	Investigating cameras	Intentional and obvious investigation of the camera mostly by sniffing	Positive
	Alert	Stopping or freezing action usually accompanied by head swivelling, sniffing and ear movement to investiage stimuli	Neutral
	Lying down	Animal relaxes on the ground, head up to be aware of surroundings	Neutral
	Suckling	Young consumes milk directly from mother's teats, reinforcing maternal bond	Positive

#### **Camera Locations**

Below shows maps of each potential camera location placed within the reserve study area (Fig. 1 and 2)

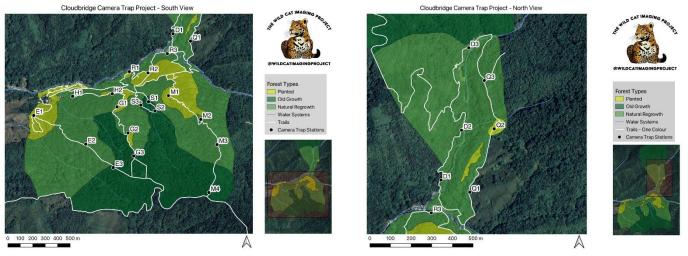


Figure 1: Possible Camera Trap Locations on Cloudbridge Nature Reserve South View (Courtesy of Ben Luke from WCIP)

Figure 2: Possible Camera Trap Locations on Cloudbridge Nature Reserve North View (Courtesy of Ben Luke from WCIP)

#### **Cameras Used and Context**

Due to logistical and technical limitations, only some of the above locations were able to be used, with every attempt made to create even sampling across the three sub-habitats. The following cameras used are listed in the table below, with some brief context on their particular site (Table 2).

Table 2: Description of Each Camera Location Used

Camera Name	Trail	Sub-Habitat Type	Private/Public	Contextual Description	Notes
E1	El Jilguero	Planted	Private	At the entrance to Jilguero Loop, near forest boundary to pastures	
E2	El Jilguero	Natural Regrowth	Private	At a large boulder commonly used as a terretorial marking spot for many mammals	
E3	El Jilguero	Old Growth	Private	Top of trail	
G2	Gavilan	Natural Regrowth	Private	Three-way junction between all forest types, but primarily Natural Regrowth	
G3	Gavilan	Old Growth	Private	Top of trail	
S2	Sentinel	Old Growth	Public	By a river, steep trail	Never recorded data
M1	Montana	Planted	Public	Planted section at relatively high elevation	Broke early in survey
M3	Montana	Natural Regrowth	Public	Natural Regrowth section at relatively high elevation	
M4	Montana	Old Growth	Public	At side entrance to Chirripo National Park	Replaced fairly late
Q2	Quetzales	Planted	Public	Small patch of Planted forest as an island in Natural regrowth	
D1	Don Victor	Natural Regrowth	Public	Relatively accessible forestry	Never recorded data
D2	Don Victor	Natural Regrowth	Public	Relatively accessible forestry	Never recorded data
R2	Rio	Planted	Public	Sloping path between Sendero Rio and Sendero Principal	Broke early in survey

### Additional methods used:

Complementary to this data, a secondary mode of data was documented: in-person observations. Due to the method's comparative infrequency and irregularity compared to the camera traps, it was used as supplementary/contextual data to the primary method. For the observations, binoculars or a long-range camera were used to safely observe *P. tajacu* in the field. Details were noted immediately after the encounter, to minimise memory degradation and improve account accuracy. Factors noted included the date, time, no. of *P. tajacu* and human observers, *P. tajacu* behaviours and time of day. Whilst care was taken during each survey to avoid disturbing the animals, human presence was regularly detected in this sampling. This provided unique opportunities to better understand how they react to direct

anthropogenic stimuli. The sampling also offered more flexible data collection since the observer(s) could pivot and visually track the animals, instead of the fixed position of the cameras.

### **Data Tabulation and Management**

As referenced earlier, all collected data within the survey was stored on an MS Excel spreadsheet, where data could be managed and sorted through efficiently. This was important as this study required the selection of certain species from the overall database for analysis. The main database contained information on the camera location, species, date, time observed and number of individuals (Appendix ii). Of all the data recorded, videos containing *P. tajacu*, humans and any large predator were filtered and entered into a separate table for further data analysis. The new table includes the previous variables, but also notes the weather, temperature, behaviour, etc. (Appendix iii).

To visualise and statistically analyse the data from the second table, R Studio was used to formulate graphs and conduct appropriate investigations into data significance. The tests used were chosen specifically for each variable to determine possible significance. For example, to test for evenness of distribution, a Chi-Squared Goodness of Fit test was often used. If this was found to be significant, further tests were conducted where appropriate, including Spearman's rank coefficient to further investigate the correlation for visualisation, Bonferroni-corrected pairwise proportion tests to pinpoint the exact significances between groups, and Kruskal-Wallis tests for when the data was unevenly distributed.

#### Results

### **Sub-habitat Preference and Group Sizes**

As a consequence of the data collected, many factors and variables had to be investigated to discern *P. tajacu* habitat preference. The primary variable was the different forest types found within the reserve. Below shows a bar chart depicting the difference in observations of the species in each forest category (Fig. 3).

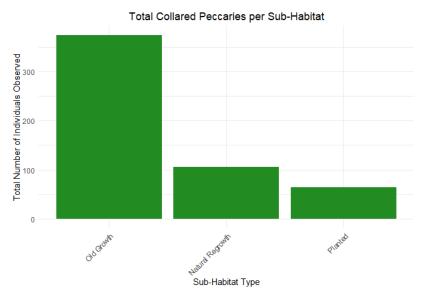


Figure 3: Bar Chart Showing the Differences in P. tajacu Observations per Sub-Habitat

The highest number of *P. tajacu* was observed in old growth forests (374), then in natural regrowth (106); the planted forests had the least (64). This data can be further analysed by investigating *P. tajacu* observations per trail, to contextualise these results further, as seen below (Fig. 4).

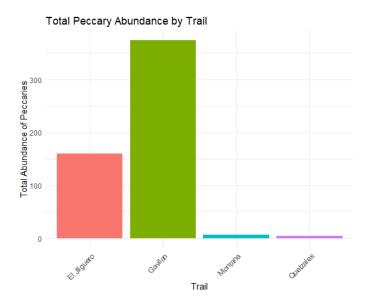


Figure 4: Bar Chart Showing the Difference in P. tajacu Observations Per Trail

The trails are composed of several forest types; combining their camera totals gives more comparative context to the trails, rather than the sub-habitat variance. Any differences observed could be suggested to be inherent to the trails themselves, rather than the sub-habitats they are present. As such, these results reveal differing totals. El Jilguero possessed the second largest sum (160), mean group size (3.64) and standard deviation (3.47). Gavilan, on the other hand, had the greatest number of observations (374), average group size (5.05) and standard deviation (4.53). Montaña (6) and Quetzales (4) had significantly reduced totals by comparison, with their average group size equal to their sums. Due to only having 1 sample each, they do not have standard deviation values. The difference was further subdivided by camera location to increase the sample size for statistical analysis, further discussed later in the paper. In descending order, the highest totals per camera were as follows: G3 (354), E2 (80), E1 (60), E3 (20), G2 (20), M3 (6), Q2 (4).

In conjunction with total *P. tajacu*, the number of juveniles observed was also noted between the forest types, which is displayed below (Fig. 5).

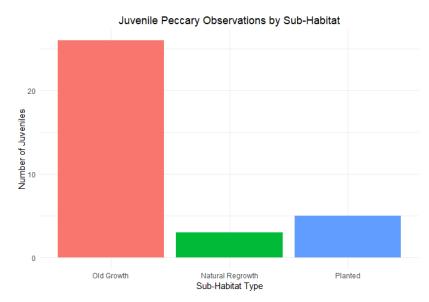


Figure 5: Bar Chart Showing the Difference in Juvenile P. tajacu Observations Per Sub-Habitat

Old Growth forests show a higher total than the other sub-habitats (26) and a higher average of juveniles per observation (1.08), whereas natural regrowth (3) and planted (5) had reduced sums. Both had an equal average of juveniles per observation (1). Compared to the other two types, old growth forests were the only sub-habitats to record more than 1 juvenile per group, with a maximum of just 2. This means it produced the greatest standard deviation (0.28); conversely, the other two types had no deviation recorded.

Another aspect investigated within *P. tajacu* distribution was the difference in group sizes across the sub-habitats, which is visualised below (Fig. 6)

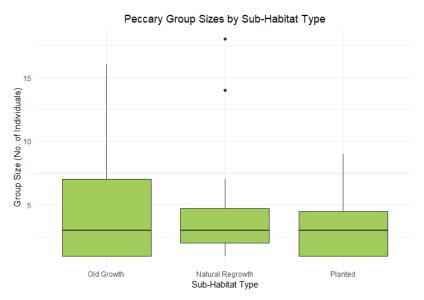


Figure 6: Boxplot Showing the Difference in Observed P. tajacu Group Sizes Per Sub-Habitat

In terms of range, natural regrowth is the greatest (min=1, max=18, range=17). This is closely followed by old growth (min=1, max=16, range=15), and then by planted (min=1, max=9, range=8). For average

group size, old growth is the highest (4.99), followed by natural regrowth (4.08) and planted (3.37). The standard deviation for each sub-habitat in descending order includes old growth (4.53), natural regrowth (3.92) and planted (2.59).

### **Potential Factors Impacting Distribution**

To gain a better contextual understanding of this data, it was necessary to investigate potential variables influencing the peccaries' choice of forest type/trail. The primary variable recorded in this regard was human presence captured on the trail cameras. Collected footage revealed that the highest number of human observations was seen in planted forests (550), closely followed by natural regrowth (513). Old growth forest observations were much fewer compared to the other two types (263). Like the *P. tajacu* observations, these results can be further contextualised by reorganising the data by trail instead, which is displayed in the graph below (Fig. 7).

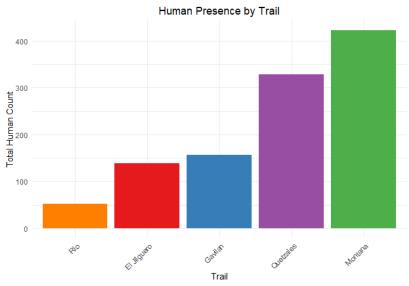


Figure 7: Bar Chart Showing the Difference in Human Observations Per Trail

From the data shown, there are clear differences between the totals observed at each trail. The greatest sum is found in Montaña (423), with the second highest belonging to Quetzales (328). After a steep drop-off, Gavilan is the next highest (157), then El Jilguero (139) and finally Rio (52). To further visualise the difference between *P. tajacu* and human observations, the graph below shows a combined stacked column chart for both per sub-habitat (Fig. 8).

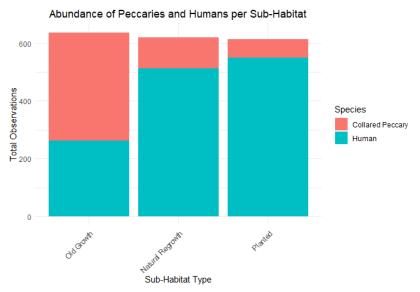


Figure 8: Stacked Column Chart Showing the Combined Observations of Humans and P. tajacu Per Sub-Habitat

Alongside the impact of human presence on *P. tajacu* distribution, observed predators were recorded to see if they also had an influence. In this measurement, pumas (*Puma concolor*), ocelots (*Leopardis pardalis*) and coyotes (*Canis latrans*) were all considered predators, since there are scientific recordings of each hunting *P. tajacu*. To visualise the results, the graph below features a clustered bar chart comparing predator numbers to *P. tajacu* observations across each trail where they were observed (Fig. 9).

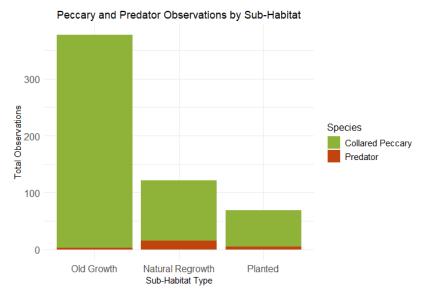


Figure 9: Stacked Column Graph Showing the Combined Observations for Predators and P. tajacu Per Sub-Habitat

Natural regrowth had the largest number of predator observations (15), distantly followed by planted (5), then old growth (3). Proportionally, the order was the same, with natural regrowth (14.2%), then planted (7.8%), and lastly old growth (0.8%).

### **Additional Factors Investigated**

Whilst the main variables measured were *P. tajacu*, human and predator presence, additional factors were also recorded to see if they had an impact on *P. tajacu* observations. The first of these is the time-of-day activity. This was displayed in two graphs below, one being a line graph for continuous time activity readings (Fig. 10). The second graph overlays the hourly activity of humans onto the *P. tajacu* activity to investigate potential correlations between the two (Fig. 11).

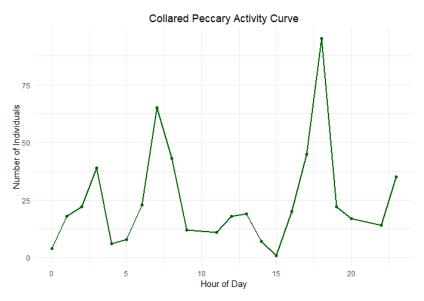


Figure 10: Line Graph Showing the Hourly Activity of P. tajacu

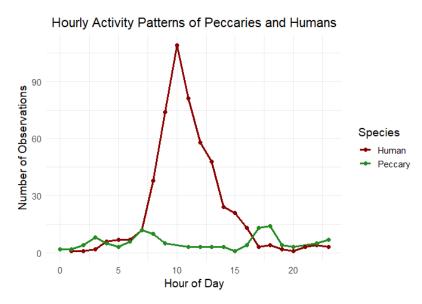


Figure 11: Line Graph Overlaying the Hourly Activity of Both Humans and P. tajacu

Fig. 10 shows the approximate hour-by-hour observations, implying three distinct peaks of *P. tajacu* activity: a minor peak between 02:30 and 03:00, a medium peak between 07:00 and 07:30 and a major peak between 17:30 and 18:00. On the overlayed graph, human activity is shown to have one long, major peak between 07:30 and 14:00.

Another variable measured was the temperature at which the *P. tajacu* were observed. To visualise this data, a scatter graph was plotted with an accompanying trend line to display any potential correlation, which is shown below (Fig. 12).

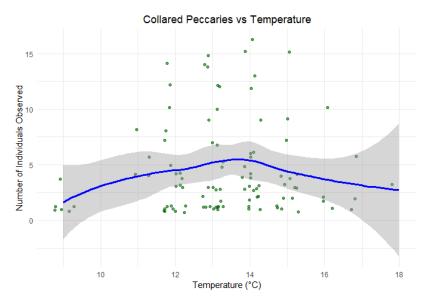


Figure 12: Scatterplot Showing How P. Tajacu Observations Changed with Temperature

The graph presents a fairly centralised plot, where the vast majority of observations were captured across a wide central range of temperatures between 11-16°C. Alongside this variable, elevation was also considered for its potential impact, which is presented in the subsequent histogram (Fig. 13).

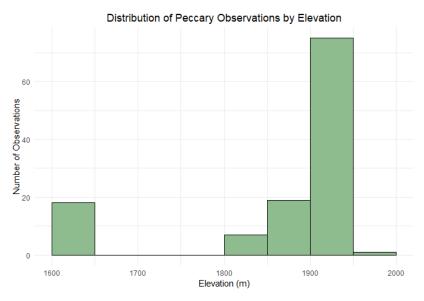


Figure 13: Histogram Showing the Difference in Observation Totals of P. tajacu by Elevation

The data shows a clear skew in the *P. tajacu* distribution, with most observations being seen between 1900-1950m (75), subsequently followed by 1850-1900m (19), 1600-1650m (18), 1800-1850m (7) and then 1950-2000m (1).

#### **Behavioural Results**

The majority of the behaviour noted was found in the traversal group type, primarily walking, often mixed in with sniffing behaviour, suggesting that olfaction is one of the strongest senses that P. tajacu possesses for receiving external stimuli. One consistent observation made was the tendency for straggling individuals to trot or run to catch up with the rest of the group, likely highlighting how the group structure reduces individual vulnerability to external threats like predation. A somewhat common intra-group behaviour observed was a reciprocal head-to-rear rubbing. This was overtly positive and may be used to strengthen social bonds within the group, as is common with other herd/social species; stronger group bonds may encourage more effective cooperation and altruistic behaviour like shared learning, theoretically improving survival rates (Marino and Allen, 2017). Conversely, when considering altruism, there was another less compassionate observation. Rarely, a single individual would be detected well outside of any group recordings, bearing an obvious limp. The impairment would limit traversal speed greatly, and so, it could be inferred that injured, sick or elderly individuals may get left behind by the group. The level of intent with this abandonment remains unclear due to a lack of direct observation on the cause and immediate effect of the injury. P. tajacu were also frequently observed to directly investigate the cameras by sniffing them for short yet distinct periods, either one at a time or only one member of the group doing so. The suckling behaviour highlighted the only opportunity where the sex of an individual could be confidently identified, as a female determinant. The other parent-child interaction observed concerned corrective behaviour administered to juveniles. This was observed very infrequently, but occurred when young P. tajacu would run recklessly, breaking the regular pattern of traversal. The behaviour was met by swift correction, presumably by the young's mother, which stifled the unruly behaviour.

#### **In-Person Observations**

As a complementary data set to the camera observations, the results for this data collection method are small, but provide some exclusive insights into peccary behaviour, which are tabulated below (Table 3).

Table 3: In-Person Observations of P. tajacu

Location	No. of Peccaries	No. of Observers	Approx. Time of Day	Behaviours	Notes
El Jilguero	2	4	Late Morning	Older juvenile suckling its mother's milk, mother was wary of observers and both retreated when more observers joined and noise increased	Initially 2 observers, increased to 4
Fields outside Cloudbridge	10	8 to 10	Early Afternoon	Flushed out of thicket up the steep field as a linear caravan, one straggler ran to catch up to the group	
El Jilguero	4	1	Late Morning	Alert to observer presence, sniffed and vocalised to other members before continuing traversal. Agitated individual raised hair on mane and clapped teeth	
Gavilan	6	1	Mid Morning	Alert, sniffing and vocalising. Briefly moved on but were spooked when surprised by observer presence. Quick flick up of head, vocalised and scattered into thicket. Usually one individual observing at all times.	Near the casita
Jilguero	5	1	Nighttime	Much more flighty than during the day, frequent, hushed vocalisations. Individuals froze when spotlighted before running for short distances. Appeared to huddle together periodically.	
Gavilan	11	3	Mid Morning	Walking and foraging a bit off-trail in the foliage. Seemingly undisturbed by observers but kept their distance.	1 juvenile, sandwiched

These results showed that *P. tajacu* generally reacted defensively, but not outright skittish of human presence, often exhibiting behaviours like increased alertness, staring, investigative sniffing, vocalising to other group members, clapping teeth, raising hair on their manes, etc. The last two listed in particular show signs of attempted deterrence, which could be interpreted as a warning or threat to the observer; however, no individuals acted in any way suggesting an imminent attack. The behavioural pattern of *P. tajacu* appeared to change drastically come nightfall, as the animal was seen to be far flightier, making short, quick dashes, followed by frozen stares as it was captured by flashlight. Vocalisations were more frequent yet hushed, and the animals seemed to huddle together more tightly.

## Special Observation – The "Sandwich" Model

A consistent observation made within this study was the positioning of juveniles within the traversing caravans of *P. tajacu*. From my observations, juveniles were found to be situated between two adults in the vast majority of situations, with two exceptions arising where the juvenile was unattended at the rear, likely due to how mature the individual was. This formation was usually placed nearer to the front of the caravan and was observed 16 times. Below shows a schematic for the arrangement in two forms, the frequent "sandwich", and the infrequent "sidewich" model (Fig. 14).

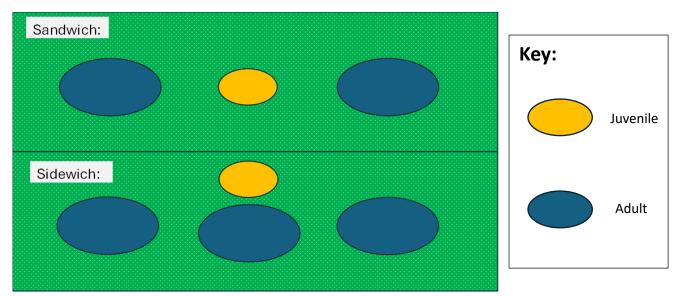


Figure 14: "Sandwich"/"Sidewich" Model

As shown in the diagram, adults usually border the juveniles from both the front and back, but for the "sidewich" model, there is an extra adult that walks by the juvenile's side. This second model was more commonly seen with very young juveniles, who presumably relied more on maternal support for protection, guidance, food, etc. More developed juveniles assumed the standard "sandwich" model.

## **Statistical Analysis**

To assess the significance of each measured variable, a variety of statistical tests were performed on the data sets. Firstly, the human-*P. tajacu* presence was measured. When comparing by sub-habitat abundances through a Spearman's rank correlation, there was a statistically insignificant p-value (0.3333); however, a perfectly negative rho value (-1) was produced. This meant that while random chance could not be confidently ruled out, there was a seemingly perfect relationship within the data presented. However, due to the added sub-habitat variable, no clear inferences could be made. The lack of a significant p-value is likely due to uneven sampling of sub-habitats, caused due to technical difficulties, which makes the results less statistically robust. To increase the sample size and reduce the impact of the sub-habitat variable, the relationship was examined per camera location. This was visualised with a correlation scatter plot shown below (Fig. 15).

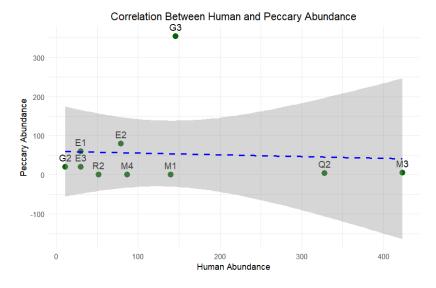


Figure 15: Correlation Plot showing the Relationship Between P. tajacu and Human Observations per Camera Location

This graph revealed a slightly negative correlation (rho=-0.182) with an insignificant p-value (0.615). This suggests the relation is likely due to chance; according to these results, however, it is important to restate that sampling remains highly uneven.

In the same vein, the predator-*P. tajacu* relationship was also investigated by sub-habitat. Using the same Spearman's test, a completely statistically insignificant p-value (1) and a rho value showing a moderately negative correlation (-0.5). This may suggest that predators reduce the presence of *P. tajacu*; however, the correlation, at least from this data, is likely to be by complete chance. Again, to reduce the influence of the sub-habitat variable and increase the sample size, the correlation was readjusted by camera location. This correlation is shown in the graph below (Fig. 16).

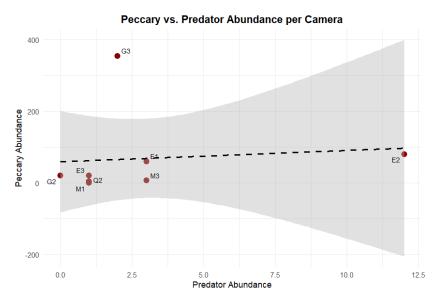


Figure 16: Correlation Plot showing the Relationship Between P. tajacu and Predator Observations per Camera Location

The correlation was revealed to be moderately positive (rho=0.482); however, the results are insignificant and likely due to chance (p=0.227).

For the intra-species *P. tajacu* factors, results were also generated. For the sub-habitat abundance of the animal, a Chi-Squared Goodness of Fit test was performed to assess the distribution of the results. This generated a significant value, suggesting that they were unevenly distributed among the forest types (p=< 2.2e-16). To investigate this further, a Bonferroni-corrected pairwise proportion test was applied to assess the differences at each possible habitat comparison; all of these results were statistically significant. In order of declining significance, the pairs were as follows: old growth-Planted (p=7.2878e-81), old growth-natural regrowth (p=2.8437e-59), and natural regrowth-planted (p=1.8556e-03). The abundance per trail was also analysed with a Kruskal-Wallis test, due to the data's irregular distribution. The p-value received was insignificant (0.4031), likely due to insufficient sample sizes. Juvenile abundance per sub-habitat was also reviewed with a Kruskal-Wallis, which was also statistically insignificant (p=0.1907) due to the same reason as with abundance per trail. Finally, the *P. tajacu* group sizes per sub-habitat were also analysed using the same test, producing another insignificant value (p=0.5858).

Regarding the other variables, various statistical tests were conducted to test their significance. For hourly temporal activity of *P. tajacu*, using a Chi-Squared Goodness-of-Fit Test, a statistically significant p-value was produced (0.0001345), strongly suggesting that *P. tajacu* activity patterns were highly non-uniform and unlikely to be due to chance. In conjunction with this, using Spearman's Rank

Correlation on the combined human and *P. tajacu* activity patterns revealed an insignificant correlation between the two species (p=0.697) and a slightly negative trend (rho=-0.084). For temperature, the p-value was found to be statistically insignificant (0.4584), with a weakly positive rho value (0.0739) indicating the apparent positive relationship between the two variables, however slight, is likely due to chance. Lastly, with elevation, the results appeared to be statistically insignificant (p=0.3571) in conjunction with a very weak negative correlation between the factors (rho=-0.033).

## **Discussion**

This study resulted in the collection and collation of many factors of data, which will each be discussed in subsections addressing comparisons to other studies conducted in various habitats.

### Intra-Species Factors of P. tajacu

On first impressions, the statistical analysis of *P. tajacu* abundance by forest type appeared to show a preference for more mature forest types, but was still present in other forests in moderate numbers, although planted forests had the least. A study in lowland Mexico supported this universal presence and suggested that P. tajacu was a generalist of forest types, including dry, flooded and subperennial. This was also true for disturbed, secondary forests, even those which subjected the species to human hunting (Reyna-Hurtado and Tanner, 2005). Another lowland survey in La Selva, Costa Rica, suggested that, generally, P. tajacu have no strong habitat preference, which differs from the results of this research (Romero et al., 2013). This may demonstrate a contrast between lowland and highland population behaviour when selecting more or less disturbed habitats. Alternatively, the animals were noted to become more habituated to human presence in disturbed areas (Romero et al., 2013); this may have made them easier to spot, potentially increasing their sample size in disturbed habitats disproportionately. Either way, more thorough research is required to determine the cause and reasoning confidently. Another factor to consider is that many of the old growth forests were at a higher elevation compared to the other forest types. Higher elevations decrease the partial pressure of O<sub>2</sub> (Forrer et al., 2023), alter floral demographics (Newcomer et al., 2022, Opler et al., 1980), humidity (Fetcher et al., 1985, Murphy, 2015), etc., which could all impact P. tajacu abundance. Consequently, the higher observation totals in old growth forests could not be confidently attributed to the sub-habitat alone. While insignificant in correlation, the group size and juvenile abundance may support an old growth preference, as group sizes appeared to have greater upper limits and averages in old growth and natural regrowth compared to planted. Juvenile abundance was highest in the old growth forests, adding further support, although statistically insignificant. Overall, to address the hypothesis, "P. tajacu will prefer old growth forest over other cloud forest sub-habitats.", this study's results appear to support it; however, the underlying reasoning, or whether it is solely due to sub-habitat change, is inconclusive. When compared to other habitats, some interesting findings come to light. One study in the Big Bend National Park, a lower-elevation, arid habitat, had higher group sizes on average (14.7) compared to the ones found in Cloudbridge, even when accounting for seasonal variation, as herds appeared to decrease in the Winter (9.9). This disparity may be down to the lower elevation of their sample sites, ranging between 1,000-1,370m above sea level (Bissonette, 1978). However, due to many unaccountable variables, no confident conclusions can be made. This lower elevation hypothesis is further supported in another study, which presented group numbers similar to the ones found in this study (5.47) at comparatively higher elevations, over 1420m in the Davis Mountains (Green et al., 2001). In a survey conducted in the Mexican tropical rainforests, a surprisingly low average herd size (2.72) although the sample size for the species was quite small (23). The largest group they recorded, however, was much larger than the biggest in this study (34) (Pérez-Irineo and Santos-Moreno, 2016). Consequently, the hypothesis, "Group sizes will be greater on average in lowland biomes compared to montane ones.", is possible, but ultimately inconclusive, due to many unaccounted variables. When considering litter sizes, in comparison with other studies, a slight difference becomes apparent. The literature consensus suggests that the average litter of *P. tajacu* is approximately 2 individuals, instead of the 1 from this study's results (Geist and Walther, 1974). This could be due to the aforementioned alterations in abiotic factors between higher and lower elevations. As these variables change, theoretically, abiotic pressure decreases, meaning that adults have access to sufficient resources and energy to breed and reproduce at higher litter sizes. Alternatively, this could also be due to the infrequent and uneven sampling of the data, which could skew the results lower than the true average. For the hypothesis, "Juvenile/litter numbers will be lower in the montane cloud forest compared to lowland habitats." The comparative results suggest it could be tentatively accepted; however, the underlying cause and impact of more robust sampling remain unclear, therefore, it remains ambiguous.

### **Factors Affecting Distribution**

From these results, there is apparent evidence to suggest that human presence is a driver of *P. tajacu* abundance within Cloudbridge Nature Reserve. Firstly, the higher numbers of P. tajacu on the Gavilan and El Jilguero trails appear to correspond to the relative lack of human presence there. The private nature of these trails limits the number of hikers on these paths to just overnight residents and researchers, which contributes to the low level of human disturbance. This potential inference must be taken with caution, as these trails were sampled at a much higher rate than the public trails, likely skewing the results in favour of the higher sampled areas. Montaña is a notable trail for this analysis, too, since it is a frequently used route, especially in the dry season, for ascending/descending Cerro Chirripó. This increases the trail's proportional human disturbance significantly, especially at night, which may contribute to the lack of *P. tajacu* sightings there. As mentioned previously, this proposal cannot be confidently confirmed by this study's results, since the sampling was highly uneven, with a minute yield of samples on the Montaña trail. The hourly time graph for humans and P. tajacu does provide more reliable supporting evidence since it accounts for all camera observations combined. While also insignificant, the graph does show a large disparity in peak activity hours for humans and P. tajacu. This suggests that P. tajacu may alter their temporal behaviour to seek times where humans are less likely to be present, i.e. the species adapts to become more crepuscular as humans are more prevalent during midday. This aligns with research conducted in Arizona, which noted P. tajacu avoiding areas of high human disturbance for feeding (Bleicher and Rosenzweig, 2018). A study in Mexico may further support this idea. It described a much more diurnal activity pattern for *P. tajacu* in comparison to the results of this paper, potentially due to the study location being more remote and less impacted by human disturbance (Pérez-Irineo and Santos-Moreno, 2016). In response to the first part of the hypothesis, "Increased human presence will negatively impact P. tajacu presence", no confident conclusion could be inferred; the potential impact of several measured and unmeasured variables may influence P. tajacu abundance rather than human presence alone. Despite this, the apparent temporal activity avoidance of humans by the animals could be evidence that supports the hypothesis, although more sampling is required to draw more reliable conclusions.

Predators had a low influence on *P. tajacu* abundance across all forest types and camera locations in this study's findings, which could be down to a few reasons. The sample size of predators was very small, especially on the public trails, which may have contributed to their lack of statistical significance. Alternatively, it could highlight how difficult a prey item, *P. tajacu*, is for many predators to kill. There are scarce reports of the animal retaliating against predators; however, they are more likely to run away (Nogueira et al., 2017). An important note regarding this subject is the lack of sampling on the Skutch trail. This trail is a remote, difficult-to-access path into dense primary forest, which had reportedly been home to sightings of many *P. onca* and *P. concolor*, which are larger predators, perhaps more capable of hunting *P. tajacu* at a consistent rate compared to smaller predators like *L. pardalis*. Sampling this trail may show a greater influence of predator abundance on *P. tajacu* sightings. Per camera location even showed an increase in *P. tajacu* abundance compared to predator abundance, although it is statistically insignificant, so it is very likely to be by chance. The hypothesis, "Increased predator

presence will negatively affect *P. tajacu* presence," could not be answered, as the results of this study were inconclusive.

### **Brief Review of Additional Factors**

In comparison to the main variables, elevation and temperature both appeared fairly insignificant in comparison. This was not a surprise due to the rigorous adaptability of P. tajacu to many different habitat types (Reyna-Hurtado and Tanner, 2005); thus, the species was unlikely to be significantly affected by changing abiotic factors (Martínez-Gutiérrez et al., 2018). Despite this, there was still a noticeable amount of P. tajacu that were detected at a higher altitudinal range. The reason for the high altitudinal preference remains uncertain as a consequence of the myriad of changing variables, meaning a change cannot be correlated with any one factor with assurance. It could be hypothesised that higher altitudes are generally less accessible to human traffic; thus, this decrease could lead to a P. tajacu increase. A notable exception to this is the aforementioned Montaña trail, which connects to the Cerro Chirripó National Park, generating higher traffic from hikers at high elevations. To make any informed assumption regarding this, a much more rigorous and focused study is required, with special attention to account for all variables, with higher sample sizes. The greater abundance at higher altitudes appears to match the old growth forests in the El Jilguero and Gavilan trails, since that sub-habitat was found only at the top of the trail; however, the existence of a correlation remains unclear. It may be due to the forest type, the reduced human traffic, the elevation itself, other unaccounted variables or a combination of factors. The temperature results also highlighted unique differences when contrasted with other biomes, especially with a desert environment. One particular study on this topic reported that P. tajacu were often inactive during the extreme temperatures of the day, i.e. midday heat and cold nights. Consequently, it was found that the animals were active during times in between, which supported milder temperatures (Bissonette, 1978). This may explain why *P. tajacu* were observed at all times of the day in this research, since Cloudbridge, as a montane cloud forest, supports a milder, less variable climate.

### **Behavioural Evaluation**

The majority of behaviours identified in this study have been discussed to varying degrees within the existing scientific literature. Regarding traversal, research reports the variety in walking up to running, including contexts for doing so, like walking during foraging and running to catch up (Byers and Bekoff, 1981). Some research delves into greater detail concerning niche one-to-one interactions, such as playing, which was not observed during this study. Reference to the reciprocal head-to-rear rubbing is also documented, suggesting that the behaviour is frequent and not unique to the cloud forest biome. It is often referred to under the moniker of "mutual grooming" and is reported not to be exclusive to any sexual combination dynamics (Geist and Walther, 1974). Interestingly, it is believed that if only one individual performs the rubbing, it may be submissive or subordinate to the other, although this was not observed in this study (Geist and Walther, 1974). This source also details antagonistic actions, like minor squabbles within the group, escalating up to full fights. Female-dominated group hierarchies were suggested in captivity, with the social structure being established through these aggressive behaviours. It is important to note that this hierarchy has only been documented in captive and controlled environments, with wild populations being much more ambiguous regarding social structure (Geist and Walther, 1974). An important group of behaviours not directly observed in this study concerned territorial marking and scent reception. While evidence of scent marking was certainly detected during surveys, neither the administration nor the reception of the signals were overtly recorded. External sources report that the scent gland is often rubbed against the substrate, and to receive the scent, the individual rubs their snout on the affected substrate (Byers and Bekoff, 1981, Geist and Walther, 1974). Some sniffing behaviour observed may belong to this reception; however, it was not definite. Sexual behaviours were not recorded at all during this study, despite the animals not having a set breeding season, although this may reduce the density of observations compared to more seasonal species (Geist and Walther, 1974). The treatment of injured individuals by P. tajacu in the scientific literature is limited; however, one paper detailed how the animals regularly visited deceased group members, reflecting the behaviour of other highly intelligent species, like chimpanzees (Pan troglodytes) and African elephants (Loxodonta Africana) (De Kort et al., 2018). This intelligence is unsurprising, considering their close relation to pigs, which studies have shown to be highly intelligent (Held et al., 2002). Another study discusses intersexual male conflict when an unfamiliar male was introduced to the group. The attack resulted in fatal injuries to the new male due to several bites to the scrotum and hind legs by the residing male (Medri and Mourão, 2016). These recorded attacks may help explain the injured individuals observed in this study. The animals were seen alone and limping from an injured hind leg. It could be hypothesised that these individuals were lone males who encountered established groups, experienced confrontation, and were left injured and alone. This is speculative as the initiation event was never observed; however, with other research showing care, even for deceased individuals of the same group (De Kort et al., 2018), it is more likely that the lone injured animals are not part of a group. The injuries are also unlikely to be a result of attempted predation, since P. onca and P. concolor tend to attack the neck and/or skull of the animal (Del Moral Sachetti et al., 2011, Mazzolli, 2013) rather than the hind legs. Neither of these areas displayed any observable damage. To revisit the idea of higher intelligence, this may be highlighted by the camera sniffing behaviour. P. tajacu would directly investigate the cameras at higher rates than most, if not all, other species recorded during the study. This exemplifies their ability to recognise unfamiliar stimuli in their environment, which may be a mechanism essential to their survival, e.g. predator detection, identifying new fruiting plants for food, etc. This is supported by the other behavioural observations concerning foraging or vigilance, which both exhibited olfactory intake. The correctional behaviour of unruly juveniles further reemphasises not only the intelligence of these animals, but also the complex relationships they form to maximise their survival. By teaching the vulnerable juveniles the importance of group protection via organised traversal, the risk of predation due to accidental isolation is likely to be reduced.

When considering the "sandwich" model, an interesting inference can be made. Literature states that in the event of disturbance, adults flush out, but the juveniles immediately drop and lie to hide, a behaviour known as tonic immobility (de Faria et al., 2020). While not directly observed, it does explain certain presumed anomalies in the secondary data set, as well as provide theories on the model observations. During in-person observations, juveniles were only seen on one occasion, which may be due to their hiding upon detection of human presence. The reasoning behind this model may be to maximise the protection of the vulnerable juveniles, which can be achieved in a few ways. Firstly, the physical presence of mature adults as a predator deterrent, secondly, more visual coverage of the environment for faster predator detection (only the adult at the back would have a blind spot from behind), and thirdly, to aid and teach navigation of foraging grounds, preventing juveniles from getting lost and isolated. It is important to note that for both models, the distance between guarding adults and juveniles varied considerably, both close and relatively far; the reason for this remains inconclusive, requiring further investigation. Reference to the observation of a "sandwich" model-like behaviour is limited within scientific literature, with the majority of referrals limited to the young following their mother near the front of the group, i.e. no mention of the adults behind the juvenile (Byers and Bekoff, 1981). Consequently, this model may be due to the linear form of the trails on which the cameras recorded, which could funnel the animals into a line formation. More research is required to investigate if this is the case, with comparisons to more open, non-linear sample contexts.

The in-person observations suggest that *P. tajacu* is a fairly defensive species during the day, which avoids unnecessary physical confrontation. The lack of violent behaviour separates *P. tajacu* from the closely related white-lipped peccary (*Tayassu pecari*). This species is also found in Costa Rica and is known to be highly aggressive, more willing to charge and bite perceived threats (Nogueira et al., 2017). The contrasting nocturnal behaviour is likely due to a few factors; firstly, many predators of *P. tajacu*, especially the wild cats, tend to be more nocturnal, thus they are more alert to the threat that these

predators present, especially when they are more abundant (Sergeyev et al., 2023). Secondly, *P. tajacu*, in particular those in the reserve, are unlikely to be habituated to human presence at night, as supported by the hourly activity graph (Fig. 11), which may have spooked the animals due to the unexpected nature of the encounter. Thirdly, and lastly, the use of a flashlight may have startled the animals due to the sudden, superfluous light stimuli, which would have overwhelmed the animals after several hours of routine darkness, to which they had become accustomed. This scenario was only recorded once, so further research into this behaviour is necessary to draw more informed conclusions. To address the second half of the hypothesis, "When confronted with human presence, *P. tajacu* will react negatively.", this can be accepted.

### **Greater Implications**

The primary takeaway from these results is the potential impact of human disturbance on *P. tajacu* behaviour and distribution. If the inferences from the findings are to be believed, there is evidence that the presence of humans alters *P. tajacu*'s temporal activity, and possibly, their choice of habitat type. Consequently, the animals appear to be active and present at higher rates during hours and locations of low human traffic. This proposed anthropogenic impact infers that the *P. tajacu*'s behaviour is altered, meaning they function in a way that deviates from their natural behaviour patterns and ecology. The influence of this on the surrounding ecosystem is difficult to determine, if it exists at all, although some change may be likely due to the animals' important role as a seed disperser and key prey item (Bigler, 1974, Byers et al., 1981, dos Santos et al., 2024, Osorto Nuñez et al., 2024, O'Brien et al., 2005). An alteration of their locality, in particular, may influence both the distribution of many plant species, depending on where they feed, and their predators. This is especially concerning with plant distribution, since changes in the lowest trophic levels are likely to have profound implications for species that rely on them in higher trophic levels (Castagneyrol and Jactel, 2012).

When considering the potential repercussions of such a topic, the impacts of ecotourism must be measured and considered carefully. Cloudbridge Nature Reserve, as a local ecotourism hotspot, has done much to revitalise and protect endangered wildlife for over 20 years, in such a unique habitat as the montane cloud forest. However, as with all locations in this sector, an appropriate balance between providing an enriching, educational experience to visitors and protecting the welfare of wildlife must be maintained, with the latter being prioritised. This is often difficult for a few reasons; people often need to see the wildlife, not only to appreciate it more, but also to build a connection and understanding of its importance (Curtin, 2009). Establishments like Cloudbridge also rely on admission fees and donations to maintain operations; presumably, people are more likely to provide this when they experience the wildlife firsthand as a consequence of their newfound connection. Without this financial aid, reserves may struggle, threatening the protection of the flora and fauna that reside there. To help regain a balance, it may be appropriate to temporarily privatise trails on certain days, to give the animals a chance to utilise otherwise busy trails to forage. Reducing the trail availability may, however, negatively impact visitor numbers as many would want access to as many trails as possible. Alternatively, there could be notices from the reserve encouraging visitors to reduce their potential for disturbance. This could be done by requesting no music be played while hiking, remaining in small groups and speaking only in hushed tones. This option is much harder to enforce and may discourage some visitors, but it facilitates access to all public trails.

## Limitations

This study was met with many limitations, which may influence the results, and especially the statistical analyses. The main limitation came from technical difficulties with the cameras, where many stopped functioning correctly during the study, for example, at R2, M1 and D1. This meant less data was collected from these locations than in others, reducing the potential sample sizes and likely skewing results unfairly. This was especially noticeable in R2 as the only data recovered featured a small collection of human recordings before malfunctioning; thus, it appears there were only humans at the

site, which is highly unlikely. There was also an insufficient number of functional cameras to cover every possible location; therefore, the overview of P. tajacu distribution was not holistic. Another limitation was the lack of control concerning many external variables like temperature, altitude, etc., which meant many measurements, like abundance and distribution, could not be determined to be down to one variable with complete confidence. Some variables were also unmeasured or weren't available for meaningful analysis. This included factors such as humidity, light intensity and floral demographics, which may have had a significant impact on P. tajacu distribution, especially the flora. Basic weather conditions were recorded as "dry", "foggy", or "raining"; however, due to this survey occurring almost exclusively in the dry season, the weather did not vary enough to produce an appropriate analysis. A major limitation was the placement of the cameras, which was limited to the trails only. Off-trail placement was trialled early in the data collection process on Sendero Rio; however, it was deemed too unsafe and difficult to access to facilitate it effectively. This is especially limiting as many P. tajacu inperson observations were seen off-trail, or in transition off-trail; consequently, this may imply that P. tajacu spend significant amounts of time off-trail, especially when humans are present. Due to the limitation on camera placement, the off-trail distribution goes undocumented. Perhaps the greatest limitation of this study was being unable to estimate the total reserve population. Since the methodology did not include tagging or radio collaring of any animals, it was impossible to enumerate unique individuals with any degree of confidence. This continued into sex identification, since adult male and female P. tajacu were hard to uniquely identify with confidence, except for mothers feeding their young.

### **Avenues for Future Study**

To continue and expand upon the research thus far, there are several options to choose from. One way to do this is to repeat the surveys during the wet season to see what differences there may be in distribution, weather-related behaviour, juvenile numbers, and more. Investigating the aforementioned variables not recorded in this survey may also reveal the impact of certain abiotic and biotic factors on *P. tajacu* distribution, with a greater focus on changing flora biodiversity. Greater efforts to survey *P. tajacu* off-trail may provide greater insight into their behaviour, potentially as a consequence of human presence. A series of more focussed studies on each variable discussed, with robust data sets, may also reveal more significant correlations between *P. tajacu* and the investigated factor. Lastly, attempts to research and estimate the total reserve population using radio collars or tagging may prove fruitful, in conjunction with more accurate sex determination, since it was not possible under this methodology.

### Conclusion

To summarise, *P. tajacu* appear to be affected somewhat by disturbance caused by human presence, both to their abundance in certain forest types and their temporal activity. Regarding other factors, the animals seem to have some statistically insignificant, yet notable, preferences in some, like elevation, and are unaffected by others, like temperature. They also appear to show certain apparent disparities compared to populations in other biomes, although the reasons for these differences are unclear, with theories surrounding elevation and flora changes.

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# **Appendix**



Appendix i: Still image from camera capture of P. tajacu



Appendix iii: Sample line from the specified table

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