Comparison of Diversity, Richness and Relative Abundance of Dung Beetles in Cloudbridge Nature Reserve

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September 2017

Deltochilum mexicanum

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1 ABSTRACT

Cloudbridge Nature Reserve on the Pacific slope of the Talamanca mountains in Costa Rica is a forest regeneration project comprising around 255 hectares of naturally regenerated or planted forest, and 28 hectares of old growth forest. The study assessed what genera of dung beetles (*Scarabaeoidea* superfamily) are present in the reserve and how diversity, taxon richness and relative abundance differed between planted and naturally regenerating forest and the old growth. Paired pitfall traps baited with dung and fermenting banana were set 50 m apart along 100m transects in the different habitat types. Flight intercepts were used on some traps to enhance capture. Three or four transects were sampled over 4 days every week, with all transects sampled once a month, between the end of November, 2016 and the end of January, 2017. The first month of sampling was conducted at the end of the rainy season and the second at the start of the dry season. Overall, 5 genera were collected, the most abundant being: *Onthophagus, Ontherus* and *Uroxys*. No significant difference was found between the forest types either overall or within genera, or in the effectiveness of either bait. There was a significant drop in overall *Ontherus* and *Deltochilum* abundance between the wet and dry seasons. High variability and large numbers of zeros in the dataset made statistical comparisons difficult and it is recommended additional study be conducted of at least 3 months, solely within the wet season.

2 INTRODUCTION

One intention of reforestation efforts at Cloudbridge Nature Reserve (Cloudbridge) is to improve its function as a natural corridor between the Chirripó National Park (Parc National Chirripó) to the east and the Talamanca Reserve to the northwest, by returning it to a state similar to the patches of remnant old growth forest in the reserve. A comparable study, conducted in a reforestation project in the Atlantic Forest in the Bahia state of Brazil, demonstrated a promising progression of *Scarabaeidae* species composition between the reforested areas and the preserved forest (Dorneles Audino et al. 2013). Former study of savanna edge forest exhibited a decrease in species richness and abundance towards the forest edge (Feer 2008). Quintero and Roslin's 2005 study of the response of dung beetle communities to forest fragmentation suggested rapid homogenization after less than twenty years, exhibiting a recovery rate twice the speed of that predicted for ant communities (Dunn 2004).

Scarabaeidae perform crucial ecosystem services, such as nutrient recycling, secondary seed dispersal, soil conditioning and aeration. Additionally, they act as transportation hosts for phoretic mites, fungi, bacteria, flies and pollen (Spector 2006). They are a valuable indicator species of environmental change, in particular of human modified ecosystems, as they are demonstrably sensitive to natural environmental gradients, land use change and resource availability (eg. Nichols & Gardner 2011). *Scarabaeidae* studies can be a cost effective means of monitoring ecosystem health due to their dependence on the presence of other animals in the ecosystem, such as dung producing animals (Spector 2006). Of particular significance to Cloudbridge is *Scarabaeidae*'s reliance on mid to large size mammals (Cambefort & Walter 1991). All six species of Costa Rican cats have been found in the reserve, along with a number of other large mammals (Cloudbridge 2017d), and a healthy dung beetle population could be an indicator of a healthy mammal population in the reserve.

The aim of this study was to assess what species of dung beetles are present in the reserve and how relative abundance, taxon richness, and diversity differ between forest types. Specifically, the study concentrated on the following hypotheses:

1) Relative abundance, taxon richness, and diversity will be greater in:
   a. the older forest types (old growth and R>30) when compared to the younger forest types (R<30 and planted),

  b. R>30 compared to R<30, and
  c. planted compared to R<30.

This study also looked at how effective fermented banana was as a bait when compared to dung, and whether or not the banana bait could be used to attract specialist species. Hypotheses were:

2) Fermented banana bait attracts specialist species not attracted to dung bait.
3) Dung bait samples will have greater relative abundance, taxon richness, and diversity than fermented banana bait samples.

As the study took place at the end of the wet season and the beginning of the dry season, differences in dung beetle community structure between the seasons were also examined with the hypothesis that:

4) There will be a difference in dung beetle relative abundance, taxon richness, and diversity between the wet and dry seasons.

3 STUDY LOCATION

The study was conducted at Cloudbridge Nature Reserve (Cloudbridge) (9.472147° N, -83.577805° W) located on the Pacific slope of the Talamanca mountains in the south of Costa Rica. Cloudbridge lies at an altitude between 1,550 and 2,600 m and is comprised of around 283 hectares of cloudforest. Approximately 28 hectares of the reserve is old growth forest with the rest composed of either naturally regenerated or planted forest. The closest area to the reserve with meteorological data was in the town of Rivas, approximately 10 km downhill of the reserve at an elevation of 875 m. In Rivas, mean annual temperature is 22.2°C and the total annual precipitation is 3484 mm (Merkel 2017). November and December typically have a mean temperature of 21.4°C with a total precipitation of 391 mm, while January and February typically have mean temperature of 21.9°C with a total precipitation of 90 mm (Merkel 2017).

Since its founding in 2002, reforestation efforts in Cloudbridge have re-established forest cover on approximately 255 hectares of degraded pastureland. The reserve is an area of great biological importance, known to be home to 298 species of birds (Cloudbridge 2017b), 47 species of amphibians and reptiles (Cloudbridge 2017a,e), and 50 species of mammals (Cloudbridge 2017d), including Puma (*Puma concolor*) and Jaguar (*Panthera onca*). At present, few entomological studies have been conducted at the reserve, identifying only 166 taxa (Cloudbridge 2017c), and data is limited. This is the first full study of the *Scarabaeoidea* superfamily in the reserve, a group commonly referred to as Dung Beetles.

The study was conducted along 15 transects spaced throughout the southern part of the reserve in four habitat types: old growth, natural regeneration over 30 years (R>30), natural regeneration under 30 years (R<30), and planted (Figure 1, Table 1).

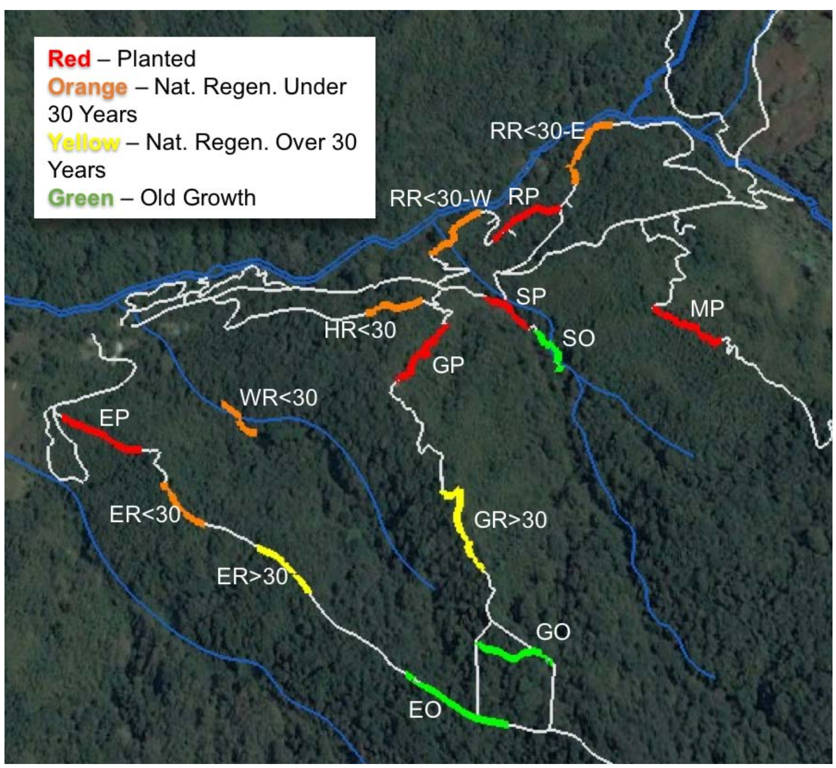

FIGURE 1: Location of study sites. First letter of site name represents the trail, the following symbols represent the habitat type: P = Planted, R<30 = Natural Regeneration under 30 years, R>30 = Natural regeneration over 30 years, O = Old Growth.

TABLE 1: Study site details.

Site	Transect Start[1]		Transect End[1]		Elevation (m)	Habitat Type[2]	Trail	Transect ID
	Latitude	Longitude	Latitude	Longitude				
1	9.47321448	-83.57245340	9.47387103	-83.57161806	1638-1646	R<30	Rio - West	RR<30-W
2	9.47343000	-83.57143000	9.47395000	-83.57034000	1653-1665	P	Rio	RP
3	9.47430588	-83.57010580	9.47523158	-83.56947145	1659-1671	R<30	Rio - East	RR<30-E
4	9.47202324	-83.57213631	9.47106351	-83.57284601	1717-1742	P	Gavilan	GP
5	9.46946190	-83.57202223	9.46834283	-83.57145067	1838-1900	R>30	Gavilan	GR>30
6	9.46728344	-83.57146081	9.46707800	-83.57049800	1941-1965	O	Gavilan	GO
7	9.47230772	-83.57349711	9.47247804	-83.57253831	1672-1684	R<30	Heliconia	HR<30
8	9.47062891	-83.57852081	9.47009859	-83.57705573	1630-1683	P	El Jilguero	EP
9	9.46954639	-83.57654570	9.46890065	-83.57586584	1719-1764	R<30	El Jilguero	ER<30
10	9.46864793	-83.57494718	9.46792876	-83.57410824	1796-1844	R>30	El Jilguero	ER>30
11	9.46683702	-83.57261182	9.46624000	-83.57111000	1917-1976	O	El Jilguero	EO
12	9.47081100	-83.57580800	9.47033018	-83.57515011	1679-1709	R<30	Water System	WR<30
13	9.47248978	-83.57144539	9.47194353	-83.57082220	1693-1728	P	Sentinel	SP
14	9.47192048	-83.57068725	9.47124926	-83.57034753	1729-1765	O	Sentinel	SO
15	9.47218577	-83.56891883	9.47165000	-83.56793000	1780-1839	P	Montana	MP

[1], Decimal degrees, WGS84 datum

[2], Habitat type: P = Planted, R<30 = Natural Regeneration under 30 years, R>30 = Natural regeneration over 30 years, O = Old Growth

4 MATERIALS & METHODS

Data was collected between 20th November, 2016, and 27th January, 2017. Traps were set for a month at the end of the wet season (late November to early December), and again during the beginning of the dry season (mid-December onwards).

Dung beetles were captured using baited pitfall traps (Figures 2 and 3). Traps were constructed from 2 L plastic soft drink bottles, 9 cm in diameter and 13 cm tall. Traps were buried so the opening was flush with the ground and covered with a plastic plate supported with wires to reduce by-catch and prevent rainwater accumulation in the trap. A cylindrical, capped bait cup (4 cm diameter, 5 cm high) was suspended from the center of the plate so that the cup hung in the center of the trap a little way down from the rim. Each cap had 11, 2 mm holes drilled in the top. A few centimeters of water with dish soap was added to the trap to help prevent beetles from escaping.

Supplementary flight intercepts (FI) were used on two of the dung traps (at 50 m and 100 m) along each transect in an attempt to increase capture rate and diversity (Ueda et al. 2015) (Figure 4). FIs improve capture rates by impeding the flight of beetles over the trap, causing them to drop down into the trap. FIs were constructed of two plexiglass sheets (20 cm x 20 cm) with slots in the center, allowing the two to be fitted together to form a cross. An indent was cut out of the bottom of each sheet (10 cm long x 4 cm high) so the FI could be fitted over top of the opening of the trap while still allowing the beetles access to the trap. A plastic rain plate was fitted over the top of the FI and fixed in place with wires.

Traps were set along 15, 100 m transects: 5 in planted habitats, 5 in R<30 habitats, 2 in R>30 habitats, and 3 in old growth habitats (Figure 1, Table 1). In a single study week, traps were set along 3 or 4 transects, with all transects surveyed over the period of a month. A total of six traps were set along each transect, at 50 m intervals to minimise interference (Larsen and Forsyth 2005). Three traps were set for each of two bait types: human dung was used as the main bait (Krell 2007), and fermented banana as a means of attracting specialist species. Canned tuna was trialed as a supplementary bait type instead of the banana during one study week in the dry season. At each 50 m interval, one trap of each bait type was set up. Traps were set between 8 am and 1 pm and left undisturbed for 48 hours before specimens were collected and preserved in ethanol.

Beetles were identified to genus level using Vaz-de-Mallo et al. (2011) *Key to Scarabaeinae of the New World* as a reference, and with the aid of Dr. Keith Philips of Western Kentucky University.

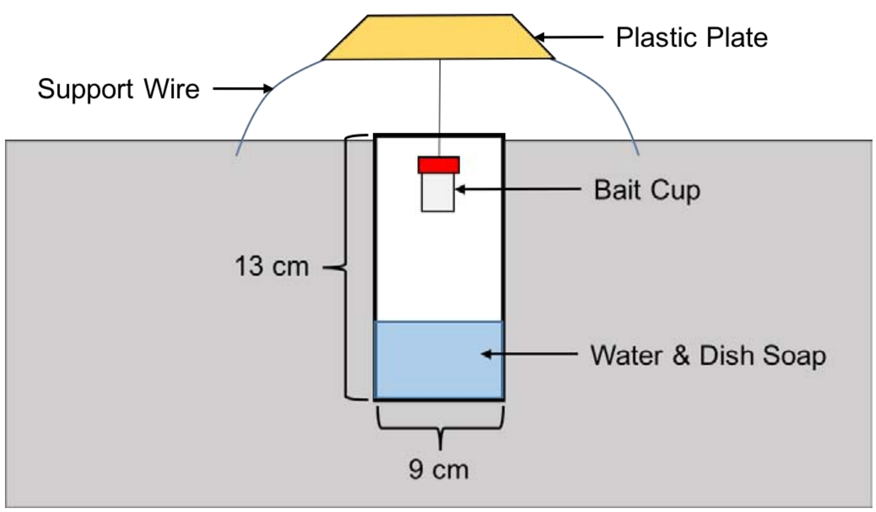

FIGURE 2: Diagram of a standard pitfall trap.

FIGURE 3: Example of a standard pitfall trap.

FIGURE 4: Example of a flight intercept.

4.1 DATA ANALYSIS

Samples were created by pooling the data for all traps on a given transect in a single collection week. Taxon richness was calculated from the pooled data for the variable of interest, as well as per sample.

Diversity was determined using the Simpson's Index of Diversity (SID) (1 = infinite diversity, 0 = no diversity).

$$D = 1 - \frac{\sum n(n-1)}{N(N-1)}$$

Where n = the abundance of an individual genus, and N = the total number of all individuals. Diversity indexes should be calculated from an equal number of samples, but the number of samples in this study were typically uneven for the variables being analysed. However, each individual sample was composed of the same number of replicates, so SID was calculated for each individual sample and then averaged to compare the variable under study.

Due to the large number of zeros in the dataset (i.e. no beetles collected in a trap or sample), and occasional very high counts, the data was very right-skewed. As such, the median rather than the mean was used as the main reporting and statistical comparison value for most tests. Statistical tests were conducted to a significance level of 0.05, although results that were significant at the 0.10 level were also reported.

Mood's Median test from Minitab Express was used for comparisons of abundance, and diversity. Mood's Median test was used as it a non-parametric test that is robust against outliers and has relatively good power for heavy-tailed distributions. For comparisons between bait types, traps of each type were paired at each trap sampling location, and the Wilcoxon Signed-Rank for paired differences test from SSP (Smith's Statistical Package) was used. When taxon richness per sample was normally distributed, a one-way analysis of variance (ANOVA) from Minitab Express was used for statistical comparison, otherwise Mood's Median test was used.

One week during sampling, tuna was trialled as a supplementary bait instead of banana. During that week, several of the tuna bait cups were removed from the traps by animals. As the presence or absence of the tuna bait in the second trap may have influenced the amount of beetles attracted to the site and, subsequently, entering the dung traps, the data from the dung traps for that week was excluded from summarized results and statistical analysis.

5 RESULTS

The data collected between November, 2016 and January, 2017 found a dung beetle community comprised of six genera, two of which were found in very small numbers. In total, 659 individuals were captured, with 13 of those unidentified to genus level. Of the five genera identified, the number of individuals ranged from: *Onthophagus*, 242 (37%); *Ontherus*, 221 (34%); *Uroxys*, 159 (25%); *Deltochilum*, 18 (2.7%); and *Canthidium*, 6 (1%). Only the four most abundant genera were analysed individually as *Canthidium* was collected in numbers too low for statistical analysis.

5.1 HABITAT

Comparing habitat types, median beetle abundance per sample was highest in R<30 at 19 (range 2-60), and generally equal between the other habitats types (medians of 11 or 12) (Table 2, Figure 5), although the difference was not significant (P-Value 0.83). Habitats had a wide range in abundance per sample (absolute differences from 58 to 79), except for R>30 which only had a total range of 17. However, the planted area's wide range was due to a large outlier, which, when removed reduces the planted range to 20. The planted outlier was due to a single sample yielding 84 beetles in one week, including 44 individuals in one trap (Rio trail, 100m). Planted and R<30 were the only habitats that had beetles in all samples.

The medians of the four most abundant genera were not significantly different between the habitats (Table 2, Figure 6). *Onthophagus*'s highest median abundance was in R<30 (9) and the lowest in R>30 (4), with the old growth and planted habitats at 6 and 5 respectively. The range in abundance was high in the planted and R<30 habitats (differences of 40 and 30 respectively), while the ranges were minimal in the R<30 and old growth (6 and 8 respectively). The median abundances between the habitats for *Ontherus* were low and similar (0 to 2). Only one individual of *Ontherus* was collected in R>30, while absolute ranges in abundances varied from 28 in the old growth to 59 in R<30. For *Uroxys*, the highest median abundance was seen in R>30 (6), with medians in the other habitats ranging from 1 in planted to 3 in the old growth. However, ranges in all but the old growth were small (4 to 10), while the old growth had a maximum sample abundance of 64. *Deltochilum* had similar medians in all habitat types (0 or 0.5) and abundance ranges of only 0-3.

As only five genera were recorded throughout the study, overall taxon richness was relatively even between the habitat types, ranging from 4 in R>30 to 5 in the other types (Table 3). Mean taxon richness per sample across habitat types were not significantly different (P-Value 0.87) (Table 3). Diversity per sample was similar between habitats as well (P-Value 0.88), ranging from 0.40±0.23 in the old growth to 0.52±0.39 in R<30.

TABLE 2: Median abundance across habitat types and genera.

Genus	Planted			R<30			R>30			Old Growth			P-Value
	Total	Median	Range	Total	Median	Range	Total	Median	Range	Total	Median	Range	
Canthidium	4	0	0-2	1	0	0-1	0	0	0-0	1	0	0-1	N/A
Deltochilum	3	0	0-2	4	0.5	0-1	4	0.5	0-3	6	0	0-3	0.63
Dichotomius	1	0	0-1	0	0	0-0	0	0	0-0	0	0	0-0	N/A
Ontherus	68	1	0-37	110	2	0-59	1	0	0-1	38	1	0-28	0.35
Onthophagus	86	5	1-41	86	9	0-30	13	4	0-6	27	6	0-8	0.67
Uroxys	15	1	0-4	17	2	0-6	21	6	0-10	79	3	0-64	0.67
Overall	177	12	5-84	218	19	2-60	39	11	0-17	151	12	0-73	0.83

R<30 = natural regeneration under 30 years, R>30 = natural regeneration over 30 years

TABLE 3: Taxon richness and diversity across habitat types.

Measure	Planted			R<30			R>30			Old Growth			P-Value
	Overall	Mean	SD	Overall	Mean	SD	Overall	Mean	SD	Overall	Mean	SD	
Taxon Richness	5	3.0	1.6	5	2.8	1.2	4	2.3	1.7	5	2.7	1.6	0.87*
Simpson's Index of Diversity	n/a	0.43	0.28	n/a	0.52	0.39	n/a	0.42	0.36	n/a	0.40	0.23	0.88*

R<30 = natural regeneration under 30 years, R>30 = natural regeneration over 30 years
*, Determined using a one-way analysis of variance (ANOVA).

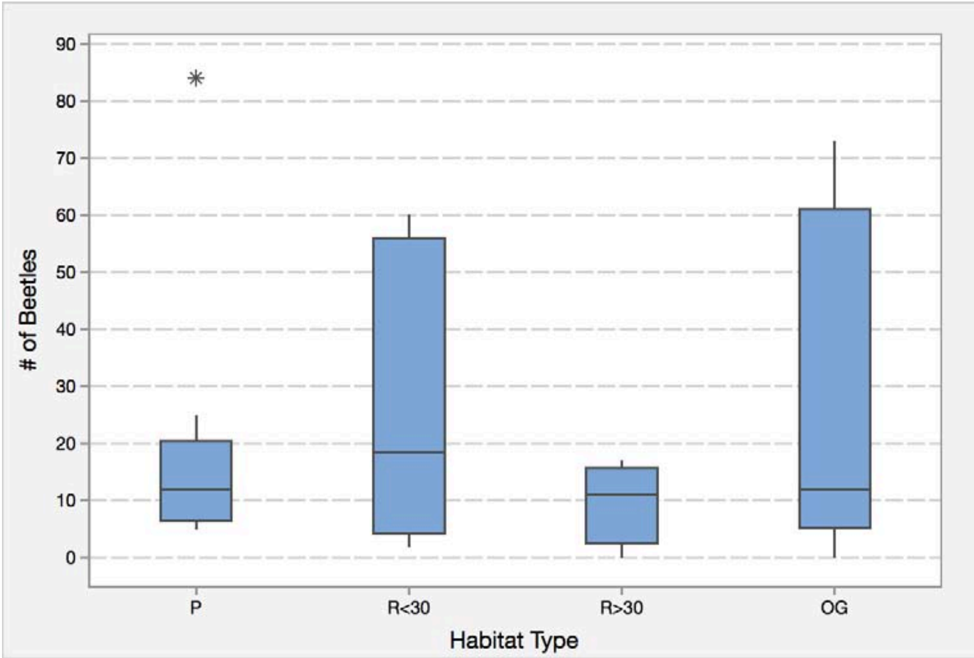

FIGURE 5: Variation in beetle abundance per sample across habitat types. P = planted, R<30 = natural regeneration under 30 years, R>30 = natural regeneration over 30 years, OG = old growth.

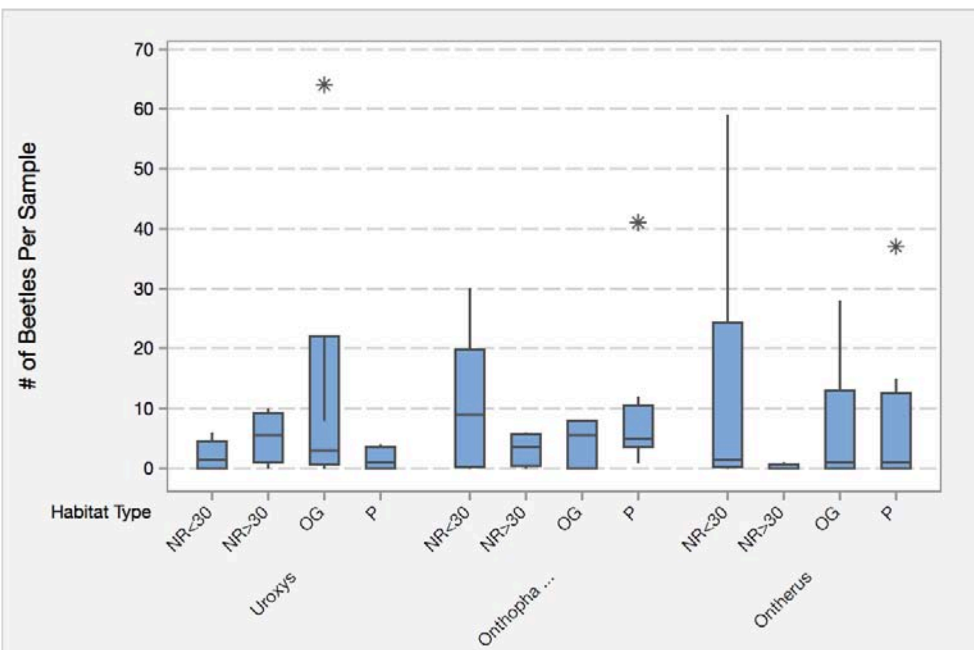

FIGURE 6: Variation in *Uroxys*, *Onthophagus*, and *Ontherus* abundance across habitat types. P = planted, R<30 = natural regeneration under 30 years, R>30 = natural regeneration over 30 years, OG = old growth.

5.2 BAIT

Dung baited traps collected almost twice as many beetles (395) as the banana baited traps (201), although median values for both groups were equal at 6 beetles per trap (ranges 0-52 and 0-78, respectively). When compared with the Wilcoxon Signed Rank test, the difference was not significant (P-Value 0.14). Broken down by individual genera, it was found that *Uroxys* and *Ontherus* showed a preference for the dung baited traps (P-Values 0.00 and 0.06, respectively), although *Ontherus* was only significant to the 0.10 level.

As two of the dung traps on each transect had flight intercepts installed to help increase capture rates, the flight intercepts may have skewed the data to increase the abundance in the dung traps. One location on each transect had paired dung and banana traps with no flight intercepts. The dung and banana traps without flight intercepts were compared on their own to determine if the same patterns were found as when all dung and banana traps were compared, and found no significant difference either overall (P-Value 0.66) or in the individual genera (P-Values: *Deltochilum* – 0.13, *Onthophagus* – 0.64, *Ontherus* – 0.81, and *Uroxys* – 0.57). This suggests that the increased abundance of *Uroxys* and *Onthophagus* in the dung traps was due to the presence of the flight intercepts and not due to a preference for the dung bait.

All five identified genera were collected in both the dung and banana baited traps. Therefore, the banana bait did not attract specialist genera into the traps. Median taxon richness per trap was 1 (range 0-4) for the banana bait and 2 (range 0-4) for the dung bait, which was significantly different to a 0.10 level (Wilcoxon, P-Value 0.07). When only the traps without the flight intercepts were compared, median taxon richness was equal at 1 (range of 0-2 for banana, and 0-4 for dung) between the two bait types and were not significantly different (P-Value 0.90). This suggests that the flight intercepts resulted in a slight increase in taxon richness per trap, but that bait type had no effect.

SID was calculated only for the traps without the flight intercepts. Overall, the banana bait traps without flight intercepts had a SID of 0.61, while the dung bait traps without flight intercepts had a SID of 0.69.

TABLE 4: Comparison of effect of bait types on abundance across genera.

Genus	Bait	All Traps				Traps Without Flight Intercepts			
		Total	Median Per Trap	Min-Max	P-Value	Total	Median Per Trap	Min-Max	P-Value
Onthophagus	Banana	84	1	0-8	0.72	32	1	0-8	0.64
	Dung	128	0	0-16		35	0	0-9	
Ontherus	Banana	84	0	0-35	0.06	53	0	0-35	0.81
	Dung	133	0	0-24		20	0	0-6	
Uroxys	Banana	26	0	0-8	0.00	13	0	0-8	0.57
	Dung	106	0	0-42		19	0	0-5	
Deltochilum	Banana	3	0	0-1	0.13	2	0	0-1	0.63
	Dung	14	0	0-3		6	0	0-3	
Canthidium	Banana	4	0	0-2	n/a	1	0	0-1	n/a
	Dung	2	0	0-1		0	0	0-0	
All Beetles	Banana	201	6	0-52	0.14	101	2	0-35	0.66
	Dung	394	6	0-78		82	1	0-15	

5.3 SEASON

Median abundances in the wet and dry seasons decreased significantly from 16 (0-84) to 10.5 (2-73), respectively (P-Value 0.03) (Table 5). Both *Ontherus* and *Deltochilum* had significant decreases in abundance between the wet and the dry season (Figure 7). *Ontherus*' median abundance decreased from 8 in the wet season to 0 in the dry season (P-Value 0.00), while *Deltochilum* decreased from 1 to 0 (P-Value 0.05). *Onthophagus* also saw a decrease in median abundance from the wet to dry season (8 to 6, respectively), although the difference was not significant (P-Value 0.86). *Uroxys* saw an increase in overall abundance from 46 in the wet season to 113 in the dry season. However, the increase was due to two large outliers, and *Uroxys*' median abundance actually decreased from 3 to 1 between the wet and dry seasons, resulting in a non-significant result (P-Value 0.17).

Overall taxon richness was 5 in both seasons. Median taxon richness per sample decreased from 4 (0-5) in the wet season to 2 (1-3) in the dry season, although the change was not significant (P-Value 0.19). Median SID per sample decreased significantly from 0.60 in the wet season to 0.32 in the dry season (P-Value 0.03).

TABLE 5: Comparison of effect of season on abundance across genera.

Genus	Season	Total	Median Per Sample	Min-Max	P-Value
Onthophagus	Wet	123	5	0-41	0.33
	Dry	119	5.5	1-21	
Ontherus	Wet	213	8	0-59	0.00
	Dry	8	0	0-2	
Uroxys	Wet	46	3	0-8	0.53
	Dry	113	1	0-64	
Deltochilum	Wet	13	1	0-3	0.08
	Dry	5	0	0-3	
Canthidium	Wet	5	0	0-2	0.23
	Dry	1	0	0-1	
Dichotomius	Wet	1	0	0-1	n/a
	Dry	1	0	0-0	
All Beetles	Wet	412	16	0-84	0.19
	Dry	247	10.5	2-73	

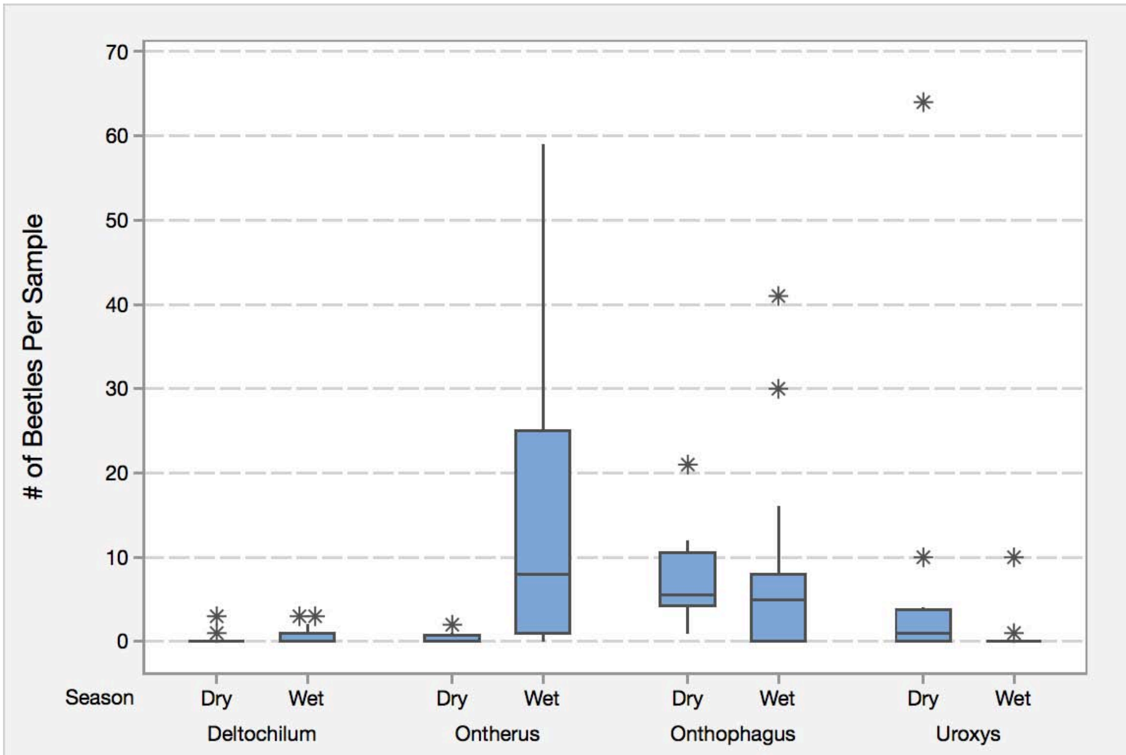

FIGURE 7: Variation in beetle genera abundance between seasons.

6 DISCUSSION

There was no clear difference in beetle abundance, taxon richness, or diversity across habitats either overall or within individual genera. Overall, R>30 had the lowest median abundance and smallest range of abundances within samples. However, as R>30 also had the fewest number of sampling sites, the lower number of samples could have reduced the probability of a large sample occurring, as large abundances per sample occurred rarely. Interestingly, the largest median abundance for *Uroxys* occurred in R>30, although the largest sample abundances for the genus occurred in the old growth. While these results are not significant, if additional data were collected, it may be found that *Uroxys* has a preference for older habitat. For *Onthophagus*, the larger median abundances and wider range in sample abundances in the planted and R<30 habitats may indicate a potential preference for the younger habitats. However, additional data would need to be collected to determine if these trends are actually significant.

In seasonally rainy environments, adults of many dung beetle species die after laying their eggs at the end of rainy season and new adult emergence occurs at the beginning of the next rainy season (Sánchez-Azofeifa et al. 2013), which is consistent with the drop in abundance between seasons seen in this study. Both *Ontherus* and *Deltochilum* had significant decreases in abundance between the wet and dry seasons. *Uroxys*' results are somewhat contradictory with a decrease in median sample abundance, but an increase in maximum sample size from 8 to 64 (Table 5). The sample with 64 *Uroxys* occurred in the first week of January, just a couple of weeks into the dry season, in the old growth. As the old growth area is cooler and more shaded, it takes longer to dry out than the other habitats, and the beetles there may not feel the effects of the onset of the dry season until later. While overall and per sample taxon richness was not significantly different between the seasons, there was a significant difference seen in the diversity between seasons.

The significant decrease in beetle abundance between the wet and dry seasons means the distribution of the beetles across habitats should be compared within the seasons to improve the accuracy of the results. However, within season comparison reduced the sample sizes for R>30 to two and the old growth to three. Given the strong right-skewness in the data, these samples sizes are not enough to make an accurate comparison.

The greatest taxon richness and relative abundance at a single trap location was found at the 100m mark on the Rio planted transect. This is noteworthy, as that area had a high-concentration of leaf litter from *Cecropia* trees – one of the key pioneer species planted in the reforestation project. The increased beetle presence may be due to the presence of White-nosed Coati (*Nasua nasua*) and other small mammals in the area, or perhaps the beetles favoured the thick leaf litter. It would be interesting to study whether there is a relationship between the *Cecropia* trees and the dung beetles.

Using fermented banana as an alternative bait for capturing specialist species was of little consequence, as no distinctive genera were identified to be attracted to the bait. However, identifying the genera to species level may uncover distinct species associated with the banana vs dung bait. There was also no discernable difference between the effectiveness of the banana vs the dung baits once the obscuring effect of the flight intercepts was removed.

7 RECOMMENDATIONS

Due to the high variability in the abundances seen in the samples and the large numbers of zeros in the data set, additional data would be required to make any definitive statements on the distribution of beetles between the habitat types. A study of a minimum of three months occurring solely within the wet season would be recommended. Adding additional sites in the R>30 and old growth habitats, such as along the Montaña trail, would make the comparisons more robust.

The sampling technique could have been improved in several ways. More information could be gathered about the habitat at each plot, most importantly soil texture, depth of leaf litter and canopy coverage, which would help identify other factors besides forest type that may affect beetle presence. Having additional environmental data may also help to explain unusually high abundances at individual trap locations.

To reduce bias associated with the bait source, for the dung bait it would be beneficial to use a composite dung sample from at least two people consuming a standardised, omnivorous diet. If supplementary baits as well as flight intercepts are used in the future, the flight intercepts should be used with both baits for more accurate comparison. Using a mesh bait cup may help improve the scent transmission of the bait and increase beetle attraction to the traps.

It would be interesting to conduct a similar study at the higher elevations of undisturbed old growth, such as the Skutch trail, where large mammals, such as Jaguar (*Panthera onca*), are known to frequent.

8 CONCLUSION

No discernable difference in the distribution of dung beetles between habitat types could be found during this study. There was no discernable difference in the effectiveness of dung or fermented banana as a bait in this study, while the use of flight intercepts increased captures of some genera. The significant drop in beetle abundance between the wet and dry seasons means that future studies in the reserve should focus on comparing dung beetle distribution between habitat types within seasons for the most accurate results. Future studies should be conducted for a minimum of three months within the wet season.

9 ACKNOWLEDGEMENTS

Thanks to Cloudbridge Nature Reserve for facilitating the research and Dr. Keith Philips of Western Kentucky University for the resources and help with identification. Thanks also to the various volunteers that helped with setting traps and to Maria Camila Ortiz Giral for her help translating this report into Spanish.

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