SNAKE COMMUNITY ECOLOGY AND CONSERVATION IN CUSUCO NATIONAL PARK, HONDURAS

by

George Lonsdale

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Author's Declaration

At no time during the registration for the degree of Research Masters has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

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Abstract

George Lonsdale. Snake Community Ecology and Conservation in Cusuco National Park, Honduras

The Mesoamerican biodiversity hotspot is threatened with agriculture related deforestation and global climate change, both of which drive widespread changes in forest composition. As the forests change, so too does the community of animals they can support; of which many reptiles have evolved micro-niches specific to these forests. Studying how these anthropogenic pressures affect the assemblages of animals that can persist there, could be vital in understanding how biodiversity will be affected on a global scale. Cusuco National Park (CNP), Honduras, is one of the most important protected sites worldwide for herpetofauna biodiversity, due to having such a high diversity of endemic herpetofauna. Despite its importance, CNP also represents one of the most threatened ecosystems in Honduras; with vast swathes of even the most protected pristine core zone being deforested and its wildlife already showing response to global climate change.

Using an established network of transects throughout CNP, Visual Encounter Surveys were used to monitor the changes in reptile biodiversity over a 13-year study period. A case study was also conducting investigating the spatial ecology and habitat preferences of *Bothriechis marchi*, the second most detected species, however, one likely that is underrepresented due to its ecology.

Diversity, richness, and evenness were found to decrease with elevation, with higher elevations being dominated by a single species, *Cerrophidion wilsoni*, whose total encounter numbers were higher than the next two species combined. Species accumulation curves for each of the surveying camps, which span the elevation gradient, have not reached asymptote, suggesting the diversity across CNP has not yet fully been described. Richness and functional guild diversity decreased with deforestation. Snake community assemblages ordinated significantly into lowland, intermediate and higher elevation communities, suggesting elevation is closely linked to snake species assemblage.

Radio telemetered snakes spent most of their time out of visually attainable range. *Bothriechis marchi* spend most of their time, stationary, in the canopy, at heights over 17 m, in closed canopy, moist broadleaf forests that are associated with rivers. One *Atropoides mexicanus* spent most of its time out of visually attainable range inside a log, undergoing ecdysis. Temperatures did not differ significantly between the log and surroundings indicating shedding sites perform a protective role for this species during a period of heightened vulnerability, rather than a thermoregulatory one.

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List of Figures, Tables, and Appendices

Taxonomic Revisions

In the interest of continuity and comparability between other papers from Cusuco National Park both published and in press, the species *Atropoides mexicanus*, will be hereafter referred to as *Atropoides mexicanus*. However, the author recognises that this species has been placed in the resurrected genus *Metlapilcoatlus* (Campbell *et al*., 2019).

Introduction

Global Threats to biodiversity

Habitat loss, unsustainable land use and global climate change are three of the greatest threats to biodiversity worldwide (Butchart *et al*., 2010; Meyer *et al*., 2016; Giam, 2017). Declines in biodiversity can be complex in nature (Mantyka-Pringle *et al*., 2015; Doherty *et al*., 2016; Giam 2017), with difficulty arising in assigning responsibility for losses with corelated causes (Harris *et al*., 2012; Mantyka-Pringle *et al*., 2015). A result of this is a large void of data pertaining to the ecological impacts of this loss of biodiversity (Collen *et al*., 2008), especially when considering baseline data in the neotropics (Roll *et al*., 2017). The tropics, home to two thirds of described biodiversity, are known to have experienced biodiversity losses to a high degree (Bradshaw *et al*., 2004), so, to reduce these gaps, greater understanding of the unique ecology of tropical ecosystems is required, including a greater level of baseline, taxa specific, community level data.

Cloud forests

Species richness and abundance are broadly inversely associated with elevation in numerous taxa (Cisneros *et al.,*2014; Acharya *et al*., 2011; McCain, 2010; Hodkinson, 2005: Gentry, 1988). However, elevation itself may not drive this trend, covariates of elevation, such as temperature or rainfall, are in turn affected by aspect and slope (Rapp and Silman, 2012), therefore will also influence habitat types, and by extension alpha and beta diversity. Cloud forests, a globally distributed and vastly understudied habitat (Bubb *et al.,* 2004), are a collection of unique forest types (Bruijnzeel and Hamilton, 2000) often limited to high elevation mountainous regions throughout the tropics. Globally, cloud forests have a large altitudinal range, 220 – 5005 masl, resulting in vast differences in rainfall and temperature averages; yet, on average, cloud forests are wetter, cooler, and more climatically stable than other montane forests (Jarvis and Mulligan, 2011). They are defined by the majority of their precipitation arriving in the form of water vapor in clouds (Muller and Stadtmuller, 1987). Forests experience many threats from land use change, deforestation, and climate change, but heightened endemism and level of habitat specialisation in cloud forests leads to the disproportionately greater effect of deforestation (Bubb *et al.,* 2004) and climate change (Ramirez-Villegas *et al*., 2014) to cause species extinctions (Segura *et al*., 2007). Changes in rainfall, temperature, humidity, and primary energy availability can put stressors on ecosystems causing species to leave an area or die (Aitken *et al.,* 2008; Bosch *et al.,*2018; Freeman *et al*., 2018). When considering the temperature decrease with elevation, species fleeing warming temperatures lower in mountainous systems must shift their ranges upslope to find their preferred conditions (Freeman *et al*., 2018). This has the overall effect of squeezing high-elevation specialists as they are outcompeted by the ascending lower-elevation generalists, without themselves a higher elevation space in which to move (Pianka, 1981). This will likely lead to the widespread extirpation of species currently restricted to the high elevations of mountain ranges, and the extinction of species endemic to these regions (Elsen and Tingley, 2015). Whilst these anthropogenic impacts may seem mechanistically clear, there may also be indirect affects by changes in climate, for example, Whitfield *et al.,* (2007) noted that a decrease in number of dry days per year alters leaf litter biomass which may have caused amphibian and reptile declines in Costa Rica.

The effects of a rapidly changing climate are of particular concern due to Mesoamerica being one of the worlds biodiversity hotspots, due to its own exceptionally high endemism and diversity (Myers *et al*., 2000). Honduras has the third highest rate of deforestation of any country in Central America, losing forest at up to 0.48% of its per year

(Sesnie *et al*., 2017) leading to an expected rapid loss of biodiversity (Oliveira Roque *et al*., 2018). In Honduras, cloud forests are found in all mountainous regions, and are protected under the Cloud Forest Act (Act 87-1987) as part of the Sistema Nacional de Áreas Protegidas de Honduras (SINAPH) (Martin and Blackburn, 2009); which protects all areas above 1800 masl, with the intent to conserve ecosystem services such as water sources for their nearest cities (Martin and Blackburn, 2009). Despite legislative protection and high elevation, Honduran cloud forests are not exempt from disturbance, with pressure from deforestation present for decades (West, 1989), so much so, it had been, albeit wrongfully, predicted that Honduras was to have lost all its cloud forest by 2021, if pre-millennium rates had continued (Mejia *et al*., 2001); Wilson and Perlman (2000) give a more conservative estimate of 2100. Within cloud forest ecosystems the purpose behind deforestation tends to be for subsistence farming and coffee agriculture (Wilson and McCranie 2004). This, coupled with other threats such as hunting, has obvious ramifications for all the biodiversity in cloud forests (Hoskins *et al.,* 2020).

Snakes as bioindicators

Snake home ranges shift relatively little over their lifetimes, allowing for changes in snake communities to be linked to ecosystem changes (Bauerle *et al.,* 1975). Generally, snakes have low capability to respond to changes in their habitat (Filippi and Luiselli, 2000), due to the specific requirements from their home ranges to fulfil specific niche and habitat needs, snakes can be considered an ideal system to study when looking at land use change and its effect on biodiversity.

Snakes and Human activity

Due to their sensitivity to anthropogenic impacts, reptiles are undergoing a mass extinction, with numbers declining in many species (Gibbons *et al*., 2000; Böhm *et al*., 2013). Declines in snake populations specifically due to deforestation have been found worldwide (Pradhan *et al*., 2014; Burgess *et al*., 2002; Shine, 1991) and snake habitat degradation has been found to significantly reduce populations (Andrade-Díaz *et al*., 2019), especially when natural forest is used in silviculture (Todd and Andrews, 2008). Despite this, snakes have received little attention in land-use change studies (Reed and Shine, 2002, Nori *et al*., 2014). Species specific habitat requirements are niche dependent, where some species thrive in edge habitat that allows for increased thermoregulation and refugia and may allow for better opportunities for hunting (Blouin-Demers and Weatherhead, 2001). Species whose specific habitat preference is determined by open spaces and increased basking opportunities may benefit from limited deforestation, allowing them to colonise new areas previously unsuitable for them (Bastos *et al*., 2005; Webb *et al*., 2005).

Human activity is known to both directly and indirectly affect the distribution of wildlife (Shackelford *et al*., 2018; Cole and Landres, 2013), however, snakes are underrepresented in the Human-wildlife conflict literature, despite snakebite being recently listed as a major global threat to humans by the World Health Organization (World Health Organization, 2019). Agricultural practices drive habitat degradation (Laurance, 2010) and human wildlife conflict (Nyhus, 2016). Higher mortality rates (Whitaker and Shine, 2000), loss of refugia and decreased activity (Marshall *et al*., 2020) have all been linked to snake communities near to settlements and agriculture (Hagman *et al*., 2012; Crane *et al*., 2016). In wild and semi-urban settings, large venomous snakes fall prey to human wildlife conflict, being persecuted by vehicles on roads, pollution (Strine *et al*., 2014), traps and being directly killed by humans (Marshall *et al*., 2018). Although some snake assemblages seem to be more resilient to land use change, from undisturbed forest to agriculture (Suazo-Ortuño *et al*., 2008), this is not true in all cases, as snake communities in Central American coffee plantations account for only half the diversity of unaltered habitat (Seib, 1985).

Snakes and prey abundance

Snakes predate a large variety of taxa which are also sensitive to ecosystem changes such as amphibians (Cortés-Gomez *et al*., 2015). On an elevational gradient, where diversity decreases, this ecosystem role may have a greater importance as the general intensity of predation decreases with decreased diversity (Camacho and Avilés, 2019). Decreases in snake abundances have been linked to decreases in prey abundance (Ujvari *et al*., 2010; Forsman and Lindell, 1997). Notably when regarding amphibians, a common food source for many snakes, which are currently experiencing a mass extinction event caused by *Batrachochytrium dendrobatidis* (*Bd*) (Stuart *et al*., 2004). Importantly, not all amphibian species are affected equally by *Bd* (Lips, 2016), and thus, a reduction in species richness from extinctions does not necessarily mean a reduction in prey biomass. However, snake populations in El Copé, Panama, have undergone a population collapse due to the reduction of amphibians in the region (Zipkin *et al*., 2020). Most species, that were not extirpated, had poor body condition as prey availability shifted. However, some species increased in abundance, becoming ecological ‘winners’, a common phenomenon post traumatic ecological events, potentially leading to homogenisation of the community (Zipkin *et al*., 2020).

Study site

All fieldwork and data collection within the two chapters of this thesis was conducted in Cusuco National Park (CNP), Honduras (Fig. 1), between 2007 and 2019. Cusuco National Park is a small, protected area within the Sierra de Omoa, north-western Honduras. Despite its size, (234km^2) CNP is extremely valuable in terms of its conservation importance, being ranked 25th in the world for its assemblage of threatened amphibians and 48th for threatened species overall (Le Saout *et al*., 2013). Numerous factors have likely influenced this ranking, including the diverse mosaic habitat that makes up CNP, a wide altitudinal range (*ca.* 20 to 2,242 meters above sea level (masl) and its situation in the Mesoamerican Biodiversity Hotspot (Myers, 1988; 2003); characterised by both high alpha-diversity and a high rate of endemism (Golicher *et al*., 2011) and intensive survey effort since at least 2007 (Green *et al*., 2012).

Cusuco National Park (CNP) was gazetted to protect all terrain over 1800 masl within an encompassing 2 km buffer zone, therefore conserving the principal water source for the country's second largest city, San Pedro Sula, and the Sula valley (Townsend and Wilson, 2008). CNP was extended in 1994 in accordance with a park management plan, to a 76.9 km^2 core zone surrounded by a 157.5 km^2 buffer zone. However, due to this never being officially recognised by the Honduran government, CNP has earned the title 'paper park', and as such, experiences issues with land use changes, lack of official protection and hunting all of which have caused a marked effect on biodiversity (Martin & Blackburn, 2009; Hoskins *et al.*, 2018).

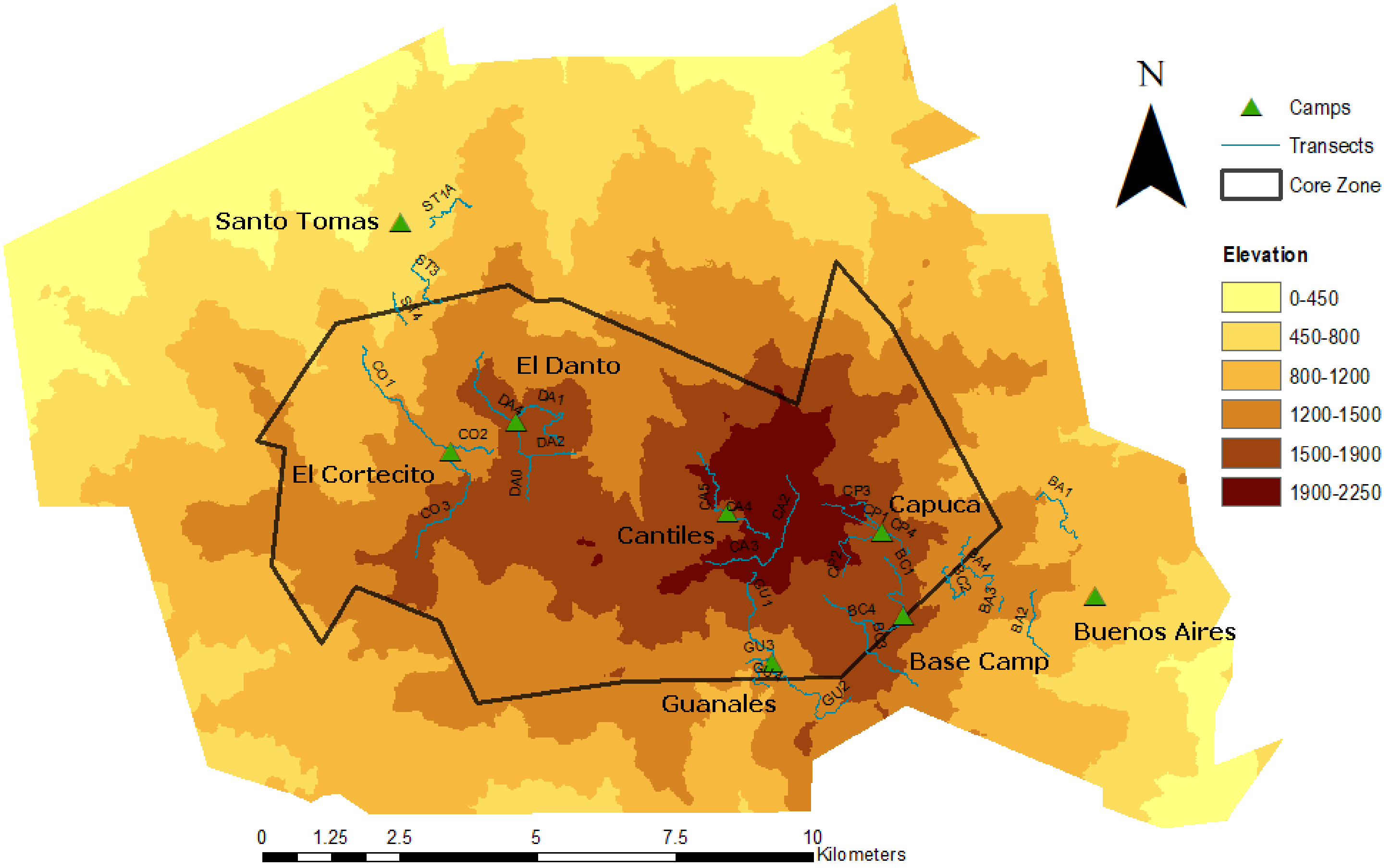


Figure 1. An Elevation Map of Cusuco National Park, Honduras. Green Triangles are camps. Blue Lines represent standardised surveying transects. Black polygon denotes the core zone. Camps and Transects are labelled. Elevation is in meters above sea level.

The two zones in CNP differ tremendously in the habitats comprising them. The largely intact core zone consists of primary and secondary lowland moist forest, pre-montane wet forest, and lower montane wet forest (Lenkh, 2005). The buffer zone contains less intact forest, being dominated by agricultural land serving cattle on the lowland slopes, turning to crop plantations of coffee, sugar cane, cardamom, and pineapple, with patches of lowland moist forest surrounding rivers and clinging to the harshest slopes. The core zone of CNP has a mean annual temperature of 14.5 °C ± 0.9 °C, with minimum 12.8 °C and maximum 16.7 °C. The mean annual precipitation is 1,832.1 ± 56.3 mm with minimum 1,711 mm and maximum 1,965 mm precipitation (Mendes, *et al*., 2011). South facing slopes between 800 and 1,500 masl are covered by semi-arid pine forest; accounting for approximately 110 km^2 of the forested area of CNP. Wet-deciduous forest covers the northern slopes between 500 and 1500 masl and is made up of a mixture of broad-leaved and pine forest. This forest type accounts for only 16 km^2 of CNP, the remaining forested area falls within the cloud forest which can be divided into broad-leaved cloud forest and dwarf forest (Green *et al*., 2012).

Cusuco National Park has a network of seven long-term biodiversity monitoring camps, which have been established since at least 2007, with one extra camp, Capuca, being utilised in 2015 (Table 1). The camps are unevenly distributed in space and elevation throughout CNP; one in the buffer zone, one on the border between the two zones, one close to the border and the rest distributed throughout the core zone (Fig. 1). Either 3 and four standardised transects radiate from each camp, ranging between 600 m and 3,100 m, following natural pathways, extinct logging trails, hunting and game trails, mountain ridges and other 'paths of least resistance' to allow for data collection.

Table 1. Details of Surveying camps within Cusuco National Park. All measurements are in Meters above sea level (masl)

Camp	Elevation of Camp (masl)	Max Elevation of Transects (masl)	Min Elevation of Transects (masl)
Santo Tomas	553	1105	660
Buenos Aires	1152	1479	1004
Guanales	1331	1975	1189
El Cortecito	1364	1696	999
Base Camp	1613	1732	1383
El Danto	1570	1730	1457
Capuca	1758	2051	1670
Cantiles	1838	2193	1789

Aims

Cusuco National Park provides an excellent case study for the impacts of deforestation and climate change on snake communities in montane cloud forests, due to it having numerous endemic vertebrates and plants, a vast elevation gradient and uphill shifts in other taxa having already been documented (Medina-Van Berkum, 2020; Neate-Clegg *et al.,* 2019). Studying the community and spatial ecology of snakes in Cusuco National Park will help to understand the dynamics of how species are distributed throughout this elevation gradient and the space use and habitat requirements of some of its most understudied species. Thus, providing the baseline data that can be continuously referred to by future studies regarding snake populations, snake communities and diversity across an elevation gradient within a neotropical cloud forest.

Chapter One – Snake community ecology along an elevational gradient in Cusuco National Park, Honduras.

Introduction

Reptiles show a high rate of endemism across montane Central America, leading to communities at altitude tending to have low evenness, skewed toward endemic or altitude adapted species (Mata-Silva *et al*., 2019). Therefore, there is a decreasing trend in the diversity of tropical snake community assemblages driven by increases in altitude (Kiorala *et al*., 2016; Chettri *et al.,* 2010; Fu *et al*., 2007), differences in climate (Moura *et al*., 2017) and decreasing temperature (McCain, 2010). Reptiles in cloud forests experience wetter, cooler and more climatically stable conditions than in other montane forests (Jarvis and Mulligan, 2011). However, cloud forests are experiencing threats from land use change, deforestation, and climate change (Bubb *et al.,* 2004), therefore, reptiles in this rapidly shifting biome may be sensitive to these anthropogenic impacts (Whiting and Fox, 2020).

The snake diversity in Cusuco National Park is surprisingly high for such a small area, with 45 species, of 33 genera, (Gilroy *et al*., 2017) representing 33% of the total diversity of Honduras (McCranie, 2011). The biodiversity within CNP is already responding to climate change and deforestation, with various taxa showing upslope shift in their elevational ranges (Neate-Clegg *et al.,* 2019, Medina-Van Berkum *et al.*, 2020). Although difficulty arises when trying to separate the effects of climate change from land-use change as they are occurring contemporaneously in montane communities (Harris *et al.,* 2012). Considering the significant upslope shift in sympatric taxa, and snake's susceptibility to the negative impacts of environmental change, it would be expected that snake communities could respond similarly to these threats. The understanding of which is imperative to reptile conservation, especially considering the lack of baseline data regarding disappearing reptile species (Roll *et al.,* 2017).

Considering both the vulnerability of snakes to anthropogenic impacts, combined with the lack of data pertaining to their trends in changing landscapes (Reed and Shine, 2002; Nori *et al*., 2014), the first chapter of this thesis provides the baseline data describing and analysing the community ecology of snakes in CNP. First, this chapter lists the diversity of snakes in CNP, comparing diversity indices between camps and comparing assemblages along a gradient of elevation, using hills numbers and rank abundance curves. Secondly, a case study is provided investigating the forest loss and associated effects on snake assemblage in El Cortecito, CNP's most deforested and still active camp. Thirdly, Detrended Correspondence Analysis (DCA) was used to investigate the drivers of diversity in CNP, and how that relates to snake assemblages at each camp and along the elevation gradient.

Methods

Study Site

This study took place between the years of 2007-2019 utilising all eight long-term forest camps in Cusuco National Park (CNP), a small, protected area within the Sierra de Omoa, north-western Honduras. Cusuco National Park is broadly separated into two zones with differing levels of protection, a largely intact mountainous core zone, surrounded by a heavily disturbed, and generally lower altitude, buffer zone (76.9km^2 and 157.5km^2 respectively). The buffer zone is dominated by agricultural land serving cattle on lowland slopes, turning to coffee and other crop plantations, with patches of lowland moist forest surrounding rivers on the least accessible slopes. The camps are unevenly distributed in space and elevation throughout CNP (Table 1); one in the buffer zone, one on the border between the two zones, one close to the border and the rest distributed throughout the core zone (Fig.1).

Data Collection

Data collection was conducted annually by Operation Wallacea Ltd (http://opwall.com) over two-month field seasons throughout the period of May-August every year from 2007-2019, with only one shorter field season in 2009 due to a coup in Honduras. The Author directly collected this data from between 2015-2019. Annual research permits were obtained from the Instituto Nacional de Conservación y Desarrollo Forestal Áreas Protegidas y Vida Silvestre (ICF) or National Institute for Conservation and Forestry Development, Protected Areas and Wildlife.

Sampling

Between 2007 and 2019 surveys were carried out in the eight camps distributed throughout the core and buffer zone of CNP. Two camps received lower survey effort, Capuca was only utilised in 2015 and Santo Tomas ceased to be surveyed annually in 2015 due to the amount of deforestation there, leading to drastic land use change and ultimately the unfeasibility of the expedition running there. All other camps have been surveyed annually for between two and eight weeks. Transects were walked daily throughout annual field seasons at a pace of approximately 500m/hr to maximise the opportunity to encounter snakes. When a snake was encountered it was caught and processed by an experienced herpetologist. Processing involves recording survey effort, specific occasion data such as time, date and weather conditions, species identification, standard morphometric measurements including snout-vent length, tail length, mass, and sex and taking DNA samples for key species. Location was logged in Universal Transverse Mercator (UTM) coordinates using a GPS (Garmin GPSMAP ® 64s) or by recording distance along the transect which is then georeferenced in ArcGIS Version 10.7 (ESRI, 2011). Elevation for each record was ascertained post-field seasons in ArcMap, by using the 'add XYZ' function for each point in conjunction with a digital elevation model. After processing all snakes were released in the same location they were found.

Data processing

Data was recorded, cleaned, and stored using Microsoft Excel (Excel version, 2011). All the data was arranged so that snake communities could be analysed at three different resolutions. The first was the highest resolution, separating the elevations spanned by a camp's transects into 10-meter bands, per year. Thus, treating each 10 m elevation band as its own discreet snake community. The second was the lowest resolution, utilising the existing network of camps as pseudo-natural groupings for snake communities. Which is arguably the most appropriate for fieldwork applications. However, due to the large uneven distribution in elevations, this may not be comparable between sites. The third resolution was to separate CNP, in its entirety, into 150 m elevation bands. This forms pseudo-communities that are less biased by camp location. However, this will still be skewed by survey effort, should there be elevation bands that overlap numerous transects from separate camps, or gaps in the transect network, where some areas will not be surveyed at all.

Data analysis

Once organised and cleaned, data was then analysed in RStudio (RStudio, 2020) using the VEGAN package (Oksanen *et al*., 2019, Vegan Package). General data exploration was done via Microsoft Excel. To assess methodological successfulness, Species Accumulation Curves (SACs) were produced using the “specaccum” function in VEGAN for each survey camp and for CNP. Population trends and Conservation statuses were downloaded from the IUCN Red List (IUCN, 2020). Shannon-Weiner’s and Simpsons diversity indices were calculated for each camp.

Functional Group diversity

Functional Group diversity was assessed on a camp-wise basis. Capuca and Santo Tomas were omitted from this analysis due to their inconsistent surveying. Snake species were grouped together based on a combination of their ecological and trophic traits into four distinct guilds, vipers and cryptic species with viper-like ecologies employing a sit-and-wait method of hunting (*e.g. Cerrophidion wilsoni, Bothrops asper, Boa imperator*);

nocturnal arboreal specialists, which tended to be of the family Dipsadidae, all were very slender with large bulbous eyes and specific head morphology for consuming soft prey such as frogs eggs or molluscs (*e.g. Imantodes cenchoa, Sibon spp.*); large cursorial snakes, which tended to be diurnal colubrids that actively hunt vertebrate prey (*e.*g. *Drymobius spp., Drymarchon melanurus, Leptophis spp.*); and fossorial snakes, which included any snakes that live underground or within the leaflitter (*e.*g. *Micrurus spp., Tantilla spp., Rhadinella spp., Omoadiphas aurula*). Proportional representation was calculated as a percentage of the total abundance of snakes at each survey camp. Changes in the proportional representation were assessed at two distinct time periods, pre- and post-a marked increase in deforestation (*Barker, R. pers. comms*), which had notable impact on the western side of CNP. Data was grouped into two timeframes 2012 - 2014 (*t=1*) and 2017 - 2019 (*t=2*) where survey effort was broadly similar, including similar number of surveys and the same number of camps open. Transects and methods were consistent between the two timeframes. Due to the concentration of deforestation on the western side of CNP, El Cortecito was singled out for further investigation. Species richness and Functional Group proportional representation were compared in the same two timeframes between transects, which have experienced varying levels of human disturbance including deforestation, land use change and regular human presence.

Rank Abundance Curves

Rank abundance curves were produced for each of the three datasets using the "Radfit" function in VEGAN. Rank abundance curves rank species based on their relative abundance within a community. Ranking the most abundant as Rank 1, the second most abundant as Rank 2 etc. Curves were then fit to one of five models to explain trends in community ecology including Pre-emption, Log-Normal, Zipf, Mandelbrot and Null models (Wilson, 1991). This was done at each of the three resolutions of community: 10 m, by camp and by 150 m elevation band. Hills numbers were also calculated for each camp and 150 m elevation band as a diversity index. Hills numbers were used over more traditional methods of calculating diversity indices because Hills number consider both species richness and evenness (Hill, 1973), placing more weight on the frequency of abundant species and discounting rare species, that would inflate diversity using indices such as Simpsons diversity index (Chao *et al*., 2014).

Detrended Correspondence Analysis

Data from each of the three community resolutions was treated to produce outputs plotting detrended correspondence analysis (DCA). This was to show what communities and locations are similar to each other and will cluster together based on their species assemblage and environmental factors. Detrended correspondence analysis was used over other ordination methods due to DCA producing clearer, more easily interpreted results (Hill and Gauch, 1980), especially when considering data spread over a gradient, which would produce a horseshoe shaped ordination using principial components analysis or nonmetric multidimensional scaling (Jackson and Somers, 1991) and dealing better with larger datasets (Hill and Gauch, 1980). Detrended correspondence analyses were then plotted and standard deviation ellipses applied around each of the natural centroids; Low, Moderate, Intermediate elevation based on Central American forest type elevations by Holdridge (1967). This was done at the three resolutions utilised for analysis with rank abundance curves. Ordination hulls link points significantly ordinated around a cluster. Ordination ellipses show one standard deviation around the cluster to imply statistical significance of a points location in relation to its nearest cluster. Species and sample ordinations were produced simultaneously and any sites located within one standard deviation can be assumed to be significantly more similar to each other than those outside of their standard deviation ellipse.

Results

From a total of 13 summer field seasons, utilising between seven and eight camps, a total of 1449 snakes were encountered. A mean of 139 ± 69 transect surveys were conducted on the standardised transect network per year, which was supplemented by a mean of 70 ± 35 annual opportunistic snake encounters. They were comprised of 44 species of 33 genera, representing five distinct snake families (Table 2.). CNP therefore houses at least 32.4% of the total ophidian diversity of Honduras. Including one Endangered species, six Vulnerable, one Near Threatened and three species endemic to CNP, all of which have decreasing populations (IUCN, 2020). The most numerous species in total over the 13-year sampling period was *Cerrophidion wilsoni* (513), followed by *Bothriechis marchi* (176) and *Drymobius chloroticus* (175). The most infrequently recorded species found in Cusuco, with only one record each were *Amerotyphlops stadelmani*, *Amastridium sapperi, Dendrophidion nuchale, Leptophis modestus*, *Oxyrhopus petolarius*, *Scolecophis atrocinctus* and *Tantilla taeniata*.

Snake abundance throughout the 13-year survey period, increased with elevation (Table 3). In the camps Cantiles, Capuca and El Danto *Cerrophidion wilsoni* (n=249; n=19; n=145) was the most numerous species. In Basecamp *Drymobius chloroticus* (n= 64) was the most numerous species. In El Cortecito, *Bothriechis marchi* (n=69) was the most numerous, and in Guanales and Santo Tomas *Atropoides mexicanus* (n=69; n=13) dominated. There is a strong negative correlation between species richness and elevation ($r_s = -0.8$, p (2-tailed) = 0.017)

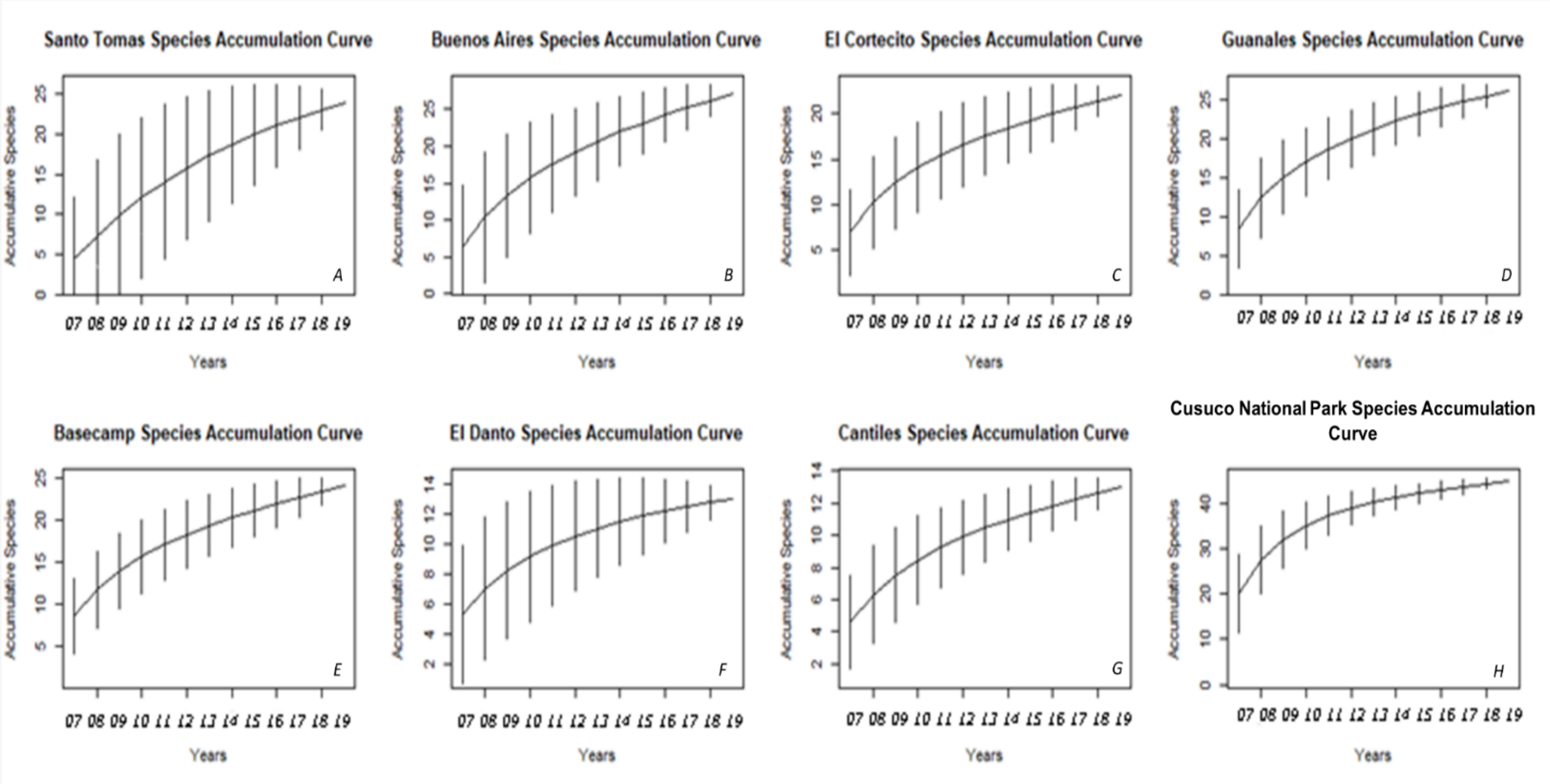
Table 2. Species list of all snakes included in this analysis. A small number of snakes have been added to the total species list for CNP (Laking *et al., in press*). Conservation Status ([LC]) was retrieved from the IUCN Redlist (IUCN, 2020) *Species whose recorded elevation fell outside the known elevation range. See Appendix 1 for full account. *† Species endemic to CNP*

Species	Average of Elevation (*masl*)	Max Elevation (*masl*)	Min Elevation (*masl*)	Number of Individuals used in analysis
Colubridae (18 species)				
Dendrophidion nuchale [LC]	563	563	563	1
Drymarchon melanurus [LC]	1448	1732	1256	4
Drymobius chloroticus [LC]	1445	1954	490	175
Drymobius margaritiferus [LC]	727	1195	472	6
Lampropeltis abnorma [LC]	1362	1528	1153	5
Leptophis ahaetulla * [LC]	1395	2012	491	40
Leptophis modestus [VU]	1613	1613	1613	1
Mastigodryas dorsalis [LC]	1398	1835	1019	37
Mastigodryas melanolomus* [LC]	803	1324	491	6
Oxybelis aeneus [LC]	1101	1163	1039	2
Phrynonax poecilonotus [LC]	1212	1296	1105	8
Scaphiodontophis annulatus* [LC]	1226	1613	730	6
Scolecophis atrocinctus [LC]	1031	1031	1031	1
Spilotes pullatus [LC]	877	1201	491	6
Stenorrhina degenhardtii [LC]	1483	1732	491	48
Tantilla schistosa* [LC]	1518	1838	1172	14
Tantilla taeniata [LC]	1320	1320	1320	1
Tantillita lintoni* [LC]	1153	1153	1153	2
Dipsadidae (17 species)				
Adelphicos quadrivirgatum [LC]	1230	1683	1089	24
Amastridium sapperi* [LC]	1352	1352	1352	1
Coniophanes imperialis [LC]	1410	1649	1172	2
Geophis nephodrymus†* [VU]	1653	2094	1339	45
Imantodes cenchoa* [LC]	1277	1704	491	47
Leptodeira septentrionalis [LC]	1197	1613	880	5
Ninia diademata [LC]	1120	1351	491	9
Ninia espinali [NT]	1767	2096	1567	9
Ninia sebae [LC]	1040	1324	491	20
Omoadiphas aurula†*[VU]	1642	2017	1089	11
Oxyrhopus petolarius [LC]	491	491	491	1
Pliocercus elapoides [LC]	1494	1626	1233	11
Rhadinella kinkelini [LC]	1513	1655	1094	7
Rhadinella montecristi [VU]	1832	2052	1370	6
Rhadinella pegosalyta†* [VU]	1633	1655	1611	3
Sibon dimidiatus [LC]	1261	1427	1215	35

Sibon nebulatus [LC]	812	1320	491	8
Tropidodipsas sartorii [LC]	1137	1758	502	7
Elapidae (2 species)				
Micrurus diastema** [LC]	1212	1694	491	39
Micrurus nigrocinctus [LC]	945	1400	491	2
Typhlopidae (1 species)				
Amerotyphlops stadelmani [VU]	1283	1283	1283	1
Viperidae (5 species)				
Atropoides mexicanus [LC]	1220	1534	491	94
Bothriechis marchi [EN]	1523	2084	686	176
Bothriechis schlegelii [LC]	672	1370	462	5
Bothrops asper [na]	1107	1283	599	5
Cerrophidion wilsonii* [na]	1766	2185	696	513

Table 3. Diversity indices of the snake assemblages at each seasonally surveyed camp in Cusuco National Park

Camp	Santo Tomas	Buenos Aires	El Cortecito	Guanales	Base Camp	El Danto	Cantiles
Species Richness	22	25	22	25	21	12	12
Abundance	73	116	190	251	248	236	308
Shannon-Weiners H	2.66	2.64	2.20	2.35	2.26	1.29	0.82
Simspons D	0.91	0.91	0.82	0.85	0.85	0.57	0.33



Santo Tomas Species Accumulation Curve

Buenos Aires Species Accumulation Curve

El Cortecito Species Accumulation Curve

Guanales Species Accumulation Curve

Basecamp Species Accumulation Curve

El Danto Species Accumulation Curve

Cantiles Species Accumulation Curve

Cusuco National Park Species Accumulation Curve

Figure 2. Species Accumulation Curves in CNP. Plots A-G: each survey camp throughout CNP. Plot H: Species Accumulation Curve for CNP in its entirety. No curves have reached asymptote. Plots A and B maintain the steepest trajectories suggesting more species will likely be found here based on the rate of acquisition.

No individual camps have reached asymptote on their species accumulation curves (Fig. 2). El Danto is the closest to reaching asymptote as of 2019, with the total curve for CNP also being close to reaching asymptote. Guanales, El Cortecito and Santo Tomas all have the steepest remaining curves.

Functional group Diversity

Snake species were assigned into four functional trait groups based on their ecology and trophic niche. El Danto is the only camp to not have all four functional groups in its community, lacking fossorial snakes (Fig. 3). Vipers make up the smallest proportion of the community in Buenos Aires, which is the smallest proportion of any of the survey camps when considering vipers. Buenos Aires has the largest proportion of nocturnal arboreal specialist species and the largest proportion of large cursorial snakes. In El Cortecito, Base Camp, El Danto and Cantiles over 50% of the snake community is just vipers (67%; 53%; 93%; 92%). Guanales has the most even community when considering functional group. El Danto has the least even community when considering functional group. The proportion of large cursorial snakes in a camp's community broadly decreases with elevation.

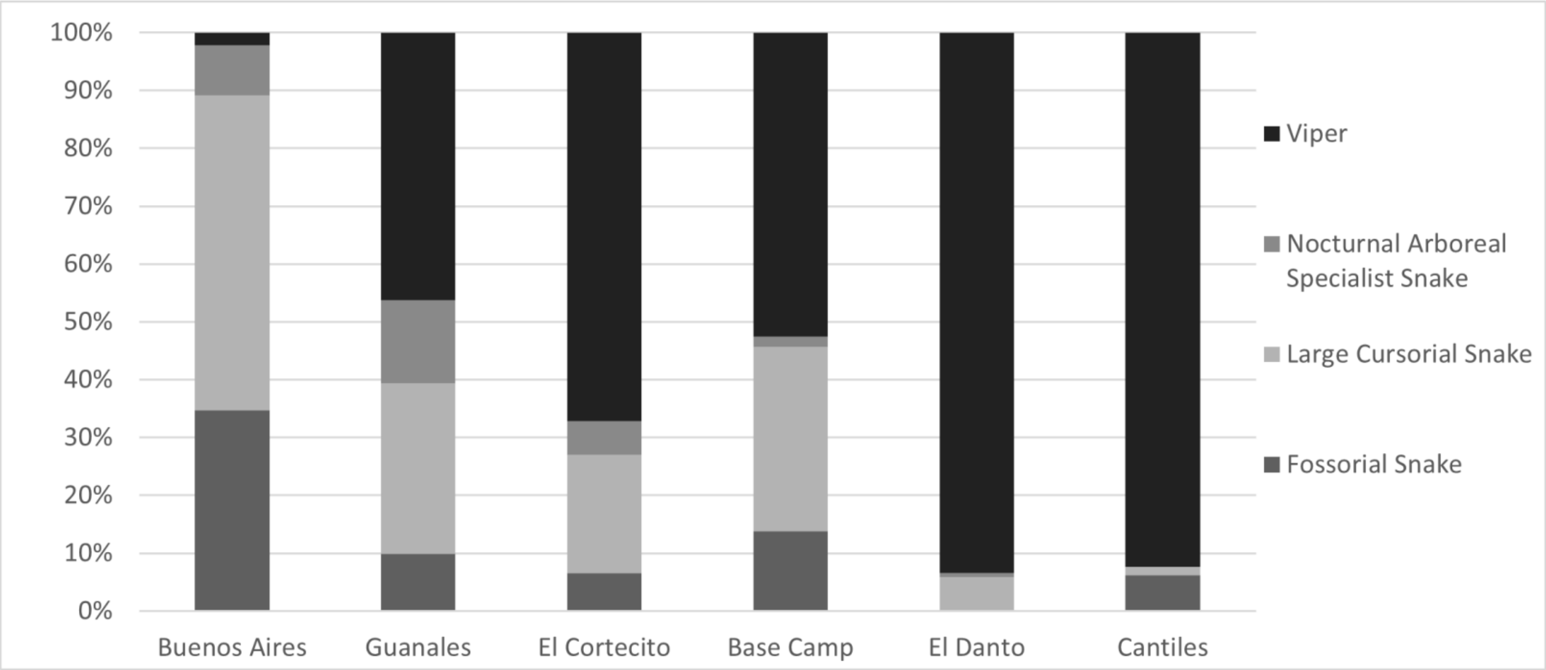


Figure 3. Percentage breakdown of four snake guilds at six seasonally surveyed camps in Cusuco National Park

Between *t=1* and *t=2* changes occurred in the functional group proportions of every camp, despite survey effort being broadly consistent. (Fig. 4). Buenos Aires has gained two functional groups. The number of large cursorial snakes in Buenos Aires at *t=1* was five. This number of records dropped to one during *t=2*. Guanales remained the most even, with proportions changing the least of all camps. Proportions of all four functional groups changed in El Cortecito, with the greatest change being in the number of viper records, dropping from 23 in *t=1* to 8 in *t=2*. At *t=2* no nocturnal arboreal specialist snakes were recorded in Basecamp. The number of vipers recorded at Base camp also dropped from 19 to 12. El Danto remained the most similar throughout the two time periods, gaining one record of a nocturnal arboreal specialist snake. Cantiles also remained very similar, however, no large cursorial snakes were recorded there in *t=2*.

At *t=1* CO1 was the most speciose transect at that camp (Fig. 5). The species richness of both CORiver and CO3 increased by one in *t=2*. Species richness of CO2 fell by one, but three functional groups were still represented, with one less viper species present. CO1 experienced the largest drop in species richness between *t=1* and *t=2*, from seven species to one and became the least speciose. The only group of snakes with any representatives in *t=2* on CO1 were the nocturnal arboreal specialists and was only represented by one individual.

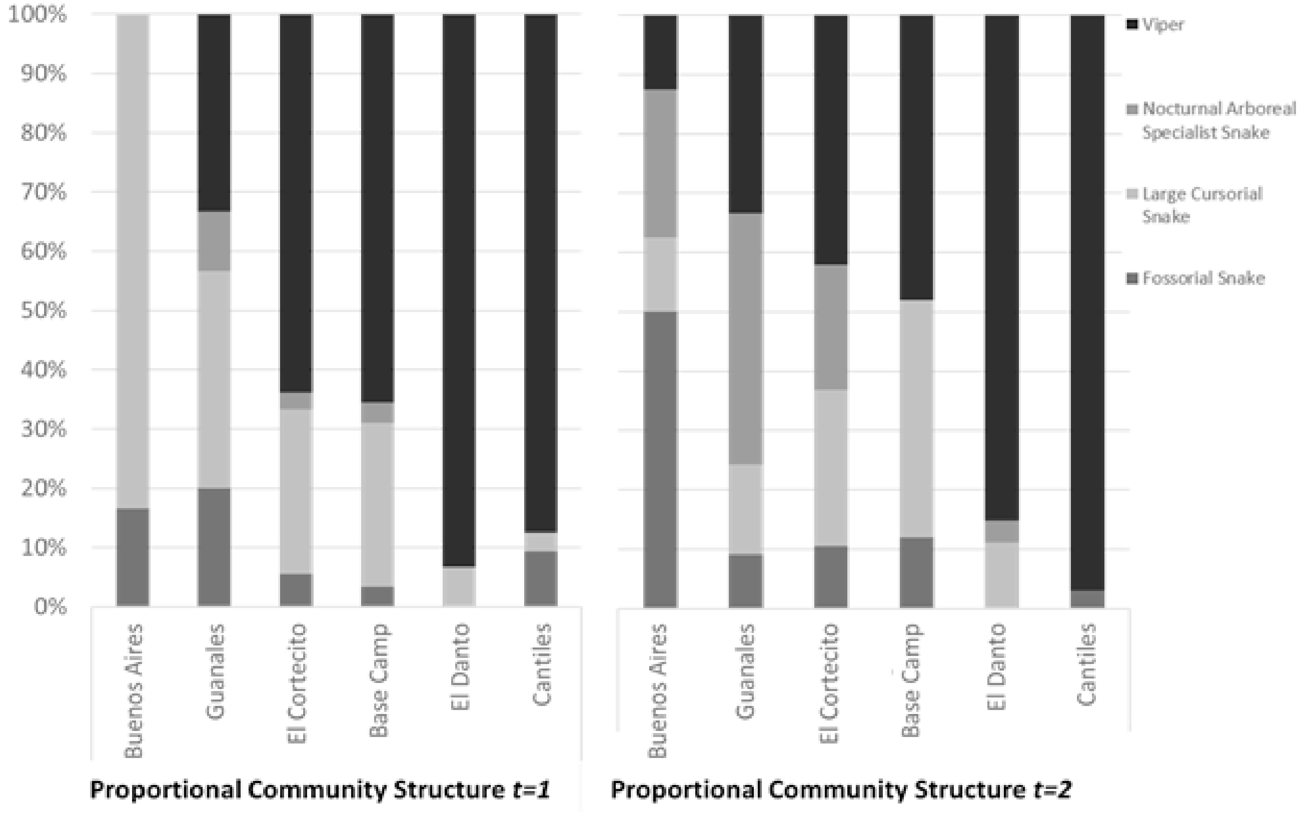


Figure 4. Percentage breakdown of four snake guilds at each of the six seasonally surveyed camps at t=1 2012-2014 and t=2 2017-2019

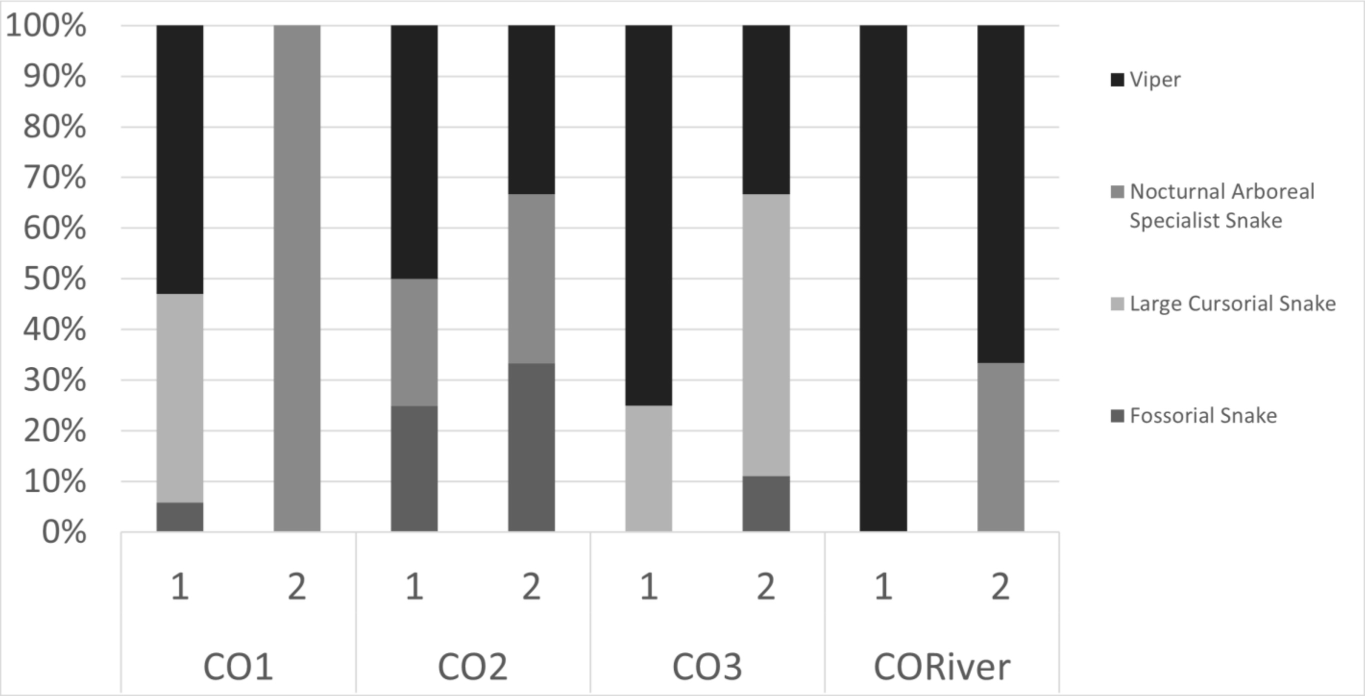


Figure 5. Percentage breakdown of four snake guilds along transects radiating from El Cortecito. t=1 2012-2014 and t=2 2017-2019.

Rank Abundance Curves

The first resolution treated 10 m elevation bands along each transect per year as a distinct community (Fig. 6). This describes the community very well at such fine scale. However, it is difficult to use when looking at wider trends. 115 communities best fit the null model. Twenty-seven communities were made up of one single species. Twenty-two communities best fit the pre-emption model. Three communities best fit the Zipf model and one best fit the lognormal model.

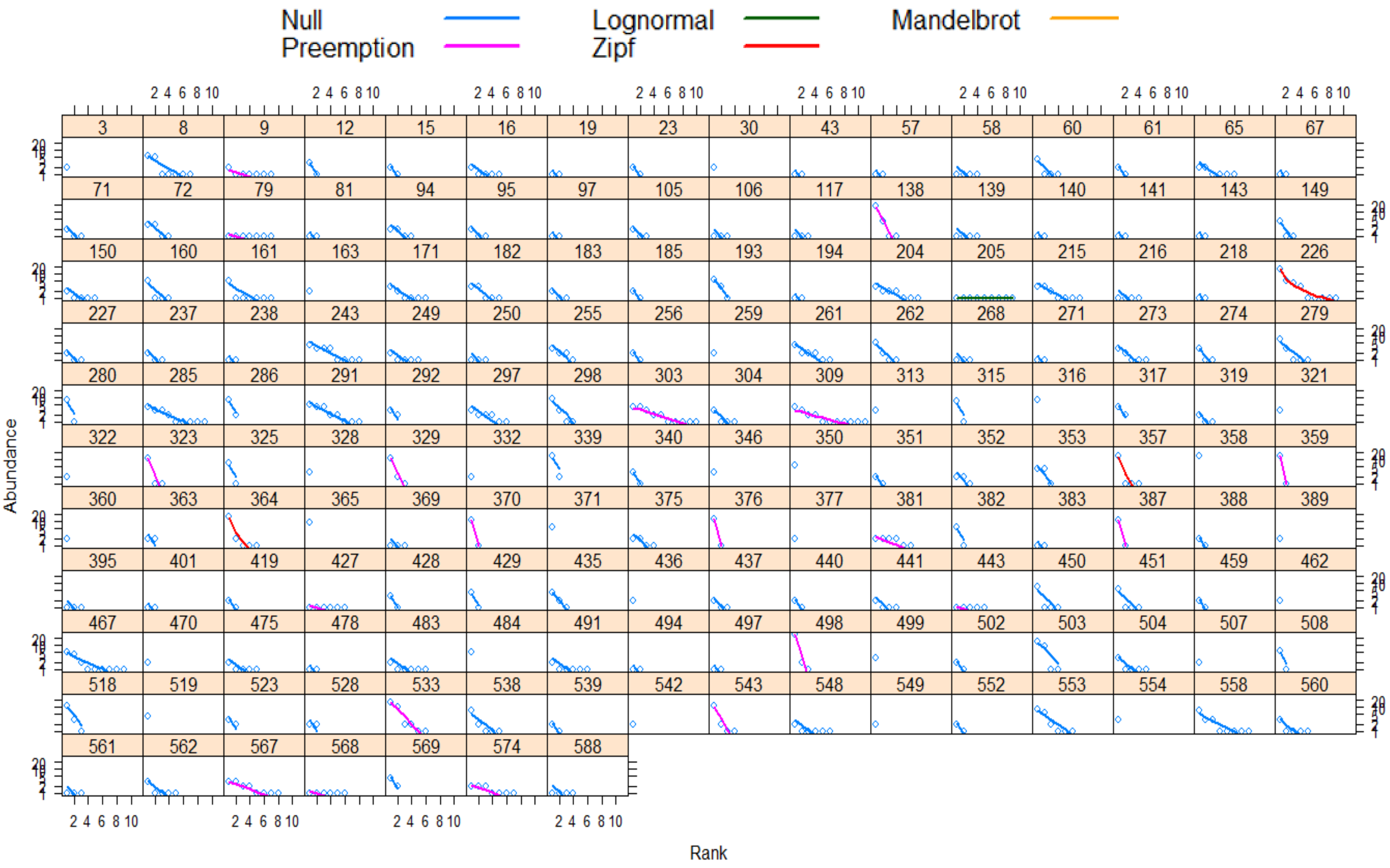


Figure 6. Rank Abundance Curves of the snake assemblages in each 10m section of each surveyed transect per year in Cusuco National Park.

The second resolution considered each camp a natural grouping for snake communities (Fig. 7). Santo Tomas has a null, broken stick, community. Out of all the camps Santo Tomas has the highest evenness. Cantiles, Capuca and El Danto all have Zipf communities due to the community being dominated by one species. Buenos Aires has the least even community fitting the pre-emption model. Species evenness decreases with elevation. Hills numbers were produced for each camp (Hills numbers q=1). Santo Tomas was the most diverse (Hills = 14.32), followed by Buenos Aires (Hills = 13.97) and as expected, diversity decreased with elevation, except for El Cortecito (Hills = 9.06), which is less diverse than the nearest elevation camps, Guanales (Hills = 14.32), and Basecamp (Hills = 9.58). Capuca was the least diverse camp (Hills = 2.20) but had the least survey effort. Cantiles was least diverse after Capuca (Hills = 2.28). Basecamp and El Danto (Hills = 3.63) had the largest disparity in Hills numbers for any two camps that are of neighbouring elevations.

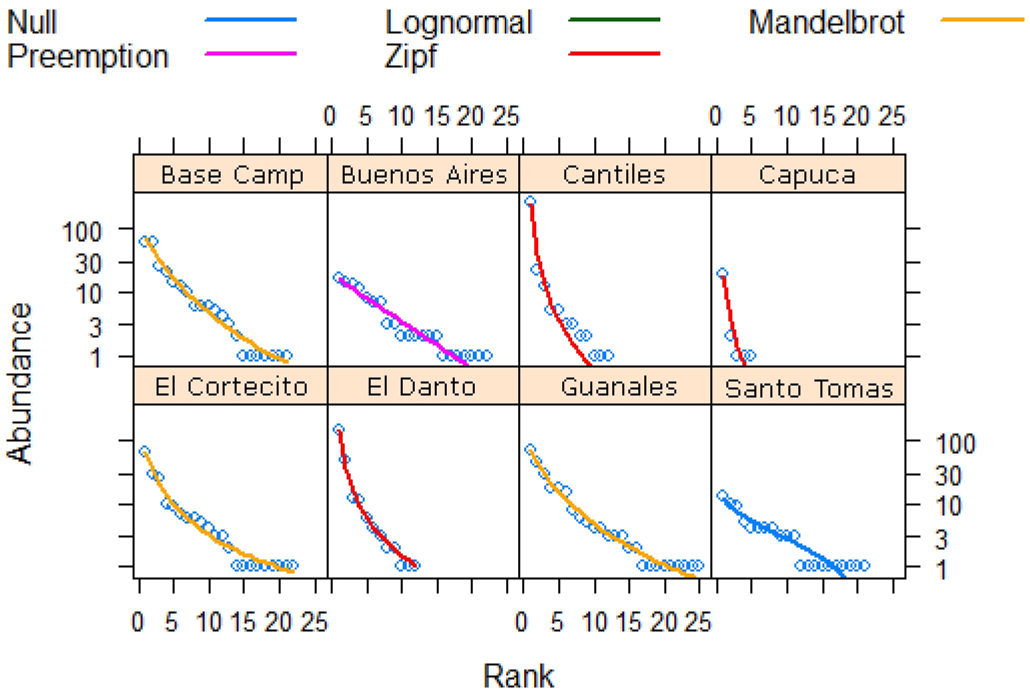


Figure 7. Rank Abundance Curves of snake assemblages in each of the seasonally surveyed camps in Cusuco National Park

The third resolution considers CNP in its entirety, dividing into 12 separate elevation bands, 11 of which are 150 m wide in elevation (Fig. 8). The 12th and highest is 89m wide. Communities *A* and *E* both fit the Pre-emption model showing high evenness. Communities *B*, *C* and *D* all fit the Null model. Communities *F* and *G* fit the Mandelbrot model and the communities at elevation bands H and above are all Zipf model. Community assemblage L could not be fit to a model as it only contained one species. Broadly, species evenness decreases with elevation, with the highest elevation bands, excluding band L, being dominated by one species. When considering Hills numbers, the diversity inversely correlates with elevation (Table 4). However, communities *B-D* do not fit this correlation. Diversity is recorded to be higher in bands where camps are situated.

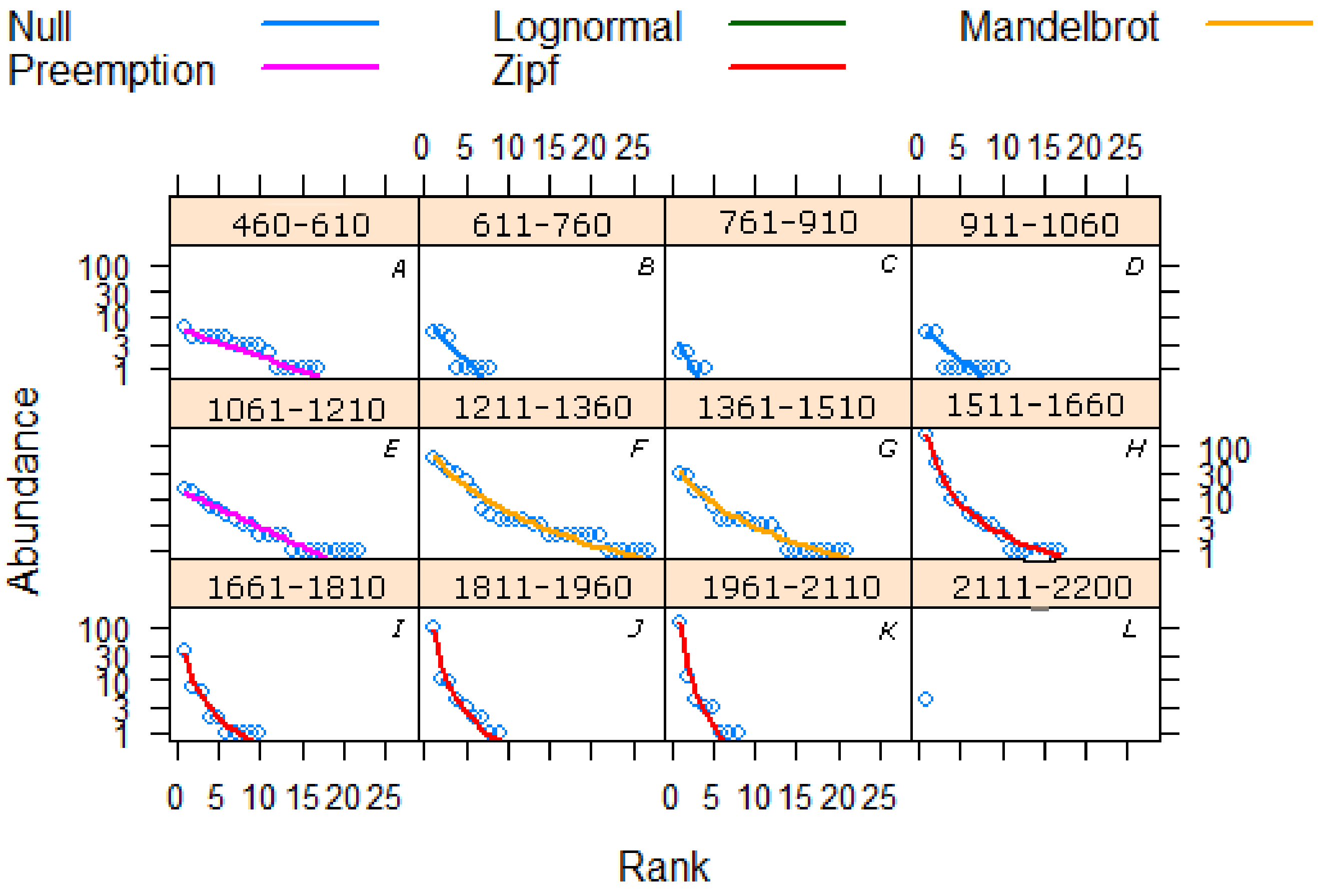


Figure 8. Rank Abundance Curves of snake assemblages in each of the 12 elevation bands in Cusuco National Park.

Table 4. Hills Numbers for each of the snake assemblages in each of the 12 elevation bands in Cusuco National Park.

Elevation Bands Hills Numbers (q=1)			
460-610	**611-760**	**761-910**	**911-1060**
14.52	6.08	3.78	7.36
1061-1210	**1211-1360**	**1361-1510**	**1511-1660**
13.97	11.44	11.07	4.30
1661-1810	**1811-1960**	**1961-2110**	**2111-2200**
3.99	2.78	2.02	1.00

Detrended Correspondence Analysis

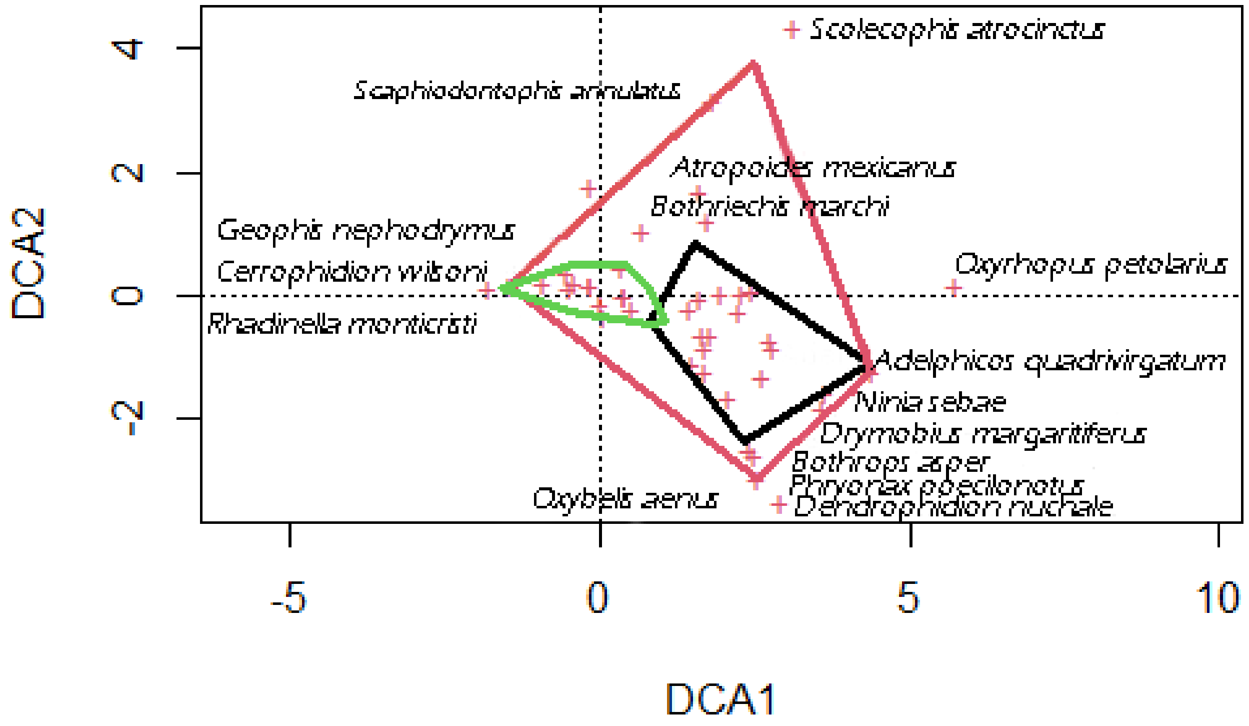


Figure 9. Detrended Correspondence Analysis ordination of the snake assemblage at each 10m elevation band along each transect per year.

The fine-scale assemblage data in the first DCA plot (Fig. 9) did not differentiate enough between assemblages to show distinct clusters. This is likely due to each assemblage not containing enough samples. However, two main clusters in species ordination can be seen, delineated by the ordination hulls in green and black. Green denotes assemblages in areas of high elevation. Black denotes assemblages in intermediate elevations. There is a small amount of overlap between these assemblages. The identity of DCA1 and DCA2 is not clear, however there is a considerable cluster of low elevation snake species ordinated around the positive side of the DCA1 axis and the negative DCA2. Whereas the high elevation species have clustered together and ordinated on the negative side of DCA1, thus indicating DCA1 is likely elevation.

The second DCA plot describes the snake communities at each of the survey camps (Fig. 10). Higher elevation camps Cantiles and El Danto are positioned within one standard deviation ellipse of cluster 3 and ordinated on the negative part of the DCA1 axis. Capuca however is situated closer to Cantiles therefore having a more closely related community assemblage. Basecamp is located outside of the 1 SD ellipse but forms part of the ordination hull to make up cluster 3. Intermediate elevation camps El Cortecito, Guanales and Buenos Aires form a natural grouping in cluster 2 and ordinated on the positive side of the DCA1 axis. Santo Tomas represents the only lower elevation camp and forms cluster 1, which ordinated on the positive side of DCA1 and DCA2. Based on camp elevations we know that DCA1 is elevation decreasing along the x axis. It is possible DCA2 is related to species ecology as all the viper species ordinated on the positive side.

The final DCA utilises the 12 elevation bands (Fig. 11). This looks broadly similar to the DCA of the camps ordination. Cluster 1 was made up of elevation Band 1, which ordinated on the positive side of DCA1 and DCA2. Elevation Bands 2-7 made up cluster 2, with bands 4 and 6 being within 1SD of each other. These all ordinated on the positive side of DCA1. Elevation bands 9-12 ordinated on the negative side of DCA1 to form a tight grouping in cluster 3, suggesting all assemblages were highly related. Bands 8, 9 and 10 fell within 1 SD of each other suggesting community assemblage was significantly similar. Based on the location of the elevation bands DCA1 is likely elevation, decreasing along its axis.

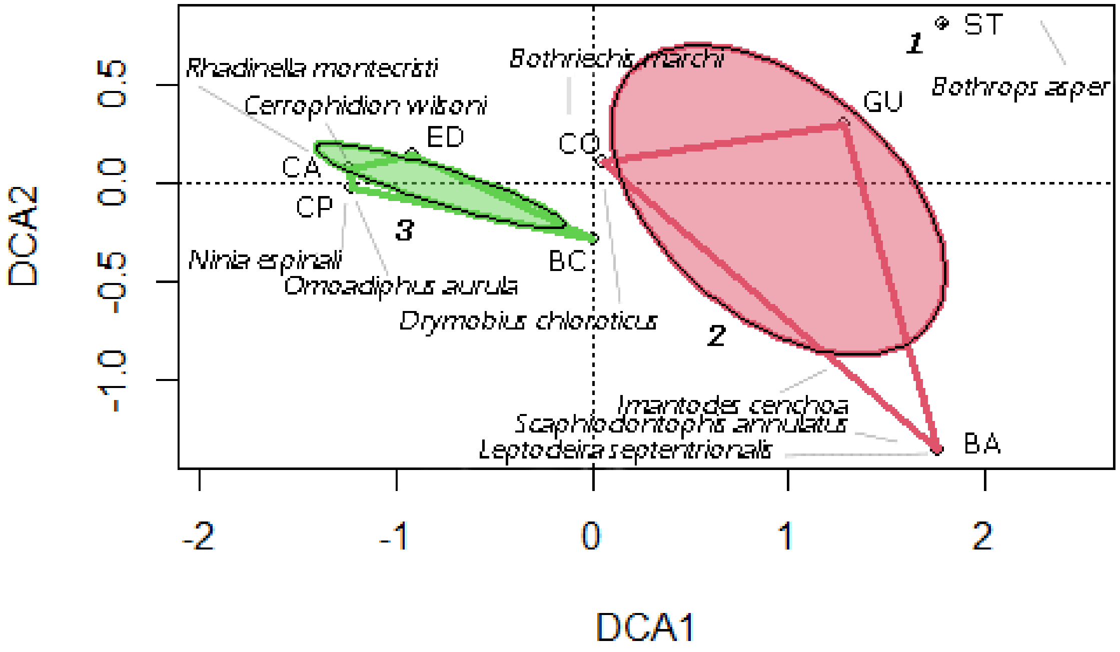


Figure 10. Detrended Correspondence Analysis ordination of the snake assemblage each of the seasonally surveyed camps in Cusuco National Park. DCA1 is inverse elevation.

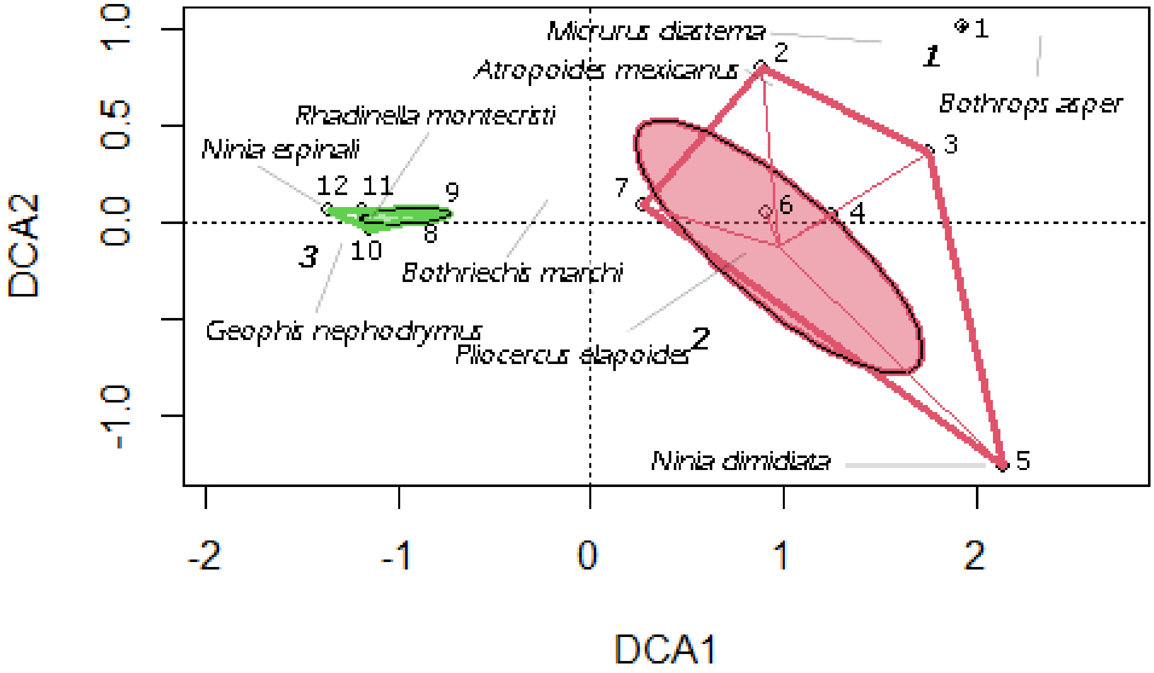


Figure 11. Detrended Correspondence Analysis ordination of the snake assemblage each elevation band in Cusuco National Park. DCA1 is inverse elevation.

Discussion

A study with a sample size this large has not been completed on snakes in the neotropics prior to this. Despite the relatively small size of CNP, snake diversity was found to be surprisingly high; housing more species than are currently recognised to be the much large Pico Bonito National Park (McCranie and Solís, 2013), another cloud forest national park on the northern coast of Honduras. Pico Bonito spans a larger elevation gradient that CNP and therefore one would expect higher overall diversity, especially when considering the small amount of human disturbance there (Jocque and Argueta, 2012). CNP's known diversity is therefore apparently testament to the sheer quantity of survey effort invested by the Operation Wallacea herpetology teams. Much like the herpetofauna of Pico Bonito, CNP's herpetofauna assemblage is littered with endemic species including the three endemic snakes (Table 1). CNP's mosaic of micro-habitats is a contributing factor into why these endemics have evolved, as well as CNP having both inland and Caribbean aspect slopes creating distinct micro-climates (Martin *et al.,* 2016).

Cerrophidion wilsoni was the most abundant species throughout CNP during the 13-year sampling period. This is due to both the extraordinary high density of this species throughout the upper reaches of CNP and most of the surveying sites and transects fitting within the species known elevation, between 1300-2620 masl (McCranie, 2011). Whilst we do not here estimate snake density, anecdotally it is very high. CNP likely presents *Cerrophidion wilsoni* with a 'snake heaven', where there is a series of ideal conditions such as low numbers of predators and competition in an isolated population, allowing them to have high numbers as seen with other species in isolated communities (Bonnet *et al.,* 2002; Martins *et al.,* 2008). Although, this apparent high density may be due to a seasonal aggregation (Graves and Duvall, 1995), an implicit bias in our survey methods. More surveying throughout the year may provide better estimates of population size.

The least recorded species, with only one record each, represent an assemblage of cryptic fossorial snakes, and three large colubrids. With the exception of *Leptophis modestus*, they all represent lower elevation species, with *Amerotyphlops stadelmani* and *Oxyrhopus petolarius* being the only species known in the list to occur over 1300 masl (McCranie, 2011). Due to the situation of the survey camps in CNP, there will always be a bias towards intermediate and medium elevation species over lower elevation species. There are more camps above 1300 masl than below, and two of the camps below 1300 masl, Guanales and El Cortecito have transects that immediately range uphill. Therefore, low elevation species are more likely to be missed. Due to Santo Tomas being the only low elevation camp, after the cessation of standardised surveying in 2015 the likelihood of finding new species to CNP here is greatly reduced.

Worldwide there are diversity gradients that are constants, such as diversity reducing with elevation. CNP is no exception, with species richness inversely proportional to elevation. Buenos Aires is the most diverse camp (Table 3), having the same species richness as Guanales but higher diversity indices. This is likely due to a compilation of factors; Buenos Aires is situated at a lower elevation than Guanales, and therefore would fall into the potential home range of more species; Buenos Aires' transects are comprised of a mixture of old growth secondary forest, open coffee plantation, shaded coffee plantations and open village/pasture. This wide diversity of habitats allows for a wide variety of niches to be filled by species.

However, snakes in Guanales are vastly more abundant than Buenos Aires (248-116). Suggesting that despite the habitat around Guanales being more homogenous (intermediate elevation pre-montane wet forest), it is able to support many more snakes. This is especially apparent when considering detectability, as snakes in more open habitats are easier to detect and the disturbed habitats around Buenos Aires are more open than the more dense, closed canopy forests surrounding Guanales. Cantiles was the least diverse camp, however, despite this Cantiles has the highest abundance of snakes. Cantiles, which is situated in the heart of the National Park (Fig. 1) has transects that radiate through primary moderate elevation rainforest, dwarf forest, and crucially a large landslide disturbed area, which occurred because of Hurricane Mitch in 1998. This south-facing landslide area (ca 240 m^2) is surrounded by broad-leaved rainforest, and itself is dominated by a rocky open space, interspersed with pine trees. This combination has led to an arid micro-climate that is significantly warmer, receives more sunlight and has less leaf litter. All of which seem to aid the presence of *C. wilsoni*, which occur in extraordinary numbers here. The author has opportunistically found upwards of ten individuals basking here within 50 m of each other on a day with lots of sun. Due to the increased thermoregulatory opportunities, other reptile species are in high abundance here, including skinks, *Scincella incerta* and *Scincella cherriei*, and the Phrynosomatid lizard, *Sceloporus malachiticus*, on which *C. wilsoni* are known to feed (Campbell and Solórzano, 1992).

In all but one camp, Basecamp, throughout the sampling period Vipers were the dominant species. With *Cerrophidion wilsoni* being dominant in the three higher elevation camps, *Bothriechis marchi* being dominant in El Cortecito and *Atropoides mexicanus* dominant in both Guanales and Santo Tomas. Interestingly the large viper *Bothrops asper* (Garman, 1883) is known to occur at three of the camps, Buenos Aires, Guanales, and Santo Tomas. In other studies, localities where *B. asper* is found it tended to be the most abundant snake (Sasa *et al.,* 2009), and yet is outside the top three species at all three of these sites in CNP.

Species Accumulation Curves

None of the Species abundance curves (Fig. 2) reach asymptote. Suggesting that throughout CNP, richness is slightly higher than our sampling effort has purported (Ugland *et al.,* 2003). These species abundance curves provide a good guide of the completeness of our surveys. However, as ectotherms are known to be sensitive to climate change (Paaijmans, *et al.,* 2013; Deutsch *et al.,* 2008) and with some taxa in CNP already 'feeling the effects' of climate change (Medina-Van Berkum *et al.,* 2020; Neate-Clegg *et al.,* 2019) and responding with uphill shifts to find more pristine habitat and cooler temperatures, it is likely these assemblages are due to change, with the higher elevation sites undergoing mass recruitment (Elsen and Tingley, 2015; La Sorte and Jetz, 2010; Stachowicz *et al.,* 2002). Perhaps even more so when considering many of the snake species in CNP tend to be small and therefore may be more profoundly affected by climate change (Woods *et al.,* 2015).

Functional Diversity

Assignment of snake species to functional guilds, was based on both ecological traits listed in McCranie (2011) and those observed by the author in CNP. It is well known that snakes are commonly persecuted by humans, through deforestation, land use change and direct killing, especially when considering venomous snakes (Marshall *et al.,* 2018; Shankar *et al.,* 2013). *Bothrops asper* is purported to be one of the most numerous snakes around Buenos Aires, according to the local people, however, is rarely recorded by our surveys or opportunistic methods. Killings of *B. asper* occur frequently around Buenos Aires. It seems likely this human influence is negating the trend of *B. asper* in becoming the most common species as seen in other locations within its range (Sasa *et al.,* 2009). The camps with the highest elevation, Cantiles and El Danto, are dominated by vipers, making up more than 90% of all snake records from these locations. Two species in the viper category, *Bothriechis marchi* and *Cerrophidion wilsoni*, occur in both these camps; in both instances the records are vastly skewed towards *C. wilsoni*, likely due to the three factors previously discussed, a combination of reduced competition at higher elevation, high prey availability and population isolation.

2015 and 2016 saw a notable increase in the amount of new illegally deforested areas appearing within the core zone of CNP (Barker, R., *pers. Comms*). When comparing the two years prior to the two years post this period, changes can be seen in the proportional representation of functional guild within every survey camp. It is difficult to attribute these changes to deforestation directly as climate change is also ongoing, which may explain why there has been some recruitment into Buenos Aires, gaining two functional groups. The proportion of vipers at basecamp dropped by ca. 20%. Basecamp is close to the lower elevation range of its most common species *Cerrophidion wilsoni* (McCranie, 2011). As a small montane viper this species may be sensitive to climate change and undergoing uphill shift, so there will be lower densities at this lower range (Woods *et al.,* 2015). Reports exist of killings of *C. wilsoni* in some areas around Base camp, close to human settlements, which would also decrease numbers. Base camp also serves as the visitors centre for CNP, and as such has numerous 'Tourist Trails' radiating from there. This extra disturbance may decrease the likelihood of encountering an individual (Goiran and Shine, 2013). Although, providing tourist numbers stay relatively low and on designated paths, snake populations may be unaffected (Sterijovski *et al*., 2011). Amongst the camps within the core zone of CNP, El Cortecito experienced the most drastic changes in proportional representation (Fig. 3). With the largest changes occurring on the transect CO1. Up to and including *t=1*, CO1 was heavily forested with mostly primary and some old secondary pre-montane moist forest, similar to that surrounding Guanales camp, with which is shares similar elevation. During the time between *t=1* and *t=2*, almost all C01 was felled (Fig. 12 and Fig. 13), leaving around 100 m of forest close to the camp. C01 follows a mountain ridge that links to nearby villages and is continuous with CO2. Clearcutting was used and evidence of coffee, cardamom and pineapple plantations being planted was clear. Some small areas of deforestation have also appeared on CO2, but this is not comparable in scale to CO1. Interestingly both transects in El Cortecito that experienced deforestation also saw decreases in species richness and in the functional group diversity. Whereas the two transects left pristine, CO3 and CORiver increased in both these metrics. Deforestation reducing richness is widely purported to be one of the leading causes of global biodiversity loss in tropical forests (Giam, 2017).

Figure 12. CO1 in 2018 during t=2. Clear cut trees lay strewn where primary pre-montane forest once stood. ©P. Medina-Van Berkum

Figure 13. A habitat plot on CO1 in 2018 during t=2. The small orange tape (central-bottom left) marks the decimated transect path. ©P. Medina-Van Berkum

Rank abundance curves

Using camps as a resolution for rank abundance is problematic (Fig. 7) as camp location was selected when Operation Wallacea first started surveying in CNP, reflecting a logistical purpose rather than one rooted in ecology. However, when considering fieldwork in CNP it is perhaps the most useful way to approach looking at the community ecology. Evenness decreasing with elevation is in line with our other results where camps at higher altitude have tended to be dominated by a single species *Cerrophidion wilsoni*. The community at Santo Tomas fit the null model, more surveying is needed to properly understand the snake community here. Hills numbers fit the global ecological trend that diversity broadly decreases with elevation.

Analysing elevation bands throughout CNP makes more ecological sense (Fig. 8), especially when considering communities that are sequential up the mountain. The most apparent result is that communities *B* – *D* all fit the null model. These elevations have extremely little to no coverage in the transect network (Table 1), most records are opportunistic here, whilst transiting between camps for example, hence why there are so many species ranked low with little abundance. More standardised surveying at these elevations is required to greater understand the snake communities. The number of species broadly decreases with elevation, when ignoring the elevation bands with null models. However, there is a large spike in richness at elevation bands *F* and *G*. This coincides with the locations of the camps El Cortecito and Guanales and Base camp, all of which are heavily surveyed and well covered with transects. This mid-elevation spike in richness is also seen in other taxa in CNP (Medina-Van Berkum *et al*., 2020) where it is suggested to be due to higher food availability, and in other taxa elsewhere (Chaladze *et al.,* 2014; Mccain, 2004). Band *L* only contains one record. This shows that snakes can occur at this elevation in CNP, but that more standardised surveying is needed at the highest elevations to greater understand these communities. Hills numbers for elevation bands follows the same diversity trends seen throughout this study whereby diversity inversely correlates with elevation. As expected, bands *B – D* do not fit this trend due to the probable underrepresentation of snake abundance here due to a reduced amount of surveying.

Detrended Correspondence Analysis

In the initial DCA plot (Fig. 9), the identity of DCA1 and DCA2 is not clear, however there is a considerable cluster of low elevation snake species ordinated around the positive side of the DCA1 axis and the negative DCA2. Whereas the high elevation species have clustered together and ordinated on the negative side of DCA1. Indicating that DCA1 is inversely related to elevation.

In both the Camp DCA (Fig. 10) and the Elevation Band DCA (Fig. 11) sites seem to fit along an elevation gradient, forming a well-ordered series from low to high elevation, ordinating into three distinct groups which represent the Holdridge (1967) forest types found in CNP. Except for Elevation Bands 2, 3 and 4 which have received less survey effort in comparison to the rest of CNP and therefore may be underrepresented in terms of species present.

Santo Tomas represents the most distinct camp in its ordination (Fig. 10). This is likely due to both its elevation, and the high number of unique species recorded there, such as:

Dendrophidion nuchale; *Oxybelis aeneus*; *Oxyrhopus petolarius*. These are all lower elevation species and would tend not to range as high as the other camps, except for Buenos Aires. Buenos Aries also ordinates away from the other camps but is still included in the group around centroid 2 due to its elevation. Due to the distance between where El Cortecito and Guanales have ordinated, despite similar elevations, suggests the communities are significantly different, which is supported by El Cortecito ordinating outside of the one standard deviation ellipse that Guanales has ordinated within. Cantiles and El Danto ordinated within one standard deviation of each other, suggesting their communities are not significantly different, which is consistent with our other results. The high elevation species shown on the ordination all ordinated close to Cantiles camp, suggesting that the higher elevation camp provides the best habitat for those species, including the Vulnerable endemic species *Omoadiphas aurula*.

Much like the camp ordination, the three lowest elevation bands ordinated close together (Fig. 11). However, they are not ordinated around the same centroid. This is because they represent a change in forest type from lowland moist forest <600 masl to pre-montane wet forest <600 masl (Holdridge, 1967). Excluding Band 1, all the bands up to and including Band 7 are ordinated around this intermediate elevation forest type. Bands 8 – 11 are all ordinated close together indicating their similarity. This is also consistent with our other results, such as the Rank Abundance Curves (Fig. 8), which show these elevation bands are dominated by one species which we know to be *Cerrophidion wilsoni*. All the high elevation bands are ordinated in the negative side of DCA1 indicating that DCA1 is elevation that decreases along the X axis.

Species Elevation records

Reptiles in Honduras have received the attention of herpetologists for at least the past 125 Years (McCranie, 2011). The abundance of new elevation records in CNP is a testament to two factors, the first being that despite the effort invested in studying the snakes of Honduras more studies are needed to understand their ecology with particular focus in globally declining habitat types such as cloud forests; and the second is the massive survey effort invested in CNP by the herpetology team on behalf of Operation Wallacea. The frequency of these range extensions, even in relatively widespread and common species, may be due in part to the lack of research currently on going in neotropical cloud forests (Bubb *et al*., 2004). However, this could be the first inclination of climate change effecting the distribution of reptiles in CNP, which has already been documented in CNP's bird community (Neate-Clegg *et al.,* 2019) and is purported to be responsible for new elevation records and elevational shifts in the Bat community (Medina-Van Berkum *et al.,* 2020).

Conclusion

Species elevation records and Species accumulation curves

Despite significant surveying in CNP since at least 2007, numerous elevation records and new park records exist in this data set, that had until now been unreported. The species accumulation curve for each camp within CNP and for CNP itself have not yet reached asymptote, which indicates that there is still diversity to find here. The combination of these results may not be independent, as climate change occurs, lowland species are likely to extend their normal ranges upslope exceeding existing range records as seen in other taxa in CNP. As these lower elevation species creep upslope there would be an expected increase in species richness that will be reflected in the respective curve.

Rank Abundance Analysis

Following the trends seen elsewhere, species richness and evenness both decrease with increasing elevation, which was seen at all levels of analysis when using rank abundance. More surveying is clearly needed to further analyse camps that have received lower survey effort. Using the more ecologically sound method of elevation bands as a basis for analysis paints a clearer picture of the trends in species richness and evenness. Understandably, there is an increase in the diversity around the elevations where the camps are, due to the increase in survey effort, which includes opportunistic surveying which occurs as people simply spend more time in the forest environment. More opportunistic surveying in different areas and elevations of CNP not accessed via the standardised transect network would increase the accuracy of this study.

Detrended Correspondence Analysis

Camps that are closer to each other in elevation have similar snake communities across CNP, indicating elevation and its confounding factors highly influence snake community assemblage, which is supported by analysis of elevation bands, which found three distinct communities representing the three Holdridge (1967) forest zones in CNP.

Functional Diversity Case Study

Along the most severely affected transects, deforestation and the subsequent land use changes seen in CNP are associated with a marked decrease in the richness of functional diversity groups present. As an isolated event, the loss of functional guilds and consequent ecosystem services is reason for concern around El Cortecito, but, with the steady increase in the rate of deforestation in CNP (Barker, R., *pers. Comms.*) the unknown effect of the loss of the snake community could have a wider effect on the food web and ecosystem in general.

Biodiversity survey methods

Implicit in the survey techniques utilised in this chapter are biases that lead to the underrepresentation of some species in the dataset. Small, cryptic, fossorial, or arboreal species are by their nature very difficult to see and record (Nordberg and Schwarzkopf, 2015; Barker and Pinard, 2001), however, despite this, the second most abundant species found in CNP throughout the 13-year sampling period was the cryptic, arboreal pit viper, *Bothriechis marchi*. Little is known about the ecology of this species, however, if they spend only a fraction of their time in a 'detectable' area, i.e., close to a river or below the canopy, It is likely that our numbers are greatly skewed to underrepresenting their abundance; there are numerous fossorial, cryptic or arboreal species in CNP, all of which may have this same bias. The second chapter of this thesis strives to understand the ecology of *Bothriechis marchi*, which may grant better understanding of how our surveys in CNP, using methods that are ubiquitous worldwide, may be missing a significant proportion of the arboreal diversity.

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“Look deep into nature, and then you will understand everything better.” Albert Einstein

Chapter 2 – Spatial Ecology of the cryptic pit vipers *Bothriechis marchi* and *Atropoides mexicanus*

Introduction

Visual encounter surveys (VES), which rely on both availability and detectability for acquiring species records (Doan, 2003), have been shown to be able to detect species at low densities, a proxy for rareness, but underperform when explaining specific ecologies and will underpredict importance of habitat out of an easily detectable range (Boback *et al.,* 2020), whether that is due to height above the ground or microhabitat type; An effect that may be exacerbated when coupled with inexperienced surveyors (Albergoni *et al.,* 2016). If the ecology of a species is only determined from when it is detected during a visual encounter survey, then its assumed abundance and behaviours may not be representative in species that are traditionally difficult to detect (Mackenzie *et al*., 2006). Thus, a different method must be employed to investigate the ecology of these species when they are not in the detectable range of the visual encounter survey.

Due to the necessity of so many species of snake to become cryptic (Allen *et al.,* 2013), in both colour and behaviour to avoid detection (Kravchuk and Watson, 2020; Endler, 1978), they have the potential to become underrepresented in datasets that are collected by VES (Mackenzie *et al*., 2006). This is especially true for cryptic, arboreal species that spend a portion of their time in the canopy and therefore out of a detectable range, which can lead to a lack of information on behaviours of these species (Kalki and Weiss, 2020), even though VES are recommended for surveying arboreal herpetofauna (Doan, 2003). Thus, a different method must be employed to investigate the ecology of these species whose ecology is not ideal for VES. To account for these differences in ecology and detectability Boback *et al.,* 2020 highlight the use of radiotelemetry as a method of acquiring the information that a typical VES misses out, such as habitat preference and presence outside of a detectable range.

Very High Frequency (VHF) radio telemetry has been used since the mid-20th century (McGinnis and Moore, 1969) and has become a widely used method for studying the spatial ecology of snakes and is especially useful to study snakes whose ecology is not fully understood. Snake home ranges (Marshall *et al.,* 2019), behavioural studies (Row and Blouin-Demers, 2006), human-wildlife conflict (Crane *et al.,* 2016; Marshall *et al.,* 2018), and habitat utilisation (Knierim *et al.,* 2019; Marshall *et al.,* 2020) have all been carried out using radiotelemetry as the main method of data collection. Being able to follow one specific individual for a long period of time also allows for detailed natural history data to be collected that is not available during a standard VES such as behaviour, diet, or habitat preferences (Reinert *et al.,* 1984).

Bothriechis marchi closely resembles what Harrington *et al.*, (2018) states to be a typical arboreal snake, both, being a member of the Viperidae and nocturnal in habits. *Bothriechis marchi* is highly endemic to an understudied region of north-western Honduras, being found only in three highland areas, Cordillera de Nombre de Dios, Cordillera de Merendon, and Sierra Sulaco. In north-western Honduras they are known from low, moderate, and intermediate elevations between 500 masl and 1840 masl (McCranie, 2011), where they occupy a variety of micro-habitats, including streamside vegetation (McCranie and Castaneda, 2005), vegetation above streams and rivers, and amongst boulders above streams (Townsend and Wilson, 2008).

They have often been detected in locations highly associated with the presence of amphibians, likely a favoured prey item (McCranie, 2011), although they are also known to feed on small mammals (Solis and Brown, 2016). Despite populations of *B. marchi* mostly occurring within protected areas, they are thought to be declining across their range (Wilson and Townsend, 2014); including in Pico Bonito National Park, one of their larger populations, where they are detected rarely (McCranie and Castaneda, 2005). In CNP they are also noted to be uncommon (Townsend *et al*., 2006). Due to this, and their cryptic colouration, detection is difficult and therefore, there may be an underrepresentation of occurrence. Despite receiving scientific interest in the fields of phylogenetics (Taggart *et al*., 2001) and toxicology (Pla *et al*., 2017), the ecology of *B. marchi* remains largely unknown; where only natural history notes detail anecdotal accounts such as dietary information. Thus, what is known and reported pertains to snakes within a detectable location i.e., close to a river or below the canopy (McCranie, 2011; Köhler, 2003), which may only represent a fraction of the behaviour and habitat use of this species. *Bothriechis marchi* is currently listed as Endangered by the IUCN, due to habitat degradation, exploitation by the pet trade, and a reduction in prey availability (Wilson and Townsend, 2014). Therefore, further understanding its ecology and detailing the extent to which its ecology may affect detectability is imperative to its conservation.

Considering the potential short comings of VES's with regards to underrepresenting cryptic, arboreal snake species, the aim of the second chapter of this thesis was to assess the likelihood of pit vipers in CNP being underrepresented. This was done by using radio telemetry to conduct the first formal investigation into the ecology of *Bothriechis marchi* and *Atropoides mexicanus* to elucidate both space-use and habitat preferences, simultaneously trialing a novel method of externally attaching radio-transmitters to reduce behavioural impacts on arboreal snakes.

Methods

Study Site

This study was carried out within the eastern portion of Cusuco National Park, Honduras. Utilising the predefined network of both terrestrial and riverine transects in the camps, Base camp, Cantiles and Guanales, surveys were conducted to search for the target species. The study period ran throughout the end of the wet season and beginning of the dry season, early June to early August, in 2018 and 2019. Visual encounter surveying methods described in the first chapter were utilised to search diurnally, through pine-oak, pre-montane wet forest, and dwarf forest, and nocturnally, along streams and rivers, known to be habitat used by *B. marchi*. Upon encounter, occasion data and survey effort were recorded, before snakes were safely captured using appropriate snake handling tools and transported in a soft, cloth snake bag to camp. After an observation period of up to 6 hours, the snake was restrained, by placing the anterior two thirds of the body into a Perspex tube (Midwest tongs ®), morphometric data was recorded, and the VHF transmitter attached.

Radiotelemetry

To all species, VHF transmitters (Biotrack pip33, Ag98, 1.8 g) were secured dorso-laterally approximately 5% of the body length anterior to the cloaca, modifying methods utilised in Riley *et al.,* (2017). In accordance with the existing literature, transmitter weight was always <5% of the body weight of the individual. The VHF transmitter was situated with the external antenna arranged caudally. Prior to adhesion, the area of skin where the transmitter would be attached was wiped with a soft cloth, water and 70% ethanol to ensure no foreign bodies would be present under the adhesive. Attachment was initiated with cyanoacrylate glue (Loctite® Super Flex) and held against the scales until dry. This was then wrapped with multiple 20mm wide strip of black or grey duct tape (Duck Tape®) to form a roughly trapezoid shaped protuberance from the side of the snake (Fig. 14). This shape was formed to create a gradual change in angle from the snake's body, to avoid foliage becoming snagged (Madrid-Sotelo and Garcia-Augayo, 2008). Following attachment of the transmitter, each snake was observed for approximately 24 hours to ensure successful adherence of the glue and subsequent tape. Once adherence was deemed successful, snakes were released at the capture location and observed for up to an hour to ensure their movement was not restricted. On one occasion the method of attachment differed to an individual of the species *Cerrophidion wilsoni*, which after capture was found to be likely gravid. So as not to circumferentially constrict this individual, this transmitter was attached solely with glue. All animals were handled, and transmitters attached in accordance with the animal ethics board (Plymouth University) under permit from the Instituto de Conservación de Forestal (ICF) (Permit Numbers 2018: DE-MP-81-2017; 2019: DE-MP-005-2020).

Figure 14. The trapezoid shaped protuberance produced by tape wrapping during VHF transmitter attachment on *Bothriechis marchi.*

After release, a tracking regime was implemented to record locations and habitat variables for each tracked snake. A 24-hour buffer period was given between the initial release and the start of data collection to reduce the bias of human disturbance from capture and transmitter attachment. VHF signals was detected using a Biotrack Sika Gold radio receiver (Biotrack, Lotek Wireless Inc, Wareham, UK) and a Yagi Flex Antenna (Biotrack, UK). UTM locations were taken with a Garmin 62s Handheld GPS (Garmin Europe Ltd, Hampshire, UK). Snakes were tracked up to three times daily, once in the morning before dawn, at mid-day and then again at after midnight. Tracking ceased only if adverse weather stopped surveying, or when the author moved camps to track other snakes. All data was recorded using a combination of paper data sheets and a Samsung Galaxy S5 (Samsung ®) in combination with a custom Open Data Kit form designed by the author and programmed by BurdGIS (BurdGIS, London UK).

Where possible, transmitters were removed from snakes at the end of the study period. Removal was completed using unbranded sterile cotton swabs lightly soaked in acetone (nail polish remover; sourced locally). This was then gently applied onto a peeled corner of the tape to remove the adhesive. This was done until the tape was completely removed and repeated on the dried glue. Care was taken not to pull at the scales of the snake with the adhered transmitter until the glue had been fully dissolved.

Habitat variables

Habitat variables were recorded based on the location where each radio-telemetered snake was found. Forest type, perch height (meters), distance to the nearest river and canopy cover (%) were all recorded for every tracking occasion. Whereas perch temperature, and microhabitat openness (%) could only be recorded when a visual was attained. Furthermore, perch temperature could only be recorded when a snake was visible and within a prescribed range that a digital infrared thermometer (Unbranded Temperature gun) could accurately detect temperature. Forest type was recorded based on the predominant tree type in the area surrounding the snake, such as broadleaf or pine forest. Forest was recorded as riparian forest if it was directly adjacent to and therefore significantly associated with a river. Perch height was recorded via two methods, a clinometer was used if the snake was visible and signal triangulation was used to estimate height if the snake was not visible. Distance to the nearest river was a categorical variable divided into four groups, of 0-5 m, 6-10 m, 11-15 m, and >15 m which was measured with a 25 m tape measure. Percentage canopy cover was estimated using a homemade canopy scope (Brown *et al.,* 2000) on which a grid of 25 evenly spaced points had been drawn. The canopy scope is held up to the eye at a set distance in front of the most open part of the canopy, above the snake's location, then the percentage of points with open sky visible behind was subtracted from 100 to give canopy cover. Microhabitat openness or microhabitat availability was the percentage estimation of how much of a 1 m^3 space surrounding the snake contained a location suitable for perching by a snake, i.e., a branch, tree trunk, fern etc.

Data was then prepared using Microsoft Excel Spreadsheet (Microsoft, 2018) and analysed in the R environment (R Core Team 2020) using packages "dplyr" (Wickham, 2021), "ggpubr" (Kassambara, 2020) and "ggplot2" (Wickham, 2016). All variables were assessed using Shapiro-wilks test for normality and either parametric or non-parametric tests depending on if the data fit a normal distribution. One way ANOVA was used to determine if the means of normally distributed continuous variables significantly differed when compared under four levels, as a species, between individuals, between life stages and between sexes. Tukey Honest Significant differences test was used to create confidence limits when making pair-wise comparison of individual snakes, sex, and life stages to a continuous variable. Boxplots were created using the functions "ggboxplot" from "ggpubr" package and boxplot from R core, to visualise data including means, upper and lower quartiles, and outliers. Levels were assigned to each categorical variable and means were compared using Chi-Squared tests to investigate significant differences between variables snakes. Simple bar plots were used to visualise this data using the function “barplot”.

Detectability

Detectability was tested by comparing physical habitat variables with visual attainment. Chi-squared was used to test the associations between categorical variables and visual attainment. One way ANOVA was used to test significance between perch height and visual attainment. Microhabitat could not be tested against visual attainment as this variable was only recorded when visual was confirmed.

Home-range Estimations

Home range estimations were created using the “adehabitatHR” (Calenge, 2006) and “sp” (Pebesma and Bivand, 2005) packages in R and ArcGIS Desktop Version 10.7 (ESRI, 2011). 95% Minimum Convex Polygons (MCP) were created for each of the five telemetered *Bothriechis marchi*. Home range estimations were visualised using “mcp.area” at different levels, ranging from 50% to 100% MCP. Kernel Utilisation densities were also created for each of the radio tracked snakes to provide models predicting utilised areas of each snake at 50%-95% models of space utilisation.

Results

Attachment Methodology

In total Eight snakes were tracked during the two summer field seasons, for a collective total of 108.5 days (Table 5). Five *Bothriechis marchi* were tracked within the Core Zone of CNP, two females and three males. SVL's of the male snakes, whose ID codes were BoMa01, BoMa03 and BoMa05, were 632 mm, 545 mm, 795 mm respectively; with masses of 90 g, 50 g and 175 g. Female snakes, codes BoMa02 and BoMa04, had SVL's of 570mm and 402mm respectively and 78 g, 28 g mass. Of all the *Bothriechis* that were tracked BoMa01 had the most tracking occasions (73), with 13 daytime, 33 night-time, 24 dawn and 3 dusk pinpoints. BoMa04 had the least number of pinpoints (6), which were comprised of 1 day, 3 night and 2 dawn occasions. BoMa04 was tracked for the least amount of time, due to time and equipment constraints of the expedition. In 2018, two *Cerrophidion wilsoni* had transmitters attached to be tracked. The first CeWi01 was a female, who upon manual palpation appeared to be gravid, so a different attachment method was used to attach the transmitter. This was found the same day close to the release site, with a small section of sloughed skin attached. CeWi02 was a larger male, who was found close to Cantiles camp. This snake stayed close to camp post release a safe distance away from "the camp shower" waterfall where it was found, for five days until the signal was lost. In 2019, one individual *Atropoides mexicanus* was radio tracked for 11 days. This was the first of its species to be studied using radiotelemetry. This individual made one significant move throughout the 11-day tracking period, to the inside of a hollowed log, where it proceeded to begin ecdysis, this was noted through the change in behaviour and change in colour of the spectacle covering the eye. Fligner-Killeen test of homogeneity was used to show temperatures recorded within the shedding site (mean = 19.02 °C), the surface of the log (mean = 19.09 °C), the ground outside the log (mean = 18.57 °C) and the ambient temperature (mean = 19.20 °C) were not significantly different ($X^2 = 12.659$, df = 12, p-value = 0.3943) (Fig. 15).

Table 5. Radio telemetered snakes tracked in 2018 and 2019 and details of which camp, attachment method, sex and how long they were tracked for.

Species ID	Year	Species	Location	Attachment Method	Sex	Attachment time
BoMa01	2018	*Bothriechis marchi*	Base Camp	Glue + Tape	M	44 days
BoMa02	2018	*Bothriechis marchi*	Cantiles	Glue + Tape	F	15 days
CeWi01	2018	*Cerrophidion wilsoni*	Cantiles	Glue	F	0.5 days
BoMa03	2018	*Bothriechis marchi*	Cantiles	Glue + Tape	M	10 days
CeWi02	2018	*Cerrophidion wilsoni*	Cantiles	Glue + Tape	M	3 days
BoMa04	2019	*Bothriechis marchi*	Cantiles	Glue and Tape	F	5 days
BoMa05	2019	*Bothriechis marchi*	Guanales	Glue and Tape	M	20 days
AtMe01	2019	*Atropoides mexicanus*	Guanales	Glue and Tape	M	11 days

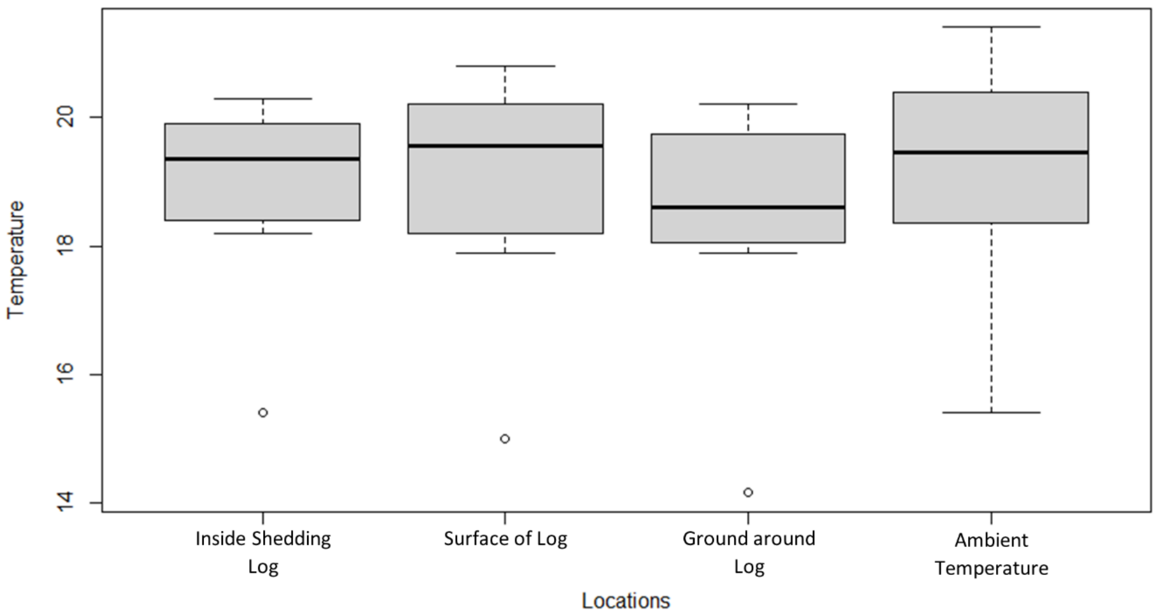

Figure 15. Temperature comparison of significant sites in and around the shedding site of an *Atropoides mexicanus* in Cusuco National Park. Central line denotes mean temperature surrounded by upper and lower quartiles. Error bars are 95%. Hollow circles are outliers.

Attachment of Transmitters

Transmitters were attached using one of two methods, a glue and tape combination or just glue. The just glue method was only considered in the special case of a seemingly gravid female. The author did not want to circumferentially restrict the abdomen of the snake. The second method, glue and tape, was more successful with attachment times of up to 44 days. Only one transmitter was able to be retrieved from the snakes whose transmitters were attached with glue and tape, BoMa03; transmitters were unable to be removed on all other snakes due to being in inaccessible locations such as the canopy. Removal was carried out using a cotton bud soaked in acetone to dissolve the tape adhesive and the glue. No bleeding, lesions or injuries were observed. Prior to the removal of the transmitter, no signs of reduction in adhesion or deterioration of the package were noted on BoMa03. Similarly, upon arboreal inspection of BoMa01 after approximately 30 days no deterioration was noted.

Habitat Preferences

Habitat variables were recorded for each individual *B. marchi.* The forest type most used by radio-tracked *B. marchi* was Moist Broadleaf forest (Fig. 16) ($X^2 = 213.41$, df = 2, p = <0.001). The other forest types used by telemetered individuals were riparian forests and moist-mixed forests. BoMa04 was the only snake to exclusively be found in riparian forest during its tracking period (Fig. 17). All others predominated in moist broadleaf forest. BoMa01 and BoMa02 also spent time in moist mixed forest. Of the telemetered individuals there was a significant association between the life stage of an individual and which forest type they were found in (X^2= 105.68, df = 2, p = <0.001).

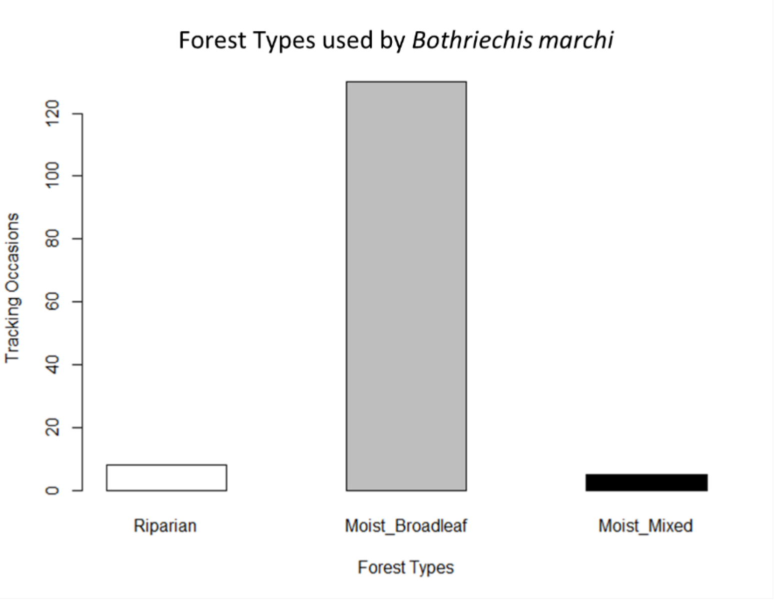

Figure 16. Forest type utilisation by radio telemetered *Bothriechis marchi* in Cusuco National Park.

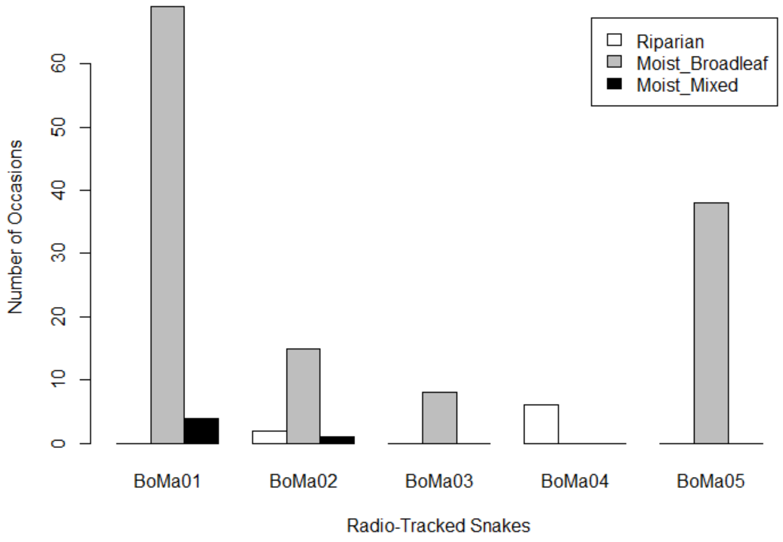

Figure 17. Forest type utilisation by each individual radio telemetered *Bothriechis marchi* in Cusuco National Park

Perch height was normally distributed across all tracking occasions of *B. marchi* (Shapiro-Wilks W = 0.867, p = <0.001). Mean perch height for the telemetered *B. marchi* was 17.04 m ±6.85 m (1sd). However, mean perch height differed between individuals, Tukey's Honestly significant difference test was used to analyse ANOVA tests on perch height and showed BoMa01 was found significantly higher than all other telemetered *Bothriechis* (p = <0.001). BoMa02 and BoMa03 had the greatest range overlap (Fig. 18) and means did not differ significantly (p = 0.99). All other comparisons of means were significantly different with p values ranging from p = 0.03, for BoMa05 and BoMa03, to p = <0.001, for BoMa05 and BoMa04. The mean perch height for BoMa05 was significantly different to all other telemetered snakes (p = ≤0.03). There is a significant association between the life stage of radio telemetered *B. marchi* and the perch height they used during the tracking period (ANOVA, sum of sq. = 1364, f = 36.28, df = 1, p = <0.001) with adults being found at a higher mean perch height than where the tracked juvenile was found (Fig. 19). Overlap in observed perch heights was discerned to be an outlier when conducting ANOVA. Sex was also determined to be significant when considering perch height (ANOVA, sum of sq. = 2169, f = 68.07, p = <0.001) with males utilising perches higher than females (Fig. 20).

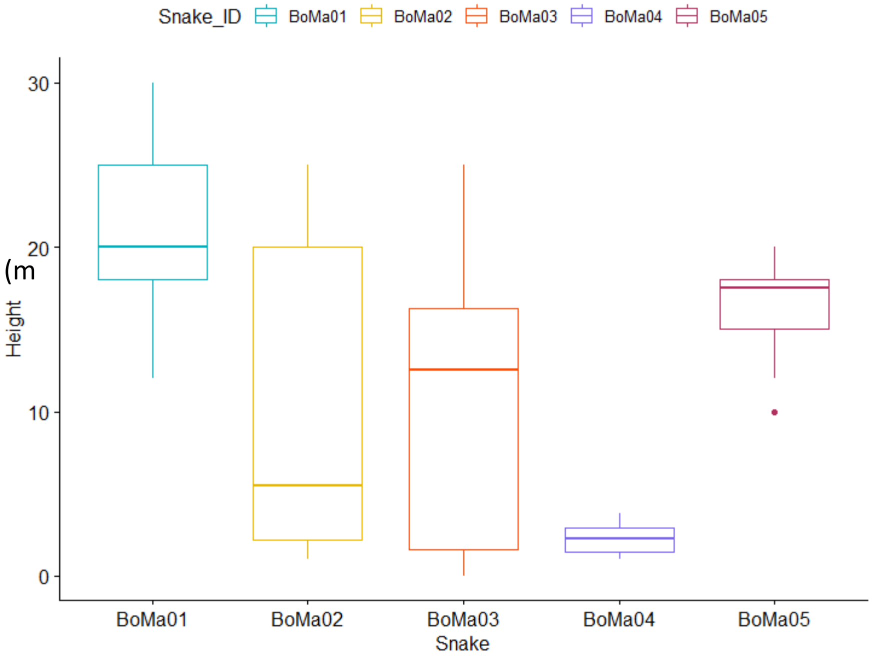

Figure 18. Perch Height utilisation by each of the radio telemetered *Bothriechis marchi* in Cusuco National Park. Central line denotes mean temperature surrounded by upper and lower quartiles. Error bars are 95%. Circles are outliers.

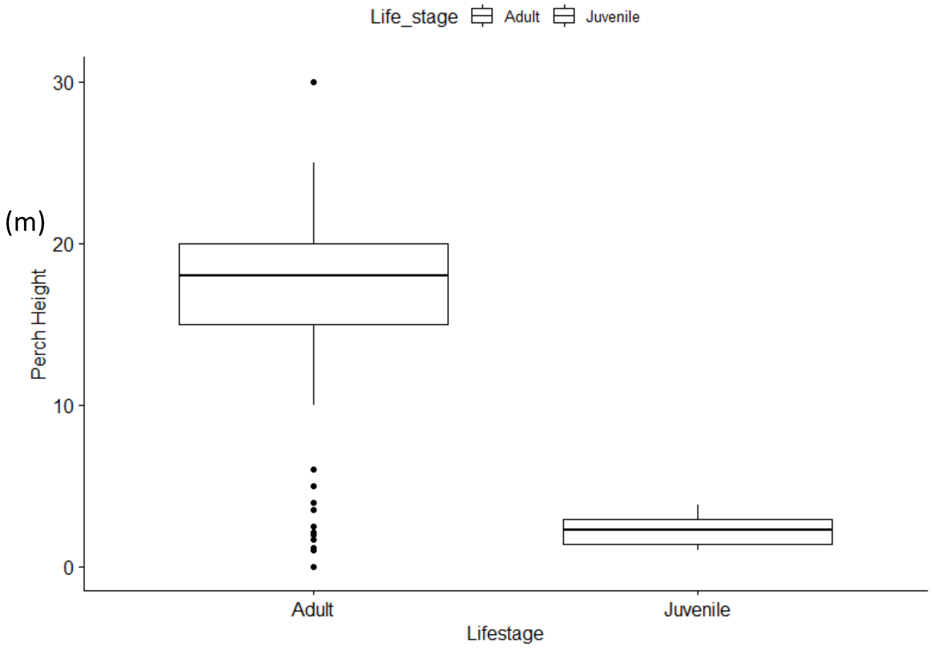

Figure 19. Perch Height utilisation by different life stages of radio telemetered *Bothriechis marchi* in Cusuco National Park. Central line denotes mean temperature surrounded by upper and lower quartiles. Error bars are 95%. Circles are outliers.

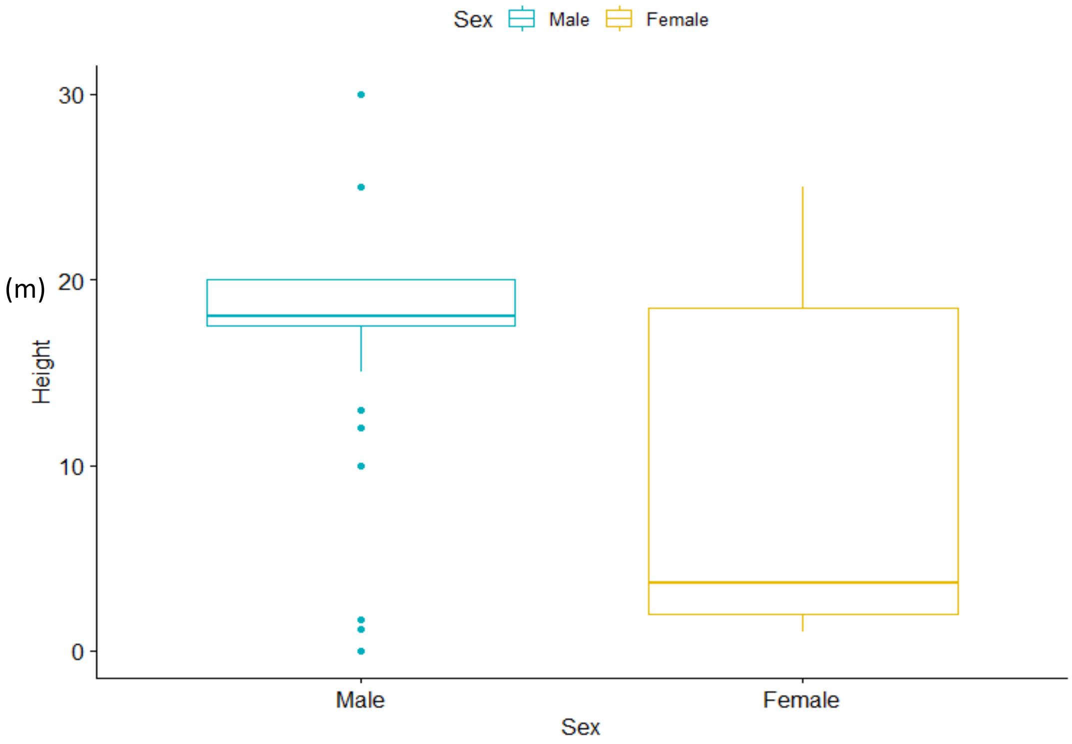

Figure 20. Perch Height utilisation by different sexes of radio telemetered *Bothriechis marchi* in Cusuco National Park. Central line denotes mean temperature surrounded by upper and lower quartiles. Error bars are 95%. Circles are outliers.

Temperature was not normally distributed (Shapiro-wilk's W= 0.96, p = 0.663). Mean temperature of perches utilised by *B. marchi* was 14.45 °C ± 1.9 ℃. Temperature could only be recorded if visual was attained on a snake, and the location the snake was utilising was within a measurable distance. Therefore, no perch temperatures were recorded for BoMa01. Perch temperature was not significantly associated with any of the individual snakes; however, temperatures were clustered close to the overall mean (Fig. 21). One way ANOVA was used to analyse variance around the means of perch temperature recorded for sex of telemetered snakes, which was not found to be significantly different (df =1, Sum of sq. = 8.12, Mean sq. =8.124, F = 2.42, p = 0.14). There was no significant difference between the perch temperature of adults when compared to juveniles (X^2= 19.44, df=12, p = 0.423), which showed high overlap in the upper quartile and range (Fig. 22).

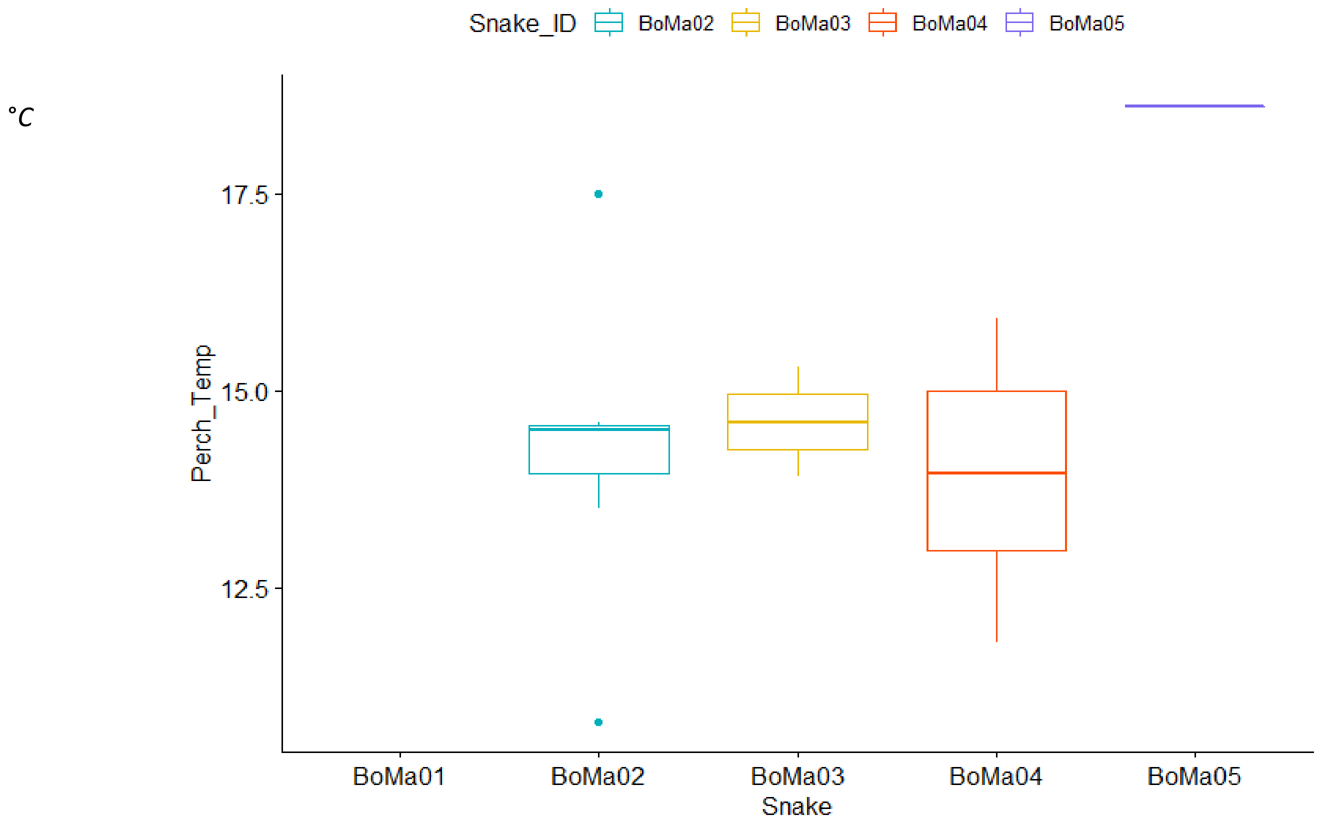

Figure 21. Perch Temperature utilisation by each of the radio telemetered *Bothriechis marchi* in Cusuco National Park. Central line denotes mean temperature surrounded by upper and lower quartiles. Error bars are 95%. Circles are outliers.

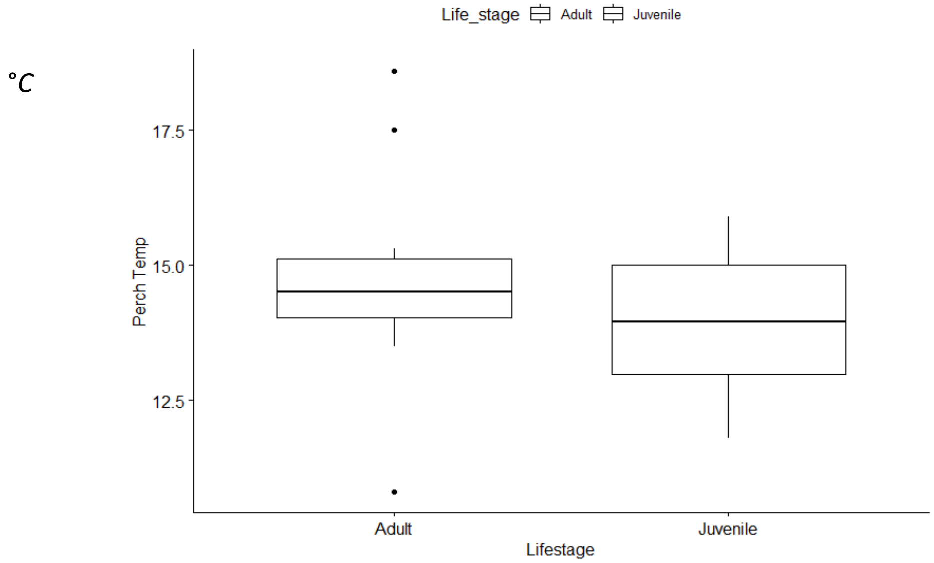

Figure 22. Perch Height utilisation by different life stages of radio telemetered *Bothriechis marchi* in Cusuco National Park. Central line denotes mean temperature surrounded by upper and lower quartiles. Error bars are 95%. Circles are outliers.

Canopy cover, which was normally distributed (Shapiro-wilks W = 0.825, p = <0.001) was recorded for 110 of the tracking occasions. Mean canopy cover of all the tracking occasions was 83.17% ± 19.66% (1SD) (Fig. 23). Canopy cover was highly associated with *Bothriechis marchi* (t= 44.34, df = 109, p= <0.001). 100% canopy cover was recorded for 36% of all the tracking occasions. 75.5% of all locations utilised by telemetered *B. marchi* had a canopy cover of over 75% (Fig. 23). One way ANOVA was used to determine a significant association between which snakes were tracked and canopy cover (df = 4, sum of sq. = 6877, F = 5.12, p = <0.001). However, there was no significant different between BoMa01, BoMa02, BoMa03 and BoMa04 (p = >0.94) (Fig. 24). BoMa05 differed significantly to BoMa01 (p = <0.001) and BoMa02 (p = 0.002), but no significant difference was found between BoMa05, BoMa03 and BoMa04 (p =

0.22). One way ANOVA was used to show canopy cover did not differ significantly between sexes (df=1, sum of sq. = 856, F = 2.25, p = 0.14) or between life stages (df = 1, sum of sq. = 83, F= 0.214, p = 0.645).

Available microhabitat measured the percentage of 1 m^3 that was available to be used by a snake to perch, for example leaves, branches, vines, and tree trunks. This was only recorded if a snake was observed on a tracking occasion. Available microhabitat was not normally distributed (W = 0.97, p = 0.85). Tukey's Honestly significant difference test shows the percentage of available microhabitat did not differ significantly between any of the tracked individuals (p = >0.8). Neither did it significantly differ between sexes (ANOVA: df = 1, sum of sq. = 148, F = 0.366, p = 0.555) or life stage (X^2 = 9.792, df =9, p =0.368).

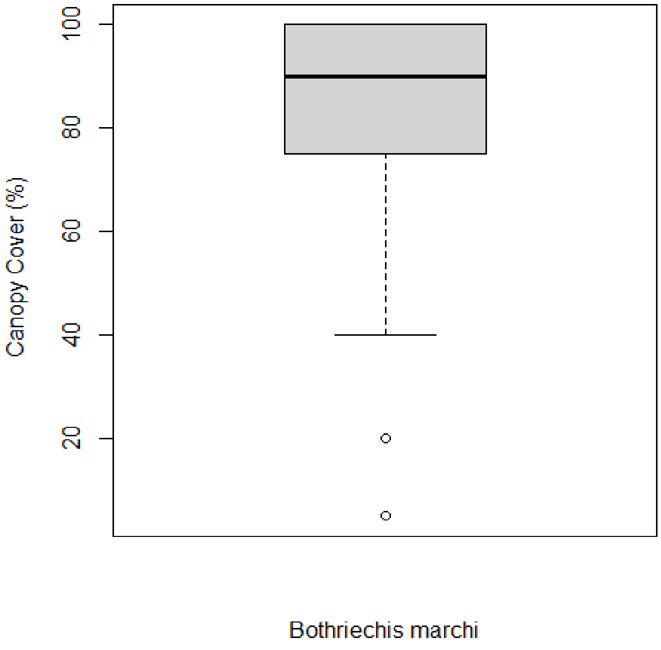

Figure 23. Boxplot of the canopy cover of sites utilised by radio telemetered *Bothriechis marchi* in Cusuco National Park. Central line denotes mean temperature surrounded by upper and lower quartiles. Error bars are 95%. Hollow circles are outliers.

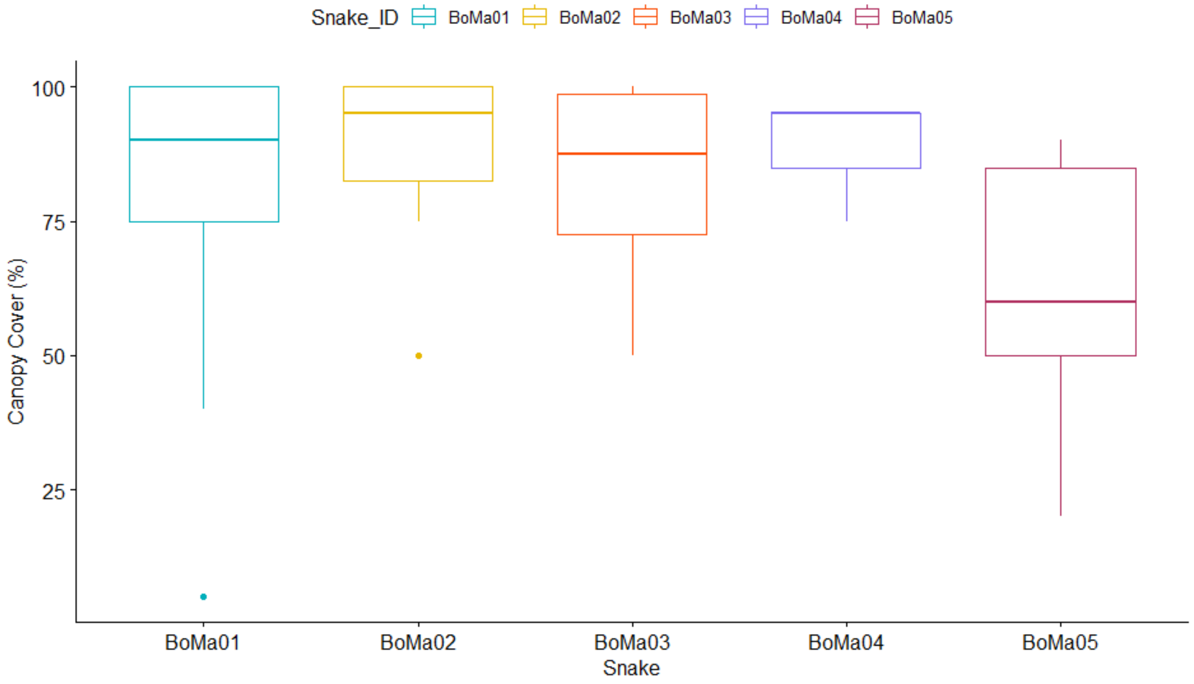

Figure 24. Canopy cover of sites utilised by each individual radio telemetered *Bothriechis marchi* in Cusuco National Park. Central line denotes mean temperature surrounded by upper and lower quartiles. Error bars are 95%. Circles are outliers.

Utilised Home-range Calculations

95% Minimum convex polygons (MCP) were produced for each of the five tracked *Bothriechis marchi*, which were then mapped onto CNP to show snake locations (Fig. 25). BoMa05 had the largest 95% MCP (Table 6.), and was found to be moving on 11 of the tracking occasions, the highest number of any of the tracked snakes. BoMa04 had the smallest 95% MCP due to being tracked for the least amount of time (Table 5.), however, was found to have moved on all tracking occasions. Although, these movements were around one tree fern, so represented little change in location. BoMa02 and BoMa03 were initially located in the same tree, several days apart, and had overlapping home ranges. BoMa03 was tracked for ten days and remained stationary for six, BoMa02 was tracked for 15 days and remained stationary for ten. BoMa01 was tracked for the longest time relative to the other *B.marchi*, however, only moved on nine occasions. Eight of which were during the night. Sex was not significantly associated with MCP size at 50% (t = -1.176 df = 2.87, p= 0.33) or 95% (t = -0.988, df = 2.011, p = 0.43).

MCP area increases with a higher percentage of points added into each polygon (Fig. 26). At 50% MCP BoMa01 and BoMa02 have simlilar utilised home ranges, 0.0363 km^2 and 0.03575 km^2 respectively. In the case of BoMa01 and BoMa05, the most significant increase in MCP size is from 90-100% of points included in the MCP. At 70% of locations added, BoMa03 plateaued, only adding 80m^2 until after 90% of the points had been added.

Kernel Utilisation (KU) Distribution models were also produced for 95% and 50% home ranges for each of the tracked *B.marchi*. The average 95% KU density model estimated the space utilised by the tracked snakes to be 0.06 Km^2 ± 0.1 Km^2 (1SD). The average 50% KU density model had a utilised space estimation of 0.009 Km^2 ± 0.02 Km^2 (1SD).

Table 6. 95% and 50% in km^2 for each of the radio telemetered Bothriechis marchi in Cusuco National Park

Species ID	Nearest Camp	Elevation (masl)	95% MCP area (km^2)	50% MCP area (km^2)
BoMa01	Base Camp	1613	0.08	0.036
BoMa02	Cantiles	1840	0.10	0.036
BoMa03	Cantiles	1838	0.03	0.003
BoMa04	Cantiles	1845	0.02	0.000
BoMa05	Guanales	1331	2.44	0.129

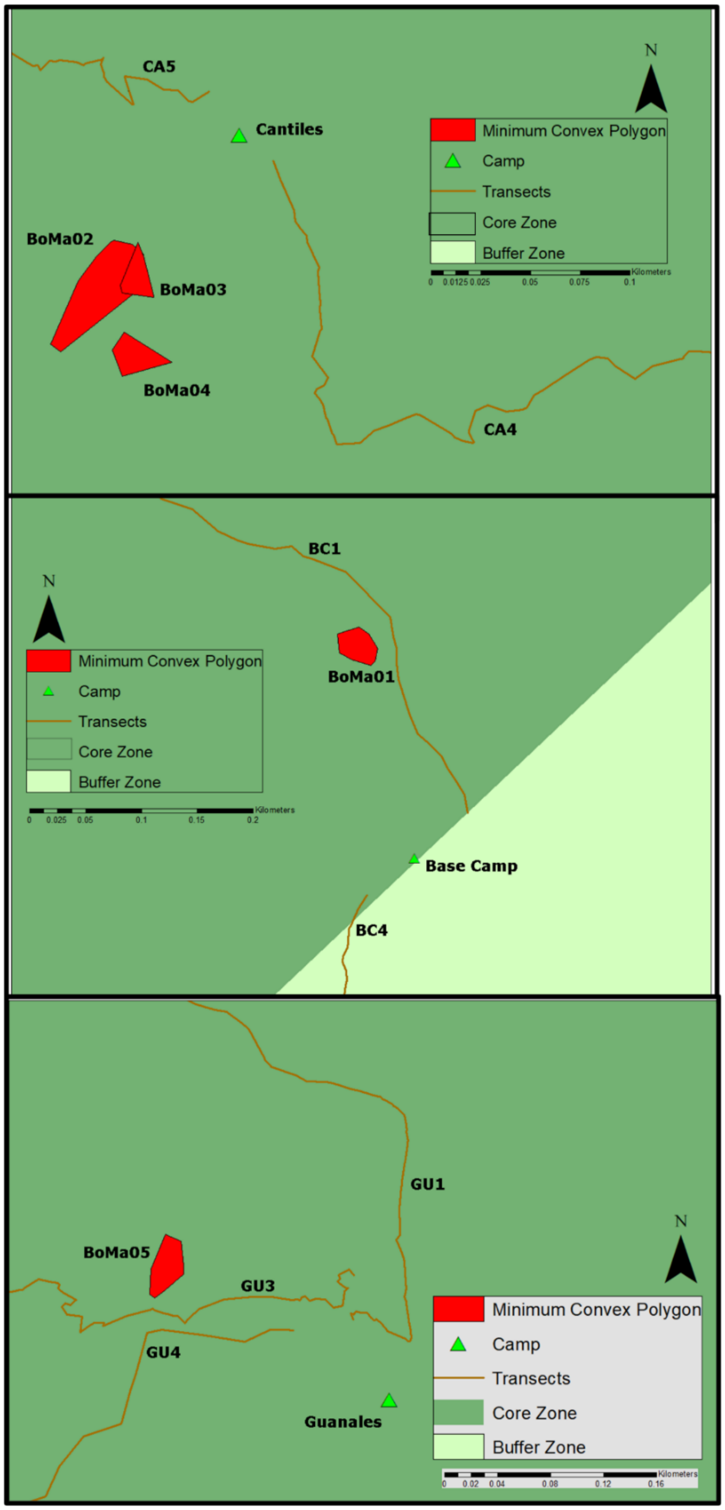

Figure 25. Map of 95% Minimum Convex Polygon for each of the radio telemetered *Bothriechis marchi* in Cususo National Park. Brown lines are stanard survey transects.

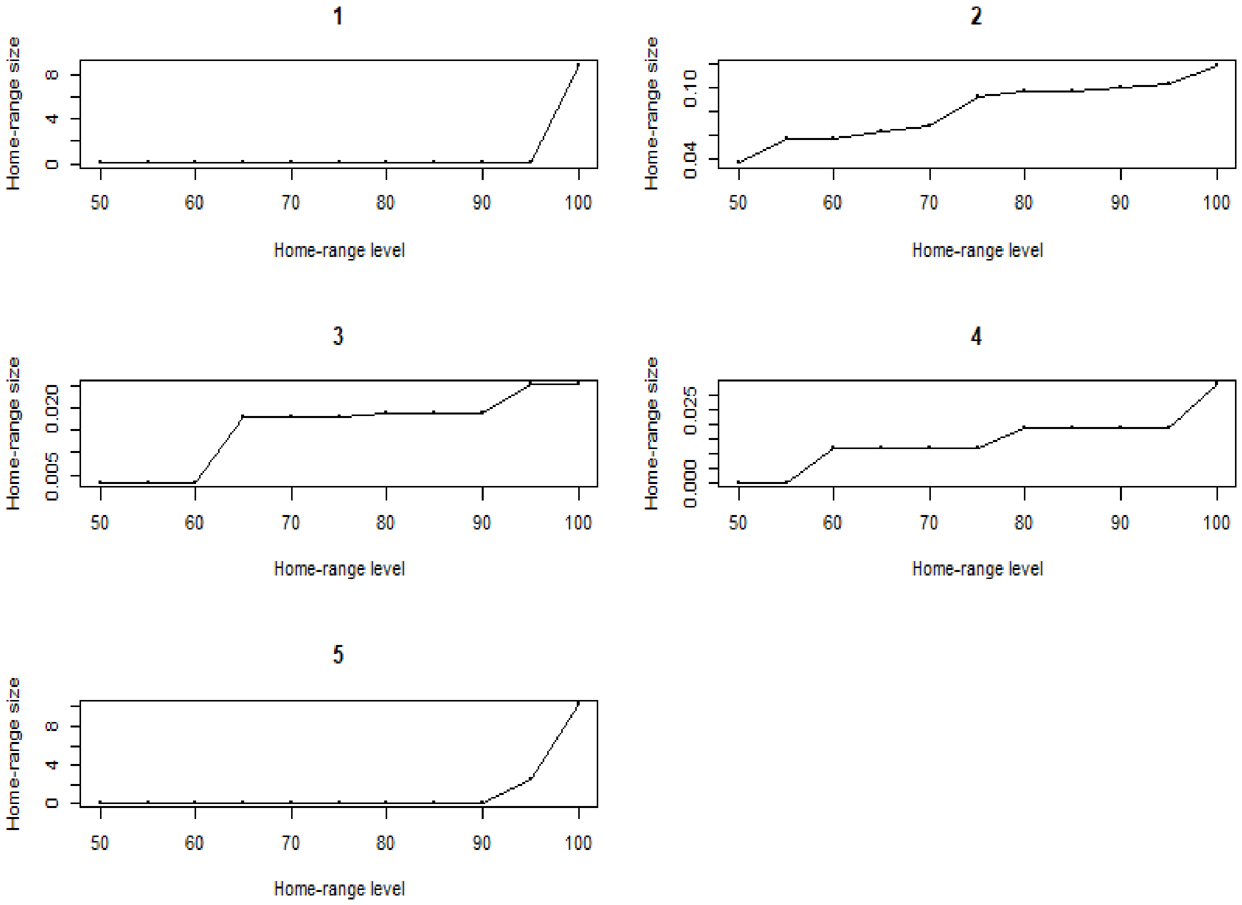

Figure 26. Minimum Convex Polygon size recruitment curves for each of the radio telemetered *Bothriechis marchi* in Cusuco National Park. Number on the grah relates to the Snake ID, i.e. 1 = BoMa01, 2 = BoMa02 etc.

Detectability

Visuals being attained of telemetered snakes was not significantly associated with the time of day ($X^2 = 2.6892$, df = 3, p-value = 0.4421). Proportions of tracks where visual was attained was highest, however, at night (n= 12), then day and dawn (n=3, n=3) and lastly dusk (n=1). Visuals were attained on snakes more frequently if a snake was closer to the nearest stream ($X^2 = 8.7756$, df = 3, p-value = <0.05) (Fig. 27). The highest number of visual encounters was of snakes that were between 6-10m away from the nearest river. Canopy cover showed no statistical significance when compared with attaining visuals of snakes ($X^2 = 16.451$, df = 13, p-value = 0.226). There was a significant difference between the heights that a snake was perched at and whether a visual was attained (df = 1, Sum of sq. = 3887, F = 197.4, p = <0.001). The mean height that a visual was attained was 3.72m (Fig. 28). The maximum height at which visual was attained was 18 meters, however, this was deemed an outlier in in the boxplot. The 1st to 3rd quartile was between 1.25m and 3.25m.

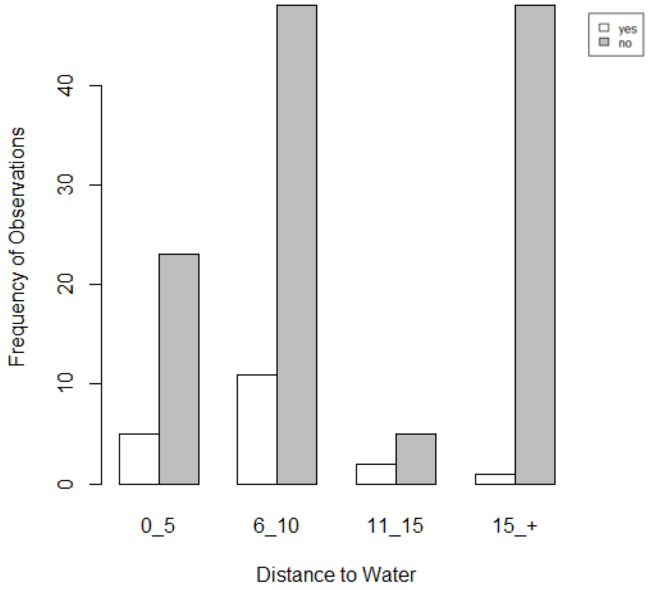

Figure 27. Visual attainment frequency of radio telemetered *Bothreichis marchi* at 4 ranges of distance to water in Cusuco National Park

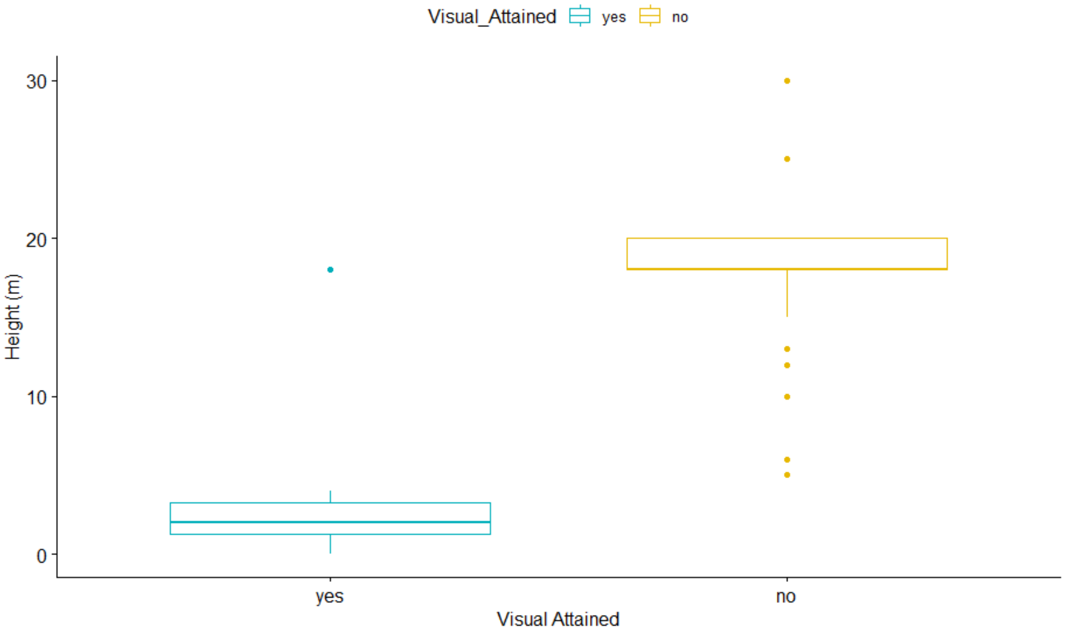

Figure 28. Mean height of visual attainment of radio telemetered *Bothriechis marchi* in Cusuco National Park. Central line denotes mean temperature surrounded by upper and lower quartiles. Error bars are 95%. Circles are outliers.

Discussion

The main aim of this study was to investigate, via radiotelemetry, the spatial ecology of an understudied and largely unknown species, *Bothriechis marchi*. Whilst there have been studies regarding the phylogeny and venom of *B. marchi* (Taggart *et al.,* 2001; Townsend *et al.,* 2013)*,* this chapter represents the first study into the ecology of this species. Likewise, the individual *Atropoides mexicanus* (Fig. 29) that was involved in 2019 represented the first of its species to be radio-tracked, as did the two individuals of the species *Cerrophidion wilsoni*.

Figure 29. AtMe01, radio telemetered *Atropoides mexicanus*. Showing trapezoid protuberance of the radio transmitter upon release.

Attachment of Transmitters

Variants of temporary transmitter attachments exist throughout the literature, such as gluing a transmitter onto the skin (Cobb *et al.,* 2005), using just tape to secure a transmitter onto the skin (Wylie *et al.,* 2011), and various combinations of the two including the novel method described in Madrid-Sotelo and Garcia-Augayo (2008), who used tape on the skin of *Oxybelis aeneus*, then glued the transmitter onto the tape, with a subsequent layer of tape on top. Riley *et al.,* 2017 reviewed the fundamentals of these methods and due to the trauma associated with gluing and taping to the skin and scales opted for the more invasive method of a sub-dermal suture. This method was not opted for in this instance due to the lack of a properly trained vet, no access to anaesthetics and a high likelihood of infection due to the high heat and humidity associated with a tropical rainforest. Similar to this study, we located the transmitter upstream of the cloaca, in this instance it was so as not to interfere with tail-prehensility common in *Bothriechis* species (McCranie, 2011; Köhler, 2003) which was not hindered by application of the transmitter (Fig. 32). Cyanoacrylate glue was used (Loctite Flexible Super Glue Flex ®, Henkel UK) to initially attach the transmitter to the scales. Grey or black duct tape was used to seal over the transmitter. A preferable colour of tape would match the colour of the snake (Tozetti and Martins, 2007). Unlike Tozetti and Martins (2007) or Wylie *et al.,* (2011) multiple strips of tape were used to ensure that the transmitter was covered, and that there was no abrupt angle changes along the snake's body, which may lead to twigs and foliage becoming snagged, as noted in in Madrid-Sotelo and Garcia-Augayo (2008).

One individual, BoMa03, was observe temporarily snagging its package, shortly after release. After pulling the transmitter package into the crook of two palm leaves (Fig. 30) feeling resistance and reversing, the snake lifted the package over the narrow gap and proceeded in the same direction (Fig. 31), with a hindrance of less than 30 seconds, similar to arboreal snakes tracked in Mexico (Madrid-Sotelo and Garcia-Augayo, 2008). No arboreal viper has been tracked using this method of attachment, and therefore it is proposed as a preferable method of non-invasive transmitter attachment for arboreal vipers, for whom short-term telemetry studies are to be carried out. Especially when considering how little impact transmitter attachment had on tail prehensility and arboreality (Fig. 32).

Transmitter removal was completed as in Madrid-Sotelo and Garcia-Augayo (2018), using acetone-soaked cotton buds to dissolve adhesives on both the tape and transmitter. Prior to dissolving this adhesive, it would be clear that pulling at the tape would needlessly lift the scales. Hence why the method of acetone was used in this instance and is recommended. Due to the amount of attachment issues experienced in one radiotelemetry study (Gent and Spellerberg, 1993), external attachment has been suggested to provide little in the way of reliability, with a review of the literature suggesting only to use external attachment if the risk of losing one single specimen is high, for example with a rare species (Ujvari and Korsos, 2000). However, the attachment reliability seen in this study is contrary to this.

One snake caused issue with attachment of transmitter, whilst in the process of ecdysis. CeWi01 almost immediately shed off the transmitter after being released, leaving a semi-opaque patch of sloughed skin still attached to the glue. If a snake is in the process of ecdysis it may be worth considering a method of transmitter attachment that allows for this, without the subsequent loss of the transmitter, for example a sub-dermal suture (Riley *et al.,* 2017). A technical issue the author encountered when tracking numerous snakes in a small area was with transmitters that were emitting similar frequencies. This caused some difficulty with locating individuals, sounding like a bouncing signal.

Figure 30. BoMa03 temporarily hindered by the palm leaves, as transmitter package caught.

Figure 31. BoMa03 moving freely, post movement reversal and lifting of the transmitter package.

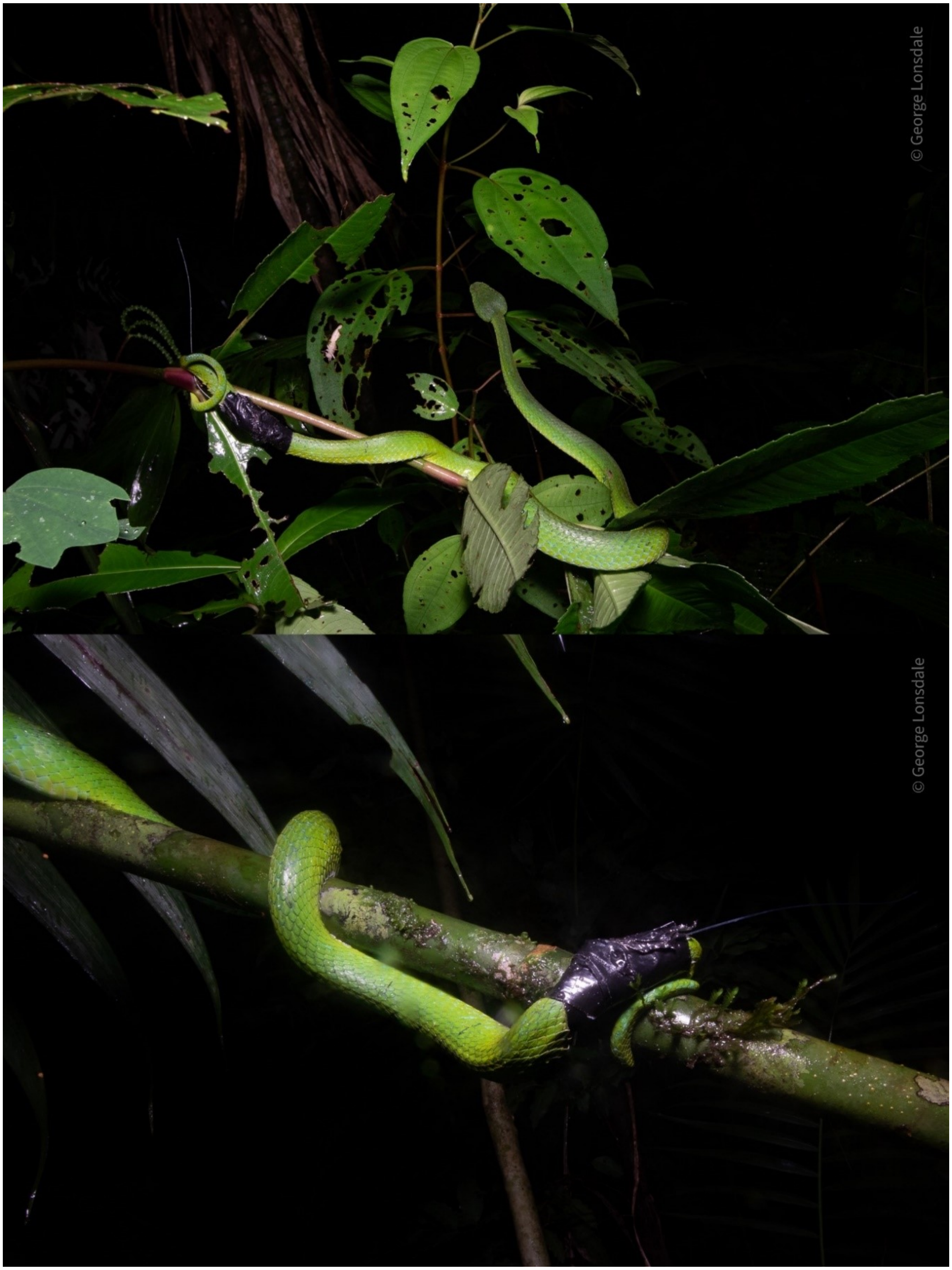

Figure 32. Radio telemetered *Bothriechis marchi* demonstrating full tail prehensility, unhindered by the radio transmitter.

Figure 31. BoMa02 demonstrating unhindered climbing ability on a smooth, wet palm branch.

Habitat Preferences of *Bothriechis marchi*

To characterise the habitat preferences of *Bothriechis marchi* is difficult due to the non-exhaustive list of variables recorded in these data. However, B. *marchi* spends most of the time stationary in the canopy of moist broadleaf forest and broadleaf cloud forest, which are associated with rivers. The preferred state is a closed canopy, with temperatures of around 15°*C,* and a relatively open vegetation, with around 60% of the microhabitat being open space.

A previous study on this species which solely utilised VES as the detection method found that *B. marchi* was found at a mean height of 1.88 m ± 1.44 m SD, suggesting that this species does use lower arboreal strata, especially in smaller individuals (Lonsdale, 2016), however, with radiotelemetry it is clear that this use of the understorey is atypical, and for a higher proportion of the time the snake is in the canopy, although it is worth noting that perch height was estimated based on triangulation of the transmitter signal if visual was not attained, which introduces an inherent error (Lee *et al.,* 1985). This error was counteracted to the best of the authors ability by gaining experience of height estimation, utilising ropes to lift transmitters into the canopy to known heights to hone estimation skills.

During this study, the snakes were stationary for most of the time. With the longest tracked individual staying stationary for several weeks at one time. It is well documented that snakes are intermittent feeders and can spend vast periods of time without moving or eating, especially those species who employ ambush predation as their main predatory method (Lillywhite, 2014), therefore it is not uncharacteristic to see *B. marchi* leading a relatively sedentary lifestyle. However, this was a short-term telemetry study (maximum time tracked = 44 days), and thus this information may only apply to this species behaviour in summer. CNP is known to get much colder during the winter months (Jones, S., *pers. Comms*.) which could alter this species behaviour from what we have seen. In temperate regions terrestrial viperid species utilise hibernacula during cooler months (Rugiero *et al.,* 2018, Gienger *et al.,* 2011, Clark *et al.,* 2008). Likewise, due to the short time-period these snakes were tracked, each location recorded is not independent of the last (Swihart and Slade, 1985) therefore, the structural conditions, such as canopy cover and habitat openness are likely autocorrelated. Lapses between tracking occasions may also introduce error into the methodology, as a snake may have moved and returned to a location between tracks, therefore utilising different habitat types. To account for this more tracks could be implemented, albeit with higher survey effort, or the implementation of a Brownian Bridge Movement Model (Horne *et al.,* 2007), which models probability bases likelihood kernels between locations to give a pathway between locations, although this would only be superior when different locations have been recorded.

Utilised Home-Range Calculations

BoMa05 had the largest home range and had the highest number of moves during the tracking period. BoMa04 has the smallest home range and was tracked for the least amount of time. As seen in other neotropical pit vipers, home range size did not significantly differ between sexes (Sasa *et al.,* 2009). However, BoMa01, which was a large individual of this species, had the third largest home range, despite being much larger than the other radio-tracked individuals; with the exception of BoMa05, the largest individual ever recorded in CNP (SVL = 795 mm, Total Length = 965 mm) and had the largest home range. Unlike in other radio tracked neotropical pit vipers (Almieda-Santos and Salmão, 2002), male *Bothriechis marchi* tend to be larger than females (McCranie, 2011), which could explain the larger home ranges, as some studies have found larger snakes exhibit larger home ranges (Clark, 1974; Shine, 1987), although the underlying drivers for that are unclear due to the scarcity of visual confirmation of behaviour exhibited during the study.

BoMa01 has the most conserved home range, only showing significant space recruitment when recording at the 95% of its MCP. A curve which resembles this is also seen for BOMA05, although at all levels from 50% and greater, home range was larger for BoMa05 than BoMa01. This similarity suggests a small home range of these snakes, with some wider reaching exploratory ranging. Both BoMa01 and BoMa05 were adult male *Bothriechis marchi*. BoM03, also an adult male, albeit a smaller adult (SVL – 545 mm), saw significant increases in home range size at the 65% level and 90% level. The plateaux's in home-range size recruitment suggest the core range of this snake during the tracking period had been accounted for in the nearest 65% of the points. Although this could be skewed due to the short tracking time of only 10 days. The further increase in home range size is due to movements that could be in relation to searching for a mate, BoMa03 was found in the exact location that BoMa02, a female, was found in 2 days earlier. It is possible BoMa03 was moving to search out this female if she was reproductive. Male mate following has been seen in other neotropical pit vipers previously during their mating seasons (Sasa *et al.,* 2009). It is unclear when the mating season would be for snakes in CNP due to its atypical seasonality. This may also explain the degree of overlap between the two individuals MCP's. The steep curves on each of the home range level plots indicates that the tracking periods failed to depict the entire home range for these individuals.

As with other studies focussing on the radio telemetry of vipers, this species has small home ranges and spends extended periods of time stationary (Sasa *et al.,* 2009, Strine *et al.,* 2018). Which means that the home range estimations made by both MCP and Kernel density contain large areas of unused space (Row and Blouin-Demers, 2006). Due to the nature of the short field seasons and the difficulty in locating the focal species, there was high variability in the amount of time snakes were tracked for. Due to this, in combination with the short period of time these snakes were tracked (Swihart and Slade, 1985) the author finds it difficult to assign these home ranges as representative of the spatial ecology of *Bothriechis marchi*. However, this rather should be treated as preliminary data to accompany a more detailed study in the future with longer tracking periods, a larger sample size and during different seasons to greater elucidate the habitat use and movement ecology of this species.

Aside from difficulty arising from the snakes themselves, conducting a radiotelemetry study in CNP presented itself with other challenges. Handheld GPS units measure the accuracy as an error rating in meters, which was accurate to 3 m in open spaces. However, due to the affinity *Bothriechis marchi* has for closed canopy forest, accuracy was often 8 m or higher. Whilst unavoidable, as this was the best equipment available to the author, it does introduce greater error and potentially the over prediction of home range estimations. Most of the tracking occasions did not result in a visual of a tracked individual being attained. This meant that the precise location of a snake, in three dimensions was an estimate based on triangulation of signal strength which introduces human error that is reduced with user experience (Lee, 1985). The author also noted significant 'bouncing' of the signals emitted by the radio-transmitters. Bounce was noted when large physical barriers such as large slopes, trees, and boulders, were close to the transmitter. Care was taken to ensure accurate triangulation when significant bounce was noted. Bounce was also noted to increase after rain, possibly due to the amount of water both in the air as clouds at higher altitude and on the leaves.

Detectability

Reptiles and Amphibians, the third largest group of arboreal vertebrates, are underrepresented in the literature (Kays and Allison, 2010). Which stems from initial biases in how herpetofauna is typically studied. The methods used in the first chapter of this thesis, VES Transect surveys are standard practice for biodiversity monitoring (Lardner *et al.,* 2019).

However, studies investigating arboreal species are vastly skewed towards the understorey (Nakarmura *et al*., 2017), visual surveying from ground level is inherently biased against cryptic and arboreal species, despite their ability to pick up rare species even at low densities, providing a long enough surveying period (Doan, 2003). Although, their effectiveness is skewed again, based on the ecology of the species being studied (Refsnider *et al.,* 2011). Radiotelemetry studies remove the need to visually encounter an individual to confirm its location, and therefore can be used as a critique of the VES surveys. As any time a visual was not attained, that individual would have been missed off a visual encounter survey. Most of the visual encounters with radio telemetered snakes occurred at night. Which is when *Bothriechis sp.* are more active (McCranie, 2011), utilising the time often to hunt or find optimal ambush locations. Although it is worth noting that during the two field seasons, no individuals were seen in ambush positions or feeding, neither were they found with a bolus indicating they had just eaten. Snakes observed during the day were extremely well camouflaged (Fig. 34), with the transmitter being required to pinpoint their location even when within a few meters. Each tracked snake had its 95% MCP situated “off-transect” which further implicates the VES method, as the snakes were not present in an area that would be detectable by a VES along the transect network.

Vegetation density plays a large role in both crypsis and detectability. Rivers often provide an open space and cross-sectional view to a forest structure, allowing for better surveying of an area, due to their often more uniform distribution of vegetation and generally lower density of tree coverage (McGarigal and McComb, 1995). Coupled with riparian zones often supporting a greater abundance of vertebrate species (Oakley *et al.,* 1985) having more visuals attained of the telemetered individuals seems inevitable. Even more so when considering the tendency of this species to feed on amphibians (McCranie, 2011), which in CNP are represented commonly by the Hylidae (Townsend *et al.,* 2006). Canopy cover was not significantly associated with visual acquisition. This is to be expected, especially when considering the non-independence, overlapping and nearby situation of utilised areas by three of the telemetered individuals (Fig. 25). Whereby, sites, which were not identical, are less independent. The primary cloud forest they were situated in was continuous, and only a river, which had a closed canopy, was between them. Crypsis plays a large role in how easy a species is to detect in its environment, but a species can only be detected if it is within a detectable range. Vegetation density and distance to an individual are factors that will determine an individual's detectable range, both of which increase when an individual is in a forest canopy. The mean height a radio-tracked *B. marchi* was seen at was 3.72 m, however the average height recorded of all tracking occasions was 17.04 m. Whilst the highest recorded visual was 18m, this was deemed to be an outlier as it was greater the upper quartile. This extraordinary visual attainment was the result of the location where BoMa05 was perched. The snake was on the thin, lower limbs of the canopy, above an uncharacteristic sparse understory. This visual was also made easier by darkness, as spotlights help to discern the bright white-green glow of a *B. marchi* from the rest of the canopy. Subsequent day time tracks did not attain visuals, but the next night track did in the same location. Indicating that the snake was likely in the same area, although some snakes show site fidelity and will return to the same site (Whitaker and Shine, 2003), and therefore detectability is reduced further in during the day in an arboreal setting.

Imperfect detection can introduce error into population estimates, distributions, and species richness (MacKenzie *et al*., 2006). Therefore, any population estimates based on occurrence data from transect surveys may have these inherent biases and therefore may not be correct, which could affect the conservation status as this species could be vastly underrepresented. Although, it seems unlikely that the population trends would differ what is described by the IUCN (Wilson and Townsend, 2014), as forests within this species range are undergoing deforestation (Gilroy *et al.,* 2017), the species is being traded on the international pet market (Raymond *et al.,* 2001), and its prey, which is amphibian based by most accounts, is declining due to *Bd* (Kolby *et al.,* 2010).

Figure 34. The ever-inconspicuous BoMa04 demonstrating incredible camouflage and low detectability on a dawn track. The top photo shows typical forest type around the river near to the MCP of BoMa02, BoMa03 and BoMa04. The lower photo shows the great difficulty in seeing them, even up close.

Shedding site - *Atropoides mexicanus*

Due to clouding of the spectacle, shedding represents a period where snakes are vulnerable to predation, undergo an intermission in feeding and some species show a narrow thermal tolerance (Klauber, 1984). Some rattlesnakes show site fidelity to shedding locations, such as rock formations, as they will adequately protect them from predators and provide sufficient opportunities for thermoregulation (Loughran *et al.,* 2015). Shedding sites can be communal (Blouin-Demers and Weatherhead, 2001), with multiple snakes utilising the same location to be afforded the same protection and because females become receptive after shedding (Aldridge and Brown, 1995). Shedding sites are therefore likely to provide a combination of the ideal thermal and hygrometric conditions for a snake to shed its skin safely and effectively. Some snakes will shed more often at higher temperatures (Semlitsch, 1979) and many snakes select retreat sites that will allow them to maintain body temperatures within an optimal range for metabolic processes (Huey *et al*., 1989). However, when comparing temperatures of the site utilised by the radio telemetered *Atropoides mexicanus*, there was no significant difference between the ambient temperature and the temperature on the ground close to the shedding site, the temperature of the surface of the log being used, or the temperature inside the shedding site. If temperature was not the driver of site selection, it is likely that inside the log represented a more humid, and well secluded site for shedding.

Conclusion

Attachment methods

The successful application of this non-invasive method of external transmitter fixation shows that short term radio telemetry studies can utilise this method in temperate, humid, and importantly very wet environments, which has been shown to be a downfall in other studies (Wylie *et al.,* 2011). The adaptation of a snake's movement to an external package was almost instantaneous, meaning the influence of disturbance by humans can be ignored faster than surgical implantation or ingestion methods, which could affect behaviour (Fitch and Shirer, 1971) and the health of a snake (Lentini *et al.,* 2011). A feature of transmitter attachment unique to this study was the dorso-lateral placement of the transmitter, anterior to the cloaca on an arboreal viper with a prehensile tail. This was shown to be key, allowing the snake to utilise full mobility whilst climbing without impairment. Care should be taken in future studies of arboreal species to ensure location of the transmitter does not impede movement, especially in the vertical environment. Transmitter attachment should consider the focal species ecology and locomotory method in both attachment location and methodology.

Habitat preferences

This study represents the first formal investigation into the spatial ecology of *Bothriechis marchi*. Closed canopy, moist broadleaf forests that are associated with rivers predominate the utilised space for this species, which spends most of its time stationary at heights over 17 m. Although, there may be an ontogenetic shift in perch height utilisation, with younger individuals using more lower vegetation than adults. Sexes may also utilise the arboreal environment differently, with females using lower height perches. However, due to the small sample size of this study broad generalisations are difficult to apply at the species level without further investigation.

This study also reports the first radio tracked individual of the species *Atropoides mexicanus*, with information pertinent to the understanding the ecdysis cycle of this species. By comparing temperatures within and around a shedding site, the ecological function of that site becomes clearer. Shedding sites likely fulfil a protective role for this species, rather than thermoregulatory. Although, consistency in temperatures around the mean could make for a more consistent climate which would aid shedding.

Detectability

Utilising radio telemetry has allowed the assessment of detectability for *Bothriechis marchi*, a cryptic, arboreal viper. Traditional methods of measuring biodiversity such as transect based VES are limited to transects, which may not traverse suitable habitat for species with specific needs. Arboreal habitats represent the most used sites for this species, but with visual attainment decreasing with perch height it is likely many of these individuals are missed. The extent of this is amplified in this study compared to a VES as the exact location of the snake was known, yet visuals were still not always attained, therefore, non-targeted surveys are much more likely to miss this species. Which could have implications on population estimates and the conservation of this species (MacKenzie *et al*., 2006).

Home Range

Home ranges and space utilisations give key information regarding the habitat preferences and spatial needs of snake species. This study suggests that larger snakes have larger home ranges. And despite males being generally larger than females (McCranie, 2011) at similar sizes they have similar sized home ranges. However, due to the small sample size and short period of tracking available the author suggests this data to treated as preliminary, to be accompanied by more detailed studies for longer periods of time to encompass an individual's utilised space entirely and documenting more movement. This study also illuminated some of the issues surrounding a radio telemetry study being conducted in a montane cloud forest, namely equipment inaccuracies due to topology and terrain, which should be considered by any further studies looking at VHF radio telemetry in montane environments, particularly wet, forested ones.

Overall Conclusions

The snake assemblage in CNP represents 32.4% of the total ophidian diversity of Honduras. Which, when considering the size of CNP shows the power of survey effort; the sheer amount of which has described this diversity, which is likely found in other montane national parks in Honduras that have received less scientific focus. Diversity, richness and evenness were found to decrease with elevation, following trends seen globally. With higher elevations being dominated by a single species, *Cerrophidion wilsoni*, whose total encounter numbers were higher than the next two species combined. However, species accumulation curves for each of the surveying camps, which span the elevation gradient, have not reached asymptote, suggesting the diversity across CNP has not yet fully been described. Deforestation in CNP was found to decrease richness and functional guild diversity in a case study of El Cortecito, a camp in the western portion of CNP which has disproportionately experienced land use change. DCA plots ordinated snake assemblages into lowland, intermediate and higher elevation communities which were distinct from each other, suggesting elevation is closely linked to snake species assemblage.

Numerous species in CNP are arboreal, fossorial, small, cryptic or have reduced detectability. As such, it becomes likely that traditional methods of surveying biodiversity underrepresent these species or miss them completely. Increasing survey effort aids detection, but detailed studies are needed to fully understand these species ecology if we are to represent populations accurately. Pit vipers fall well into the reduced detectability category. With *Bothriechis marchi*, an arboreal, cryptic, pit viper likely experiencing it strongest. No studies pertaining to the ecology of this species have been done, yet known ecology is assumed based on anecdotes from opportunistic observations. Radiotelemetry, using a novel method of transmitter attachment for arboreal vipers, tracked the movements of five *Bothriechis marchi* and one *Atropoides mexicanus* to investigate ecology. *Bothriechis marchi* spends most of its time out of a visually detectable range, stationary, in the canopy, at heights over 17 m, in closed canopy, moist broadleaf forests that are associated with rivers. *Atropoides mexicanus* provided novel data pertaining to the purpose of shedding sites in this species, which seemed to perform little in terms of thermoregulation, but served to protect the snake during a period of heightened vulnerability. Most individuals of each species, during most of their tracking periods were visually undetectable, and spent significant amount of time there. Thus, any study wishing to assess populations, or monitor biodiversity in locations where low-detectability species occur, should consider this in their study design by either dedicating survey effort to such species, or altering their questions.

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Appendix 1 – Snake Elevational Range extensions.

Notable Species Accounts and Range Extensions

Amastridium sapperi **Werner, 1903:** One male individual (SVL 248 mm, Tail Length 111 mm, Mass 11 g) was caught on 24 June 2017 in Guanales camp at 1352 masl. Conditions were sunny and the snake was moving across the trail at the start of GU2 between areas of dense leaf-litter. This individual had 140 ventral scales and 49 sub-caudal scales and was identified by scalation characters in combination with the distinctive colouration of the nuchal band, which is unmistakable when comparing to any other snakes known to be found within CNP. This represents the first record of this species in CNP. This record is 582 m higher than McCranie (2011) suggests they occur in Honduras.

Bothriechis marchi **Barbour and Loveridge, 1929:** *Bothriechis marchi* was the second most detected species during the 12-year survey period. By all accounts, this species occupies premontane wet forest at low and intermediate elevations of between 500-1840 masl. (Köhler, 2003; Wilson and McCranie 2003; McCranie, 2011; Solis and Brown 2016). During our study period we found numerous individuals above 1840 m, including the highest individual record from close to Cantiles camp at 2084 masl. The author suggests more consistent nocturnal surveying at these higher altitudes within CNP to further understand their distribution along this elevation gradient.

Cerrophidion wilsoni **Jadin *et al*., 2012:** The most numerous snake found in CNP throughout the 12-year survey period with more than 500 being encountered. This species is known to occur in lower montane rainforest between 1400 and 3491 masl (Jadin *et al*., 2012), with the species description reporting on other records as low as 1220 masl. During our survey period we found individuals as low as 696 masl which represents a huge potential area increase for this species. Although it seems to be much more abundant at higher elevations within CNP.

Geophis nephodrymus **Townsend and Wilson, 2006:** *Geophis nephodrymus* represents the most encountered of the three known endemic snake species to CNP. Within CNP it is known to occur between 1545 and 1780 masl (Townsend 2009). During the 12-year surveying period 45 individuals were encountered at elevations between 1339 – 2094 masl (mean elevation 1653 masl) extending the known elevation range both higher and lower than previous literature estimates.

Imantodes cenchoa **Linnaeus, 1758:** *Imantodes cenchoa* is surely one of the most widely distributed snakes in Central and South America, being recorded from South Mexico south to the Chaco region of Argentina at elevations of 0-1500 masl (Cisneros-Heredia 2006). In CNP this species is most commonly recorded in the buffer zone and edge of the core zone at camps Buenos Aires, Guanales and El Cortecito, however less common records come from both Basecamp (1613 masl) and the transects around Cantiles, where our highest record for this species is reported from at 1758 masl. This represents a significant increase in elevation for a snake so widely distributed, which may have an incredible increase in the amount of space now known to be available to it. Notably in CNP, this species seems to persist in coffee plantations and around villages, even being found inside houses.

Leptophis ahaetulla **Linnaeus, 1758:** Similar to *I. cenchoa*, *Leptophis ahaetulla* has a trans-continental distribution, with various sub-species recognised throughout central and south America from South Mexico to Argentina at elevations of 0-1680 masl (Uetz *et al*., 2020). During the 12-year survey period data used in this thesis, 40 records of *L. ahaetulla* were recorded at elevations of 491 – 2012 masl representing a significant increase in upper elevation range. Anecdotally, populations are sparse above the previously reported elevation boundaries.

Mastigodryas melanolomus **Cope, 1868:** Individuals of this species are reportedly rare in Honduras (Uetz *et al*., 2020) occurring at low and moderate elevations (McCranie 2011) of up to 1500 masl (Köhler 2003). However, in CNP, this species was numerous, especially around coffee fincas with the maximum elevation record at 1324 masl This species may have been missed from these elevations in the past prior to land use change, as they are likely more easily seen basking on the open ground of plantations, although, they are still easily missed due to the rapidity at which they move after short periods of basking.

Micrurus diastema **Duméril *et al*., 1854:** In Honduras, *Micrurus diastema* is known from lowland moist forest, premontane wet forest, and lower montane wet forest between 45 and 1680 masl (McCranie 2011) In CNP this species has been recorded at 1694 masl, which, although not the greatest elevation increase reported here, is still significant considering the toxicity of this species venom and the potential that peoples encountering it may be increased at higher elevation. Likewise, as the distribution of highly venomous coral snakes has been used to describe the distribution of mimicry, and the presence of coral snakes likely improving outcomes for such mimics (Wilson *et al*., *in press*) this increase in elevation range could help describe snake assemblages and survivorship at higher elevations.

Omoadiphas aurula **Köhler *et al*., 2001:** The second most encountered endemic species of snake in CNP during the 12-year survey period was *Omoadiphas aurula* with 11 individuals recorded. The type locality at 1250 masl represents the lowest currently recognised elevation for this species up to 1900 masl (McCranie 2011). However, we encountered individuals within a much wider range of elevations between 1089-2017 masl, extending both the upper and lower elevation limits for this species. Increasing the range of this species to lower elevations increases the amount of space able to be utilised greatly, however, it is still likely endemic to this small region, as the mean elevation was significantly higher, at 1642 masl.

Scaphiodontophis annulatus **Duméril *et al*., 1854:** Reported from near sea level to 1550 masl in seemingly all available terrestrial forest types up to and including premontane wet forest (McCranie, 2011). In CNP this species has been recorded at elevations up 1613 masl in the forest clearing which makes up basecamp, the site of the CNP visitors centre. This forest clearing tends to be depauperate of snake species, when compared with even the edge forest surround, however, lizards of the genus *Scincella* are seemingly more abundant due to the enhanced thermoregulatory opportunity, which likely drew this snake out of its regular leaf litter habitat (McCranie 2011). The increase further increases the overlap between the range of this species and *Micrurus diastema*, which individuals of this species seem to mimic with the anterior portion of their body.

Tantilla schistosa **Bocourt, 1883:** By all accounts, *Tantilla schistosa* is found from 300 to 1680 masl in lowland, premontane, and lower montane moist forest. In CNP this species is more widespread being found at elevations up to 1838 masl firmly solidifying its position as a member of intermediate elevation forests.

Tantillita lintoni **Smith 1941:** *Tantillita lintoni* is the smallest representative of the caenophidia present in CNP. Its distribution along the Caribbean versant of central America is limited to elevations up 900 masl (Wilson 1988; McCranie 2011). In CNP we encountered two individuals of this species on the road above Buenos Aires Village at 1153 masl, one of which was dead on the road.