

MONITORING THE HABITAT AND SPATIAL ASSOCIATIONS OF TWO
THREATENED PRIMATES ALONG A CONSERVATION AREA
IN WESTERN ECUADOR

by

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LIST OF ABBREVIATIONS

Abbreviation	Description
BSLL	Bosque Seco Lalo Loor
JCR	Jama-Coaque Reserve
TFCC	Three Forests Conservation Corridor
TFCA	Three Forests Conservation Area
TMA	Third Millennium Alliance
IUCN	International Union for Conservation of Nature

ABSTRACT

The Chocó rainforest in coastal Ecuador is an internationally recognized biodiversity hotspot that has been more than 95% deforested for logging and agricultural purposes, which has reduced wildlife habitat and isolated remaining habitat patches. In response to rapid deforestation, the Three Forest Conservation Corridor (TFCC) was established to promote connectivity among local reserves and create the Three Forests Conservation Area (TFCA). As managers from these reserves plan to acquire land to expand the protected area, a better understanding of threatened species' habitat associations, such as two threatened primates: the Ecuadorian capuchin (*Cebus aequatorialis*) and the Ecuadorian mantled howler (*Alouatta palliata aequatorialis*), is required to inform management and acquisition decisions. I recorded activity and distribution of both primate species using twenty acoustic monitoring devices and trail cameras deployed in the forest canopy at stations spread across the TFCA. I assessed the influence of habitat type (agriculture and three forest types [cloud, dry, and wet]), vegetation structure, and landscape composition on occupancy and local presence using single-season occupancy models. I also mapped total detections of both primate species to identify areas of frequent use. Models that included covariates were compared to null models using AICc, and goodness-of-fit-tests. Although the 90% confidence interval of regression coefficients overlapped '0', the model that included a positive relationship with station height was the best model for Ecuadorian mantled howlers and the model that included a negative relationship with distance to edge was the best model for

Ecuadorian capuchins. The lack of significance likely was due to the limited number of canopy stations as well as a low detection probability, a common issue when studying rare species. Maps indicated that cloud forest on the northeastern edge of the TFCA were frequently used by both species. I suggest preserving the remaining intact forests with tall trees to aid in both species' conservation. Additionally, results will guide future areas for protection and corridor expansion.

I. INTRODUCTION

Global biodiversity is in decline largely due to high rates of habitat loss via land conversion and fragmentation (Heywood 1995; Butchart et al. 2010; Hansen et al. 2013). Fragmentation is a process in which an expanse of habitat is transformed into smaller patches separated and isolated by a different matrix of habitats (Wilcove et al. 1986). For many species, fragmentation leads to restrictions on movement and dispersal (Kindlmann and Burel 2008). Small-scale movement restrictions (i.e., daily movement disruptions) lead to poor condition of individuals due to increased energy expenditure to obtain resources (Smith et al. 2013), whereas large-scale dispersal movement restrictions (i.e., preventing long-distance dispersal) caused by severe habitat isolation can lead to inbreeding depression due to the lack of gene flow (Kenney et al. 2014). Fragmentation can be especially detrimental to large mammals, such as primates, given their large home ranges and the increased exposure to poaching while navigating fragmented landscapes (Bicca-Marques 2003).

Promoting habitat connectivity among habitat patches has proved to be a successful strategy to mitigate the impacts of fragmentation in tropical systems (Campos and Jack 2013). One way to increase habitat connectivity is through the establishment of conservation corridors (Beier and Noss 1998) that link forest patches occurring in otherwise ‘uncrossable’ landscapes. Such connectivity can be accomplished by strategically planting trees or encouraging farmers to retain various vegetation patches intact. Despite the recognized importance of corridors for increasing connectivity, there is little research on the effectiveness of conservation corridors in the tropics (Caro et al. 2009; Yaap 2018). Given the high degree of ecological specialization in the tropics

(Laurance and Bierregaard 1997), species may be especially sensitive to edge-effects (Laurance and Laurance 1999) and more research is necessary to understand the spatial requirements of tropical species to use a conservation corridor.

Fragmentation in western Ecuador is extensive due to the extreme deforestation in this region (Haro-Carrión and Southworth 2018; Dodson and Gentry 1991). It is estimated that as much as 98% of the primary forest of western Ecuador has been lost (Haro-Carrión and Southworth 2018), and much of the remaining forest exists in discrete isolated patches surrounded by agriculture (Dodson and Gentry 1991). This deforestation has caused conservation issues for many native and endemic species. Approximately 15% of native mammalian species are threatened with extinction, including three of the four primates existing in western Ecuador (IUCN 2020).

Primates are often advocated as ‘umbrella species’, meaning that conserving forest swaths large enough to maintain healthy primate populations inherently protects many species in their range that rely on the microhabitats within the primate territories (McCann et al. 2003; Lambert 2011; Campos and Jack 2013; Freire Filho and Palmeirim 2019). In addition, many primates provide ecosystem services in the form of seed dispersal for tree species crucial to forest health and structure (Terborgh 1992). Commonly, primates also function as ‘flagship’ species, or those that engage public support for conservation action due to their positive perception as charismatic species (Caro and O’Doherty 1999). Unfortunately, many neotropical primate populations are in decline due to habitat fragmentation and hunting (Peterson and Heemskerk 2001; Hilário et al. 2017). It is estimated that 38.2% of neotropical primates currently are threatened with extinction (IUCN 2020). Within the neotropics, Ecuador is listed as the fifth most

speciose country for primates with 22 species, 11 of which are listed as threatened or endangered, and four of which reside in western Ecuador (Tirira 2017).

Two of the four primate species that occur in western Ecuador, the Ecuadorian capuchin (*Cebus aequatorialis*) and the Ecuadorian mantled howler (*Alouatta palliata aequatorialis*), are patchily distributed throughout the entirety of western Ecuador (Cervera et al. 2018). Both primate species are experiencing population declines due to extensive habitat fragmentation and conversion (Tirira 2011; Campos and Jack 2013; Cervera et al. 2015). Although there is evidence that Ecuadorian capuchins and Ecuadorian mantled howlers utilize regenerating forest (Campos and Jack 2013; Papworth and Mejia 2015), the extent of usage of this habitat remains unknown.

The Ecuadorian mantled howler is currently listed as “Vulnerable” by the International Union for Conservation of Nature (IUCN) (Cuarón et al. 2008) but listed as endangered in Ecuador (Tirira 2011). Population decline of Ecuadorian mantled howlers is attributed to habitat loss and poaching (Cuarón et al. 2008). These primates form troops of 5-12 individuals (Cervera et al. 2015) and have a relatively small troop home range (estimated as 1.3 – 60 hectares [ha]; Neville et al. 1988; Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Arroyo-Rodríguez and Dias 2010). This species is strictly herbivorous, primarily consuming leaves with fruits as a supplement, and several of their food sources are absent from fragmented forests (Arroyo-Rodríguez and Mandujano 2006). Therefore, highly fragmented forests likely cannot indefinitely sustain populations. As Ecuadorian mantled howlers act as seed dispersers and are noted to utilize regenerated and replanted areas (Papworth and Mejia 2015), it is vital to understand proper habitat management to support this species.

The Ecuadorian capuchin is listed by the IUCN as “Critically Endangered”, predominantly due to intense deforestation throughout its range as well as poaching. Ecuadorian capuchins appear on a list of the ‘25 most threatened primates in the world’ (Schwitzer et al. 2019), and the authors state that research on how landscape disturbances affect this species is needed. A predictive model estimated that Ecuadorian capuchin distribution may be driven by greater canopy cover, low human population density, mild seasonality, and annual precipitation less than 2 m (Campos and Jack 2013). The model estimated 5028 km² of suitable habitat remains for the Ecuadorian capuchin; however, this estimate includes unprotected forest patches that may be subjected to further fragmentation where the species may undergo local extinction (Campos and Jack 2013). By some estimates, in a few decades the range of this species has been reduced to ~1% of its original distribution (Albuja and Arcos 2007). Further, there is limited information on the habitat features driving the local presence of Ecuadorian capuchins. These primates have a varied diet, largely consuming fruits, as well as small vertebrates and invertebrates (Albuja and Arcos 2007). However, despite Ecuadorian capuchins exploiting a wide variety of food sources, the larger troop home range requirements exhibited by this species (500 - 560 ha) showcase that habitat connectivity is crucial to fulfill their energetic requirements and allow the persistence of this species (Jack and Campos 2012).

To improve local habitat connectivity, the Jama-Coaque Reserve (JCR) in western Ecuador—a protected area that works with local community members to preserve the last remaining patches of the coastal Chocó rainforest—established the Three Forest Conservation Corridor (TFCC) in collaboration with the local towns of Camarones and Tabuga, the neighboring Bosque Seco Lalo Loor (BSLL), and the IUCN-Netherlands.

The TFCC is important because it forms a contiguous 1500-ha protected area known as the Three Forests Conservation Area (TFCA) that spans three ecologically distinct forest types: dry forest, moist forest, and cloud forest. These forests are located along an elevational gradient, which facilitates seasonal movement of wildlife across the landscape and protects clean water resources for local communities. This initiative is currently underway and requires a better understanding of the two threatened primate species' habitat and spatial requirements to inform management decisions regarding future land acquisition and management of properties immediately buffering the corridor.

Previous efforts to assess the habitat and spatial associations of the Ecuadorian capuchin and the Ecuadorian mantled howler have been limited due to methodology employed (i.e., visual surveys: Campos and Jack 2013; Cervera et al. 2015). Recommendations have been made by neotropical primatologists to use passive methodologies (such as trail cameras) to monitor these primates and increase detectability (Campos and Jack 2013). Although terrestrial trail cameras have been utilized to successfully monitor the Ecuadorian capuchin (Guerrero-Casado et al. 2020), my study is the first to utilize trail cameras in the canopy paired with acoustic recorders to monitor these two species.

Objectives of the Study

The objectives of this study were to: 1) assess the spatial distribution of the Ecuadorian capuchin and the Ecuadorian mantled howler across the TFCA; and 2) examine the influence of habitat and spatial features at two spatial scales (micro- and macro-) on the use of various areas within the corridor. I hypothesized that habitat usage

of these species will vary across the conservation area and predicted that the primates would use the forested areas more frequently than agricultural areas. I further predicted a positive relationship between canopy cover and intensity of usage for the Ecuadorian capuchin and the Ecuadorian mantled howler due to their primarily arboreal locomotion (Campos and Jack 2013; Cervera et al. 2015).

Significance of Research

For the TFCC to be successful, the habitat and spatial requirements of these species must be identified; thus, the results of this research will directly inform management efforts in the areas immediately adjacent to the TFCC and TFCA. Areas that are identified as potential movement barriers for these primates will be prioritized for restoration (if currently farmland) through sustainable agroforestry or for preservation (if currently forested and locally owned). Third Millennium Alliance (TMA, the NGO that owns and manages JCR) is working collaboratively with communities to incentivize sustainable agriculture through improved economic opportunity and inform local farmers on how to create a more ‘wildlife-friendly’ landscape based on the data gathered. Additionally, these results might fill a knowledge gap concerning habitat use of the two primate species within recently created corridors, which are especially crucial for maintaining habitat of the “Critically Endangered” Ecuadorian capuchin (Campos and Jack 2013).

II. METHODS

Study Site – The Three Forests Conservation Area

This study was conducted along the western coast of Ecuador within the TFCA (Figure 1), located approximately 11 km south of the equator in the Manabí province. The TFCA covers 1,500 ha and includes BSLL, JCR, and the TFCC which encompasses 350 ha of forested ridgeline between the two ecological reserves. The three forest types the TFCA spans are defined by annual precipitation received or elevation. Dry forest is described by average annual precipitation of 100 – 200 cm, wet forest is characterized by > 200 cm of precipitation, and cloud forest is defined by an elevation of > 450 meters above sea level. Agriculture in the TFCA is largely characterized by current and abandoned pastureland. The TFCC exists along an elevational gradient from sea level to ~650 meters above sea level. The climate is defined by a marked dry season from June through December and an intense rainy season from January through May (Vera Barahoma 1993). Some of the pasturelands bordering the TFCA were included for this study.

Canopy Station Placement

I monitored the use of the TFCA by the Ecuadorian capuchin and the Ecuadorian mantled howler with twenty AudioMoth (version 1.1, Open Acoustic Devices, United Kingdom) acoustic recorders (hereafter AudioMoths) and twenty Browning Trail Cameras (Browning Dark Ops Pro XD, Browning Trail Cameras, Birmingham, Alabama) (hereafter ‘trail cameras’). Prior to placement of canopy stations, I created a map in QGIS (version 3.14, QGIS Development Team) to systematically space survey points that

would represent canopy station locations. I laid a grid over the sampling extent with cells spaced 1 ha² (totaling 1764 cells) and placed a point in the center of a randomly selected cell. Following this process, I created a 75-ha buffer around each point and excluded all cells (from further selection) within that buffer. A 75-ha buffer area was specified given that it is intermediate in size between the home range of the Ecuadorian capuchin and Ecuadorian mantled howler. I repeated this process until twenty points were placed (Figure 1).

On the ground, I visited the generated GPS points and identified target trees for climbing (within 100 m of the generated GPS coordinates, and physically connected to the surrounding canopy). Once I identified qualifying trees, I determined placement of the canopy station based on perceived suitability of movement for primates (i.e., connecting to other trees, without several small branches to obstruct movement, and wide enough to support larger animals) and set the climbing line with a Big Shot (Bartlett Arborist Supply, Marlette, MI, U.S.A.). I then climbed into the canopy and mounted one AudioMoth and one trail camera (Figure 2), which I will refer to as a canopy station. I mounted the trail cameras to the tree facing a branch that was suitable for wildlife movement, and the AudioMoth slightly below to prevent water buildup on the device. I angled both devices to prevent disturbance to the natural movement of arboreal species. I removed some vegetation to reduce the instances of non-target stimuli photos (i.e., wind-blown movement of leaves) and set the trail cameras to collect 3 photos in rapid succession with a 10 second delay and installed 64 GB SD cards. I set the AudioMoths to record 10 minutes every hour between 0600 – 1900 hrs and installed 128 GB SD cards. Due to limited supply, I only placed one Kestrel (D2 DROP) (Nielsen-Kellerman

Company, Boothwyn, PA) microclimate sensor (hereafter Kestrel) in each of the four habitat types at a canopy station. I set the Kestrels to record hourly temperature, relative humidity, dew point, and heat severity index. Initial establishment of the canopy stations was completed on 5 January 2020, prior to the start of the rainy season.

To ensure equipment function, I conducted maintenance (replacing batteries and SD cards, removing any non-target stimuli, and adjusting camera angles) every 12-38 weeks. I conducted the first round of maintenance on 6 January 2020 and started with stations placed earliest. Delays due to the Covid-19 pandemic prevented me from returning to Ecuador to complete the second round of maintenance until 9 October 2020. During this period, I moved three of my canopy stations due to anthropogenic disturbance compromising the safety of the canopy stations (i.e., chainsaw scars). Additionally, I acquired more kestrels and placed one in each of the remaining sixteen trees.

To assess potential habitat and spatial associations, I recorded the following covariates: elevation, canopy cover, vertical obstruction, number of trees connecting to the canopy station tree, height of the canopy station, and DBH (diameter at breast height) of the tree (Neam and Lacher 2015) at each canopy station. I recorded canopy cover from the height of the canopy station using a convex spherical densiometer in each cardinal direction, then averaged the four measures and converted the canopy cover measures to be on a scale of 100, instead of 96. I also recorded vertical obstruction, the percentage of cover from nearby surrounding vegetation, from the level of the canopy station using light contrast in Canopeo (Oklahoma State University Department of Plant and Soil Sciences, Stillwater, OK) in each cardinal direction and averaged the four measures. From the level of the canopy station, I also counted the number of trees connected to the

canopy station tree. I used a laser range finder to measure height of the canopy station to the ground, and I recorded 3 measures to ensure an accurate reading. As many of the trees had large buttress roots, I measured DBH at the point where the roots no longer extended beyond the trunk (Figure 3). Additionally, I used satellite imagery from 2020 to estimate proximity to an artificial edge (e.g., habitat edge created by slash-and-burn techniques for cattle grazing), human dwellings, and a river (Neam and Lacher 2015). I considered the variables that were measured at the tree as the micro-level variables, this includes canopy cover, vertical obstruction, connecting trees, height of the canopy station, and DBH. I considered the variables that were measured with satellite imagery as the macro-level variables, this includes distance to artificial edge, human dwellings, river, and elevation.

Acoustic Analysis

I identified the Ecuadorian capuchin and Ecuadorian mantled howler vocalizations utilizing Kaleidoscope Pro (version 5.19, Wildlife Acoustics). For Ecuadorian mantled howlers, I used the following parameters: 100 – 750 Hz frequency range, 0.5 – 5 s vocalization length, and 0.5 maximum inter-syllable gap (Bergman et al. 2016). I then manually identified vocalizations that populated within the given parameters. As Ecuadorian mantled howlers can be heard at a distance > 1 km, I conducted a decibel analysis to only include vocalizations that occurred close to the canopy station (< 5 m). Given mantled howler vocalizations have been noted to be 90 dB from 5 m (Whitehead 1989), I filtered detected calls through Raven (Cornell Lab of Ornithology) and Equation 1 from Merchant et al. (2015) to determine the decibel level of vocalizations:

$$\text{SPL} = M + G + \left(20 * \log_{10} \left[\frac{1}{V_{pp}} \right] \right) + (20 * \log_{10} [2^{N_{bit}-1}])$$

Where SPL is sound pressure length (dB), M is the sensitivity of the microphone (-18), G is the gain set for the recorders (-30.6dB), N_{bit} is the sampling depth (24), and V_{pp} is the peak-to-peak voltage. I collected the peak voltage (V_p) in Raven and calculated the units based on a max kU of 32.77 on Raven and maximum microphone voltage of 3.6.

$$V_p = \text{Peak}/32.77 * 3.6$$

I then converted the peak voltage (V_p) to the root-mean-square voltage (V_{rms}).

$$V_{rms} = V_p * 1/\sqrt{2}$$

Finally, I converted the root-mean-square voltage to peak-to-peak voltage (V_{pp}) for the decibel analysis.

$$V_{pp} = V_{rms} * 2(\sqrt{2})$$

Based off these equations, I only included calls that had a V_p of 30 or greater as that would convert to a dB of 90, which would suggest that only calls from 5 m or closer were included in later analyses.

I used the following parameters to populate vocalizations of Ecuadorian white-fronted capuchins: 1500 – 3000 Hz frequency range, 0.5 – 5 detection length (Gros-Louis, 2006). I identified the vocalizations of Ecuadorian capuchins using a cluster analysis with vocalizations from an online database and vocalizations collected during analysis. I examined the files that clustered with identified vocalizations as the frequency range of these primates overlaps with several native bird species. Given that Ecuadorian capuchin calls are not known to travel as far as those of Ecuadorian mantled howlers, I did not conduct a dB analysis for this species. I collaborated with experts at the

University of Texas - Austin to confirm identification of different Ecuadorian capuchin vocalization types (e.g., contact, aggression) prior to including the vocalization in the analyses. Although I noted the time of calling, for statistical purposes, acoustic detections were collapsed into a daily event.

Statistics

I developed a suite of hierarchical, single species, single season occupancy models in package ‘unmarked’ (Fiske and Chandler 2011) using RStudio (version 4.04, R Core Team 2021). For these models I used canopy station as the spatial unit and week as the temporal unit, species detection/non-detection status when the station was active as the response variable, micro- and macrolevel environmental variables as predictors of wildlife occupancy and activity, and weather variables as predictors of wildlife detection and activity. I pooled detections by trail camera and Audiomoths. I elected to conduct occupancy models given their ability to account for imperfect detections and use of ‘detection’ and ‘non-detection’ data (Mackenzie et al. 2002; Tobler et al. 2015; Rich et al. 2016; Dertien et al. 2017). For both primates, I considered a week to be my unit of temporal replication for the occupancy calculation of Ecuadorian mantled howlers and local presence for the Ecuadorian capuchins where occupancy and local presence differ in whether canopy stations are considered spatially independent. A week as a unit of temporal replication was decided to relax the assumption of constant availability.

One of the assumptions of occupancy (Ψ) estimation is that sites are independent meaning that the detection of a species at one canopy station should not depend on if it was detected at another at the same sampling occasion (Mackenzie et al. 2002), which is

met for the Ecuadorian mantled howler. Due to the large home range of Ecuadorian capuchins relative to spatial positioning of canopy stations, I could not assume that the canopy stations were independent. To account for the violation of this assumption, I estimated local presence (θ) which does not assume the canopy stations are independent and instead considers each to be a subunit (herein used to indicate a non-spatially independent part of the unit [the TFCA]), meaning that the local availability is not static and may vary over time or subunits given the area is occupied (Hines et al. 2010; Bailey et al. 2014). For the Ecuadorian capuchin, I conducted local presence and detection models separately given the instability of models conducted with both variables present. I defined the model parameters according to Bailey et al. (2014): Ψ is the probability the sampling unit is occupied, θ is the probability the subunit is occupied, p is the probability of detecting the species. Given the limited data available for weather variables, I created separate models where day (24-hour period) was considered the temporal unit to compare the impacts of minimum daily relative humidity, high daily temperature, and the standard deviation of each on the detection probability of these primates in the dry season and in the rainy season. I elected to focus on minimum daily relative humidity and maximum daily temperature given that the Mexican black howler (*Alouatta pigra*) spends more time resting on warmer and drier days (Aristizabal et al. 2018), and the standard deviation of both variables to understand if greater fluctuation of these variables effects detection probability (Janmaat et al. 2006; Aristizabal et al. 2018).

I conducted a pairwise correlation test and eliminated any variables that had a coefficient of >0.7 as well as a ‘corvif’ correlation test to determine if any variables were multicollinear (variation inflation factors were > 3) (Zuur et al. 2010). None of the

variables were collinear. I then standardized all variables to have a mean value of 0 and a standard deviation of 1 (Schielzeth 2010) and eliminated nonsignificant ($P > 0.05$) variables in a backwards stepwise manner for detection and occupancy models (Kéry et al. 2013). Given the number of canopy stations ($n=20$), global models would not converge, so I built one ‘starting’ model with the microlevel covariates, and another with the macrolevel covariates. Once I built the models, I used the model selection procedure with the ‘modSel’ function and selected the model with the lowest AIC value. If models were considered competing ($\Delta AIC < 3$), I selected the model with the fewest variables, favoring parsimony. I then used the ‘fitStats’ function to ensure the best model properly fit the data. If the model violated the assumptions of ‘fitStats’ (i.e., χ^2 p-value < 0.05), I checked the next competing model for proper fit.

To visualize the distribution of both primate species across the conservation corridor, I created a separate table of total detections (detections here considered daily) by canopy station. I loaded these data with coordinates in to QGIS and used the ‘heatmap’ option to create these maps. I also used these heatmaps to visually assess which of the habitat types both primates were detected in.

III. RESULTS

From December 2019 – January 2021, I monitored primates with trail cameras and acoustic recorders for periods between 64 – 397 nights for a total of 5,980 trap nights and 204,688 images. I collected a total of 49,337 files from the AudioMoths for a total 8,223 recorded hours. A gap exists in the data due to the Covid-19 pandemic (Table 1). I coded the observation and site-level covariates as displayed in Table 2.

Detections throughout the TFCA

Detection probability of the Ecuadorian mantled howler throughout the entire survey period and TFCA was 0.05. Ecuadorian mantled howlers were detected most frequently in forested areas with detections only occurring at one agricultural site (Figure 4). On a site level basis, the greatest number of Ecuadorian mantled howler detections were at CF04 (89 of the 241 total detections; Figure 4), a cloud forest site at the northeastern corner of the TFCA.

Detection probability of the Ecuadorian capuchin throughout the survey period and TFCA was 0.01. Ecuadorian capuchins were largely detected in cloud and wet forest with only 1 detection in dry forest and no detections in agriculture (Figure 5). Throughout the corridor, Ecuadorian capuchins were most frequently detected at CF04 (10 out of 43 detections) a canopy station in the northeastern corner of the TFCA (Figure 5).

Habitat and spatial covariates

The mean elevation was 395.25 m.a.s.l. \pm 152.58 (standard deviation). The mean canopy cover was 70.59% \pm 15.57% (SD), meanwhile the mean vertical obstruction was

32.51% \pm 14.43% (SD). The number of connecting trees averaged 8 trees with a range of 1 to 36 trees. The mean height of the canopy station was 17.02 m \pm 7.13 m, meanwhile the mean DBH was 81.42 cm + 35.63 cm. The mean distance to river was 0.17 km \pm 0.13 km, mean distance to human dwellings was 1.59 km \pm 0.69 km and the mean distance to artificial edge was 0.49 km \pm 0.32 km (Table 3).

Ecuadorian mantled howler detection and occupancy probability

Throughout the sampling period, I detected the Ecuadorian mantled howler 240 times with a naïve occupancy of 70%. Of the detections, 37 were unique acoustic detections and 200 were unique camera detections, with only 3 detections overlapping. In the dry season, daily minimum RH (%) was included in the best fit model (Table 4; SSE = 0.49, $\chi^2 = 0.41$, Freeman Tukey = 0.47). Low relative humidity had a weak positive affect on Ecuadorian mantled howler detection probability (transformed $\beta_{\text{low.RH}} = 0.73 \pm 0.37$ SE, $z = 1.95$, p-value = 0.05; Table 11; Figure 9). During the rainy season, high temperature and low relative humidity were included in the best fit model (Table 5; SSE = 0.42, $\chi^2 = 0.07$, Freeman Tukey = 0.46). High temperature had a significant negative effect on detection probability (transformed $\beta_{\text{high.temp}} = -0.52 \pm 0.16$ SE, $z = -3.22$, p-value < 0.01; Figure 10), whereas low relative humidity did not have a significant effect (transformed $\beta_{\text{low.RH}} = -0.23 \pm 0.15$ SE, $z = -1.51$, p-value = 0.13; Table 10), however the model excluding low relative humidity did not fit the data (SSE = 0.45, $\chi^2 = 0.04$, Freeman Tukey = 0.48). The estimated detection probability in the dry season (0.09 \pm 0.02 SE) was similar to the detection probability in the rainy season (0.07 \pm 0.01 SE).

The best fit occupancy model for the Ecuadorian mantled howler based on the binned data included canopy station height on detection and occupancy (Table 6; SSE = 0.52, $\chi^2 = 0.15$, Freeman Tukey = 0.46). Although canopy station height was included in the best fit model for occupancy (transformed $\beta_{\text{height}} = 6.35 \pm 4.24$ SE, $z = 1.50$, p-value = 0.13), the 95% confidence interval overlap '0' (CI: -1.90, 14.6; Table 8). However, the best fit model had a 55x better fit than the null model (Table 6). Predictive plots indicated that Ecuadorian mantled howler occupancy probability increased from 0.10 to 0.85 as canopy station height increased from 12 m to 16 m (Figure 6). The estimated proportion of area occupied by Ecuadorian mantled howlers is 0.71 (95% CI: [0.70 – 0.80]).

Ecuadorian capuchin detection and local presence probability

Ecuadorian capuchins were detected 42 times, with a naïve occupancy of 50%. There were 3 unique acoustic detections, and 39 unique camera detections. For detection probability during the rainy season, the best model included minimum RH as a predictor (Table 5). Although the best model fit the data (SSE = 0.49, $\chi^2 = 0.75$, Freeman Tukey = 0.51), this model is not significantly different from the null, given that the confidence interval overlapped '0' (Table 10). In the dry season, there were too few Ecuadorian capuchin detections to conduct any reliable models. For Ecuadorian capuchin detection based on the binned data, the best fit model included distance to river and height of canopy station (Table 7; SSE = 0.50, $\chi^2 = 0.81$, Freeman Tukey = 0.49). Distance to river had a significant negative affect on Ecuadorian capuchin detection (transformed $\beta_{\text{river}} = -0.75 \pm 0.32$ SE, $z = -2.40$, p-value = 0.02), whereas canopy station height had a significant positive affect on detection (transformed $\beta_{\text{height}} = 0.78 \pm 0.24$ SE, $z = 3.16$, p-

value < 0.01 ; Table 9).

The best fit model for Ecuadorian capuchin local presence included distance to artificial edge as a predictor (Table 6; SSE = 0.42, $X^2 = 0.20$, Freeman Tukey = 0.44). Although distance to artificial edge was included on the top model for Ecuadorian capuchin local presence (transformed $\beta_{\text{edge}} = 0.84 \pm 0.58 \text{ SE}$, $z = 1.45$, p-value = 0.15), the 95% confidence interval overlapped '0' (CI: -0.30, 2.00; Table 8), likely due to a small sample size. Predictive plots indicate that Ecuadorian capuchin local presence increased from 0.1 to 0.8 as distance to artificial edge increased from 0.1 km to 1.2 km (Figure 7). The estimated proportion of area used by Ecuadorian capuchins is 0.54 (95% CI: [0.50 – 0.75]).

IV. DISCUSSION

Detections from the monitoring efforts affirm that both primate species are using the TFCC, however, there were some areas that appear unused by both species. Ecuadorian capuchins were not detected in any agriculture sites whereas Ecuadorian mantled howlers were only detected at one agricultural site that bordered forest (Figure 5, Figure 4). While both primate species had a greater number of detections in the cloud forest than other forest types, I was unable to test whether these differences were significant. Ecuadorian capuchins were only detected once in the dry forest of the TFCA, but another trail camera study solely detected Ecuadorian capuchins in the dry forest (Guerrero et al. 2020), which suggests that the distribution of the cameras may have been limited given there were only three canopy stations in this habitat type. It is interesting that the Ecuadorian mantled howlers were only spotted in the edge agriculture site, given that studies on habitat use have indicated they utilize replanted and regenerating areas (Papworth and Mejia 2015; Fedigan et al. 1998). However, the regenerating areas within one of these studies were largely bordered by forest (Papworth and Mejia 2015). This distinction may indicate that the locations of the canopy stations in replanted areas of the ‘agriculture’ habitat type may be too far from an edge for the Ecuadorian mantled howlers to move into.

The evidence from this study did not support my prediction that the Ecuadorian capuchin and Ecuadorian mantled howler increased usage in areas with high canopy cover. However, in previous studies that identified canopy cover as a potentially important habitat variable for these primates, satellite imagery was used, whereas I used a microscale approach with a spherical densiometer and the minimum cover at any location

in this study was 43% compared to 0% in previous studies (Campos and Jack 2013; Cervera et al. 2015). The limited variability of my approach to canopy cover suggests that a microscale approach may not be appropriate for these primate species; however, it is also consistent with the findings in one study that a threshold of habitat suitability is reached above 25% cover for the Ecuadorian capuchin and occurrence does not increase once this level of cover is reached (Campos and Jack 2013). Similarly, I measured connectivity on a microscale approach where a macro-scale approach, such as the use of LiDAR to classify percent cover, may accurately indicate if connectivity (instead classified as percent tree cover within a specified buffer versus a limited area) affects presence of these primates. In this study, some canopy station trees had a few trees in the immediate vicinity, but there was little to no connectivity beyond a small area to facilitate movement, which may have influenced the results.

The results from the local presence models suggest that the presence probability of Ecuadorian capuchins increases as the distance to an artificial edge increases (Figure 7) and can indicate a negative edge effect. In the context of anthropogenic disturbance, edge effect is defined as the changes in a previously undisturbed habitat due to the creation of an artificial edge through anthropogenic activities, such as logging and livestock grazing (Lovejoy et al. 1986). Negative edge effect indicates a decrease in the density of a species as the proximity to the artificial edge increases (Ries et al. 2004). In neotropical primates, the response to an edge seems to be related to their dietary requirements: primates that are largely folivores tend to increase in density around edges (Coley 1980; Lenz et al. 2014), whereas primates whose diets consist of fruits tend to decrease around edges due to the reduction in availability of that food source (Johns

1997). Ecuadorian capuchins have a varied diet; however, it has been suggested that the principal component of their diet is fruits and invertebrates (Van Schaik and Noordwijk 1988; Albuja et al. 2018), which may explain the decrease in presence probability with a decrease in distance to artificial edge.

Greater occupancy probability of Ecuadorian mantled howlers correlated positively with canopy station height. This result suggests that managers intending to promote the presence of Ecuadorian mantled howlers could consider planting trees that reach a maximum height of 15 m or higher (Figure 6). Ecuadorian mantled howlers have been noted to consume seeds of *Inga edulis* (Figure 8), a pioneer tree that can grow up to 30 m in height (Lim 2012). Further, previous research indicates that folivorous primates, like the Ecuadorian mantled howler, consume the leaves of quick growing pioneer species as their leaves produce weaker chemical defenses to prioritize growth (Coley 1980; Williams-Linera 1990; Lenz et al. 2014). Given my results, I would recommend that managers in the process of restoring pastureland in western Ecuador focus on planting tree species such as *Inga edulis* that are native to western Ecuador and can grow to a height of >15 m relatively quickly to restore the canopy and promote the activity of natural seed dispersers such as Ecuadorian mantled howlers. However, given the large confidence envelope, weak effect size, and the method this covariate was collected (measuring the height of the canopy station versus the height of the tree) this correlation should be examined by future researchers.

Few studies have used trail cameras to monitor the Ecuadorian mantled howler and the Ecuadorian capuchin, and those that have were restricted to ground level cameras (Guerrero et al. 2020; Lizcano et al. 2015). The study by Guerrero et al. (2020) focused

specifically on Ecuadorian capuchins with a similar sample effort (20 cameras with 5,785 trap nights) and resulted in 8 unique detections compared to 39 in this study, whereas Lizcano et al. (2015) focused on all medium and large mammals with a lower sample effort (60 cameras with 3,735 trap nights) and had 3 detections for each primate species compared to 200 unique camera detections for the Ecuadorian mantled howler. These results likely suggest that canopy trail cameras are more effective compared to ground cameras for surveys of the Ecuadorian capuchin and Ecuadorian mantled howler, which reflects their arboreal nature.

Though trail camera surveys are rare, the most used methods to monitor the Ecuadorian mantled howler and Ecuadorian capuchin are visual encounter surveys or acoustic triangulation (for the howlers) (Cervera et al. 2018; Karunos et al. 2016; Cervera et al. 2015; Campos and Jack 2013; Jack and Campos 2012). Studies that use visual encounter surveys and acoustic triangulation for Ecuadorian mantled howlers have high success rates and can obtain additional data such as sex ratios, troop size, and age ratios (Cervera et al. 2018; Cervera et al. 2015) that are not necessarily obtainable with a trail camera and/or an acoustic recorder. Therefore, I would not recommend passive monitoring as a reliable alternative to visual encounter surveys and acoustic triangulation for Ecuadorian mantled howlers. In the case of Ecuadorian capuchins, where visual encounter surveys often result in fewer than twenty encounters (Cervera et al. 2018; Karunos et al. 2016; Cervera et al. 2015), except for studies carried out with the intent of a census (Jack and Campos 2012), I would recommend the use of these passive monitoring methods to confirm presence in an area.

It is important to note that this study was limited in several aspects. First, many

studies utilizing camera traps to monitor species for occupancy do not consider a single trail camera as the unit of measure, and instead have several trail cameras within each defined site (Clare et al. 2015; Tobler et al. 2015; Cove et al. 2013). The placement of twenty canopy stations was determined to balance accommodating the relatively smaller home range size of the Ecuadorian mantled howlers and the larger home range size of the Ecuadorian capuchins for the limited area available, and as such I was unable to measure occupancy for the Ecuadorian capuchins. Detection probabilities for both primates were also low (<0.1), which may indicate the need for different survey design or methods to improve this estimation. I was limited in comparing the true effectiveness of acoustic detections and camera detections given the difference in data acquisition length, the challenge in identifying Ecuadorian capuchin calls, and the restrictive measures placed in determining whether an Ecuadorian mantled howler call was to be included in the analyses. Battery life of the AudioMoths is approximately four months for the programmed settings and given my inability to check the canopy stations until October of 2020, all AudioMoths had stopped recording by April 2020, whereas most cameras were still taking photographs. In identifying Ecuadorian capuchin calls, I encountered problems attempting to create an advanced classifier, and various types of capuchin vocalizations frequently clustered with bird calls, so it is probable that capuchin vocalizations from the manual identification process were low-biased leading to an underestimation of detection probability throughout the TFCA. Additionally, although Ecuadorian mantled howler monkeys were recorded at every site, only the loudest calls were included. There is a chance my criteria for inclusion was too stringent, especially given how differing weather conditions alter how sound travels and may have led to a

bias in not including acoustic detections on days that were windy, since wind causes howler calls to attenuate at quicker rates and creates noise interference on the part of the detector (Garstang 2004). Lastly, as with the AudioMoths, there were issues with some cameras running out of battery before others (and, in one case, a camera being stolen), which caused variability in detection days across canopy stations and may have resulted in primates not being detected at canopy stations with limited sampling time.

Future Studies

Existing literature on the habitat associations of the Ecuadorian capuchins and Ecuadorian mantled howler are sparse and lacking in fine-scale resolution. Future studies should build upon the framework provided in this study and explore the potential impact tree height has on Ecuadorian howler occupancy, and whether these primates will travel in shorter trees or if tall trees are a necessity for travel. Further, the impact of distance to an artificial edge on Ecuadorian capuchins should be examined to potentially determine at what size a forest patch is uninhabitable for this primate. For this study, agriculture land use was synonymous with pastureland; however, I have observed Ecuadorian capuchins and Ecuadorian howlers utilizing land bordering agroforestry properties and I think it is necessary to further understand the extent to which primates will use these landcover types. Although I cannot be sure that these relationships conclusively exist, the large confidence intervals are likely due to small sample sizes and a larger study would be more telling. I would recommend implementation of these passive survey methods to further study the Ecuadorian capuchins, and further exploration into how weather patterns influence the detection probabilities of both species as we were limited by a lack of

consistent weather data. Further, I think it would be advantageous to explore the ability of close-to-ground-level AudioMoths to record Ecuadorian capuchin vocalizations. Given that Ecuadorian capuchins are known to descend to the ground (Guerrero et al. 2020; Albuja et al. 2018) and the cost-effectiveness of AudioMoths, this implementation could provide a means to allow for a simultaneous, coordinated monitoring effort of the Ecuadorian capuchins across its remaining range.

Conclusion

I would recommend that the TFCA should first prioritize acquiring land in the northeastern bounds of the corridor for expansion (Figure 4, 5). This area was a hotspot for both primate species, and it is likely that protecting this area would benefit both species. While I cannot provide any conclusive remarks about the habitat and spatial associations of either primate given the limited number of detections, there is potential to expand on the evidence of microlevel associations of these species. Further, this study has demonstrated that the use of canopy trail cameras and acoustic recorders is a viable survey method, although it may serve best in conjunction with visual encounter surveys.

V. TABLES AND FIGURES

Table 1: Length of data acquisition by AudioMoths (AM Rec.), trail cameras (Cam. Rec.), and Kestrels (Kestrel Rec.), as well as days not recording (NR) between January and October of 2020 by site throughout the TFCFA ($n = 20$). Length was recorded in days.

Site	AM Rec.	AM NR 2020	Cam. Rec.	Cam. NR 2020	Kestrel Rec.	Kestrel NR 2020
AG01	221	170	391	0	251	112
AG02	205	169	374	0	88	-
AG03	64	259	64	259	41	-
AG04	207	167	305	0	89	-
AG05	216	158	305	0	90	-
CF01	139	256	395	0	246	132
CF02	125	205	318	30	88	-
CF03	174	162	166	210	16	-
CF04	181	177	393	0	88	-
CF05	226	165	391	0	89	-
CF06	139	213	131	234	88	-
CF07	177	139	63	219	48	-
CF08	178	138	63	219	48	-
DF01	226	156	326	56	23	-
DF02	219	168	387	0	169	192
DF03	133	254	387	0	89	-
WF01	232	152	232	152	255	123
WF02	239	152	391	0	58	-
WF03	196	181	377	0	92	-
WF04	131	224	289	0	0	-

Table 2: Code used for observation-level and site-level covariates to build occupancy and local presence models for the Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) and Ecuadorian capuchin (*Cebus aequatorialis*) throughout the TFCA.

Covariate	Code
<i>Observation-level Covariates</i>	
High Daily Temperature (°C)	HighTemp
Daily Standard Deviation of Temperature	StDevTemp
Minimum Daily Relative Humidity (%)	LowRH
Daily Standard Deviation of Relative Humidity	StDevRH
<i>Site-level Covariates</i>	
Canopy Cover (%)	Canopy
Number of Trees Connected to Monitor Tree (count)	Conn
Vertical Cover (%)	Vert
DBH (cm)	DBH
Distance to River (km)	River
Distance to an Artificial Edge (km)	Edge
Distance to Human Dwellings (km)	Neighbor
Elevation (m.a.s.l.)	Elev
Height of the Canopy Station (m)	Height

Table 3: The minimum (Min.), maximum (Max.), mean, and standard deviation (SD) of the site-level covariates estimated to assess occupancy and local presence of Ecuadorian mantled howlers (*Alouatta palliata aequatorialis*) and Ecuadorian capuchins (*Cebus aequatorialis*) throughout the TFCA ($n = 20$).

Covariate	Min.	Max.	Mean	SD
Canopy (%)	43.23	94.01	70.59	15.57
Conn (count)	1.00	36.00	8.05	7.13
Vert (%)	8.71	61.20	32.51	14.43
DBH (cm)	33.00	145.00	81.42	35.63
River (km)	0.00	0.50	0.17	0.13
Edge (km)	0.11	1.15	0.49	0.32
Neighbor (km)	0.45	2.73	1.59	0.69
Elev (m)	130.00	642.00	395.25	152.28
Height (m)	4.40	29.50	17.02	7.13

Table 4: The most supported single species detection models for the Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) throughout the TFCA ($n = 19$) in the dry season (Oct - Nov), where Ψ indicates covariates influencing occupancy probability, p indicates covariates influencing detection probability, K is the number of parameters on the model, AIC is Akaike's Information Criterion, ΔAIC is the difference in reported AIC, and w_i is the AIC weight.

Models by Species	K	AIC	ΔAIC	w_i
<i>A. p. aequatorialis</i>				
$\Psi(\cdot), p(\text{LowRH}, \text{StDevTemp})$	4	171.92	0.00	0.39
$\Psi(\cdot), p(\text{LowRH})$	3	172.02	0.11	0.37
$\Psi(\cdot), p(\cdot)$	2	173.92	2.01	0.14
$\Psi(\cdot), p(\text{LowRH}, \text{HighTemp}, \text{StDevTemp}, \text{StDevRH})$	6	174.90	2.98	0.10

Table 5: The most supported single species detection models for the Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) and the Ecuadorian capuchin (*Cebus aequatorialis*) throughout the TFCA ($n = 20$) in the rainy season (Jan. – Mar.), where Ψ indicates covariates influencing occupancy probability, θ indicates local presence probability, p indicates covariates influencing detection probability, K is the number of parameters on the model, AIC is Akaike’s Information Criterion, ΔAIC is the difference in reported AIC, and w_i is the AIC weight.

Models by Species	K	AIC	ΔAIC	w_i
<i>A. p. aequatorialis</i>				
$\Psi(\cdot), p(\text{LowRH}, \text{HighTemp})$	4	452.72	0.00	0.47
$\Psi(\cdot), p(\text{HighTemp})$	3	453.03	0.33	0.40
$\Psi(\cdot), p(\text{LowRH}, \text{HighTemp}, \text{StDevTemp}, \text{StDevRH})$	6	455.51	2.79	0.12
$\Psi(\cdot), p(\cdot)$	2	461.55	8.83	0.01
<i>C. aequatorialis</i>				
$\theta(\cdot), p(\text{LowRH})$	3	100.05	0.00	0.67
$\theta(\cdot), p(\cdot)$	2	101.50	1.44	0.33

Table 6: The most supported single species models for the Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) and the Ecuadorian capuchin (*Cebus aequatorialis*) throughout the TFCA ($n = 20$), where Ψ indicates covariates influencing occupancy probability, θ indicates covariates influencing local presence probability, p indicates covariates influencing detection probability, K is the number of parameters on the model, AIC is Akaike's Information Criterion, ΔAIC is the difference in reported AIC, and w_i is the AIC weight.

Models by Species	K	AIC	ΔAIC	w_i
<i>A. p. aequatorialis</i>				
$\Psi(\text{Height}), p(\text{Height})$	4	684.00	0.00	0.98
$\Psi(\cdot), p(\cdot)$	2	739.20	55.62	<0.01
<i>C. aequatorialis</i>				
$\theta(\text{Edge}), p(\cdot)$	3	299.96	0.00	0.26
$\theta(\cdot), p(\cdot)$	2	300.54	0.58	0.20
$\theta(\text{Height}), p(\cdot)$	3	300.67	0.71	0.19
$\theta(\text{River, Edge}), p(\cdot)$	4	301.72	1.76	0.11
$\theta(\text{Height, Vert}), p(\cdot)$	4	302.02	2.06	0.09

Table 7: The most supported single species detection models for the Ecuadorian capuchin (*Cebus aequatorialis*) throughout the TFCA ($n = 20$), where Ψ indicates covariates influencing occupancy probability, θ indicates covariates influencing local presence probability, p indicates covariates influencing detection probability, K is the number of parameters on the model, AIC is Akaike’s Information Criterion, ΔAIC is the difference in reported AIC, and w_i is the AIC weight.

Models by Species	K	AIC	ΔAIC	w_i
<i>C. aequatorialis</i>				
$\theta(\cdot), p(\text{Height, River})$	4	291.74	0.00	0.42
$\theta(\cdot), p(\text{Height, Vert})$	4	293.30	1.56	0.19
$\theta(\cdot), p(\text{Height})$	3	293.31	1.57	0.17
$\theta(\cdot), p(\text{Height, Vert, Conn})$	5	293.45	1.74	0.17
$\theta(\cdot), p(\cdot)$	2	300.54	8.80	0.01

Table 8: The coefficient values (coeff.), standard errors (SE) and 95% lower and upper confidence interval (LCI and UCI, respectively) for the weekly binned data for the best single season models for the Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) and the Ecuadorian capuchin (*Cebus aequatorialis*) throughout the TFCA ($n = 20$).

Variables by Species	Coeff.	SE	LCI	UCI
<i>A. p. aequatorialis</i>				
Ψ (Intercept)	3.02	1.83	-0.56	6.60
Ψ (Height)	6.35	4.24	-1.95	14.65
p (Intercept)	-1.82	0.14	-2.09	-1.54
p (Height)	0.89	0.14	0.62	1.15
<i>C. aequatorialis</i>				
θ (Intercept)	0.22	0.54	-0.83	1.27
θ (Edge)	0.84	0.58	-0.29	1.97
p (Intercept)	-2.47	0.18	-2.81	-2.12

Table 9: The coefficient values (coeff.), standard errors (SE) and 95% lower and upper confidence interval (LCI and UCI, respectively) for the best detection model of the Ecuadorian capuchin (*Cebus aequatorialis*) throughout the TFCA ($n = 20$).

Variables by Species	Coeff.	SE	LCI	UCI
<i>C. aequatorialis</i>				
θ (Intercept)	0.92	0.75	-0.55	2.38
p (Intercept)	-3.14	0.28	-3.69	-2.59
p (Height)	0.78	0.24	0.32	1.28
p (River)	-0.75	0.32	-1.38	-0.12

Table 10: The coefficient values (coeff.), standard errors (SE) and 95% lower and upper confidence interval (LCI and UCI, respectively) for the best detection models in the rainy season (Jan – Mar) for the Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) and the Ecuadorian capuchin (*Cebus aequatorialis*) throughout the TFCA ($n = 20$).

Variables by Species	Coeff.	SE	LCI	UCI
<i>A. p. aequatorialis</i>				
Ψ (Intercept)	0.28	0.47	-0.63	1.19
p (Intercept)	-2.67	0.15	-2.95	-2.39
p (LowRH)	-0.23	0.15	-0.53	0.07
p (HighTemp)	-0.52	0.16	-0.83	-0.20
<i>C. aequatorialis</i>				
θ (Intercept)	7.77	36.9	-64.58	80.12
p (Intercept)	-5.37	0.45	-6.26	-4.48
p (LowRH)	0.71	0.41	-0.09	1.51

Table 11: The coefficient values (coeff.), standard errors (SE) and 95% lower and upper confidence interval (LCI and UCI, respectively) for the best detection models in the dry season (Oct – Nov) for the Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) throughout the TFCA ($n = 19$).

Variables by Species	Coeff.	SE	LCI	UCI
<i>A. p. aequatorialis</i>				
Ψ (Intercept)	-0.53	-0.98	-1.59	0.53
p (Intercept)	-2.56	0.28	-3.11	-1.99
p (LowRH)	0.73	0.37	<-0.01	1.46

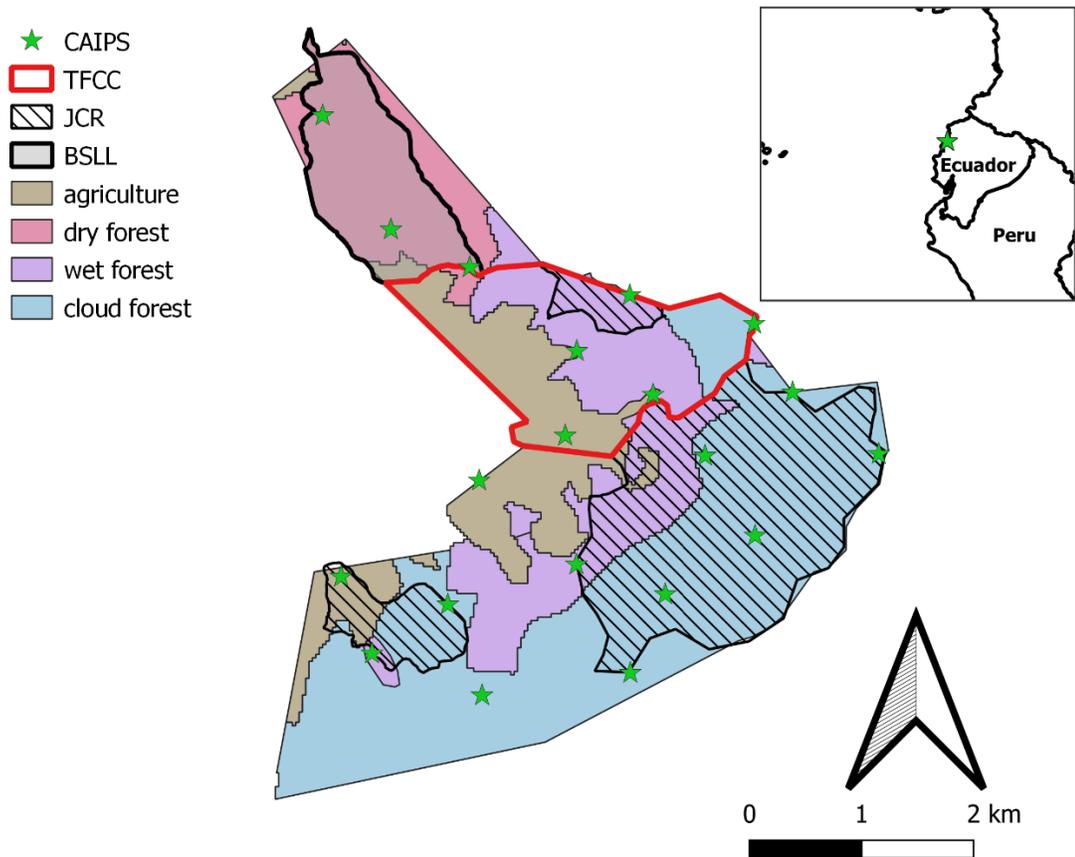


Figure 1: Map of the three forests conservation area. Each green star represents a canopy station in the corridor that was systematically generated. Colors represent different habitat types: light blue is cloud forest, light brown is agriculture, purple is wet forest, and pink is dry forest. The red outline indicates the boundaries of the TFCC and the property boundaries of the two reserves (BSLL and JCR) are outlined. The boundaries of the TFCA represent areas with access to place canopy stations. The green star in the inset maps displays the location of the TFCA within Ecuador.



Figure 2: Canopy station – the AudioMoth is positioned slightly under the tree to decrease chance of water buildup and in a weatherproof case that has a membrane to allow sound to pass and a silica packet in the event moisture enters. The camera is mounted on an arm and positioned so it will not interfere with wildlife movement and is facing the main branch. Not photographed is the kestrel.



Figure 3: Canopy station tree with large buttress roots. Dashed red line indicates where the DBH was measured.

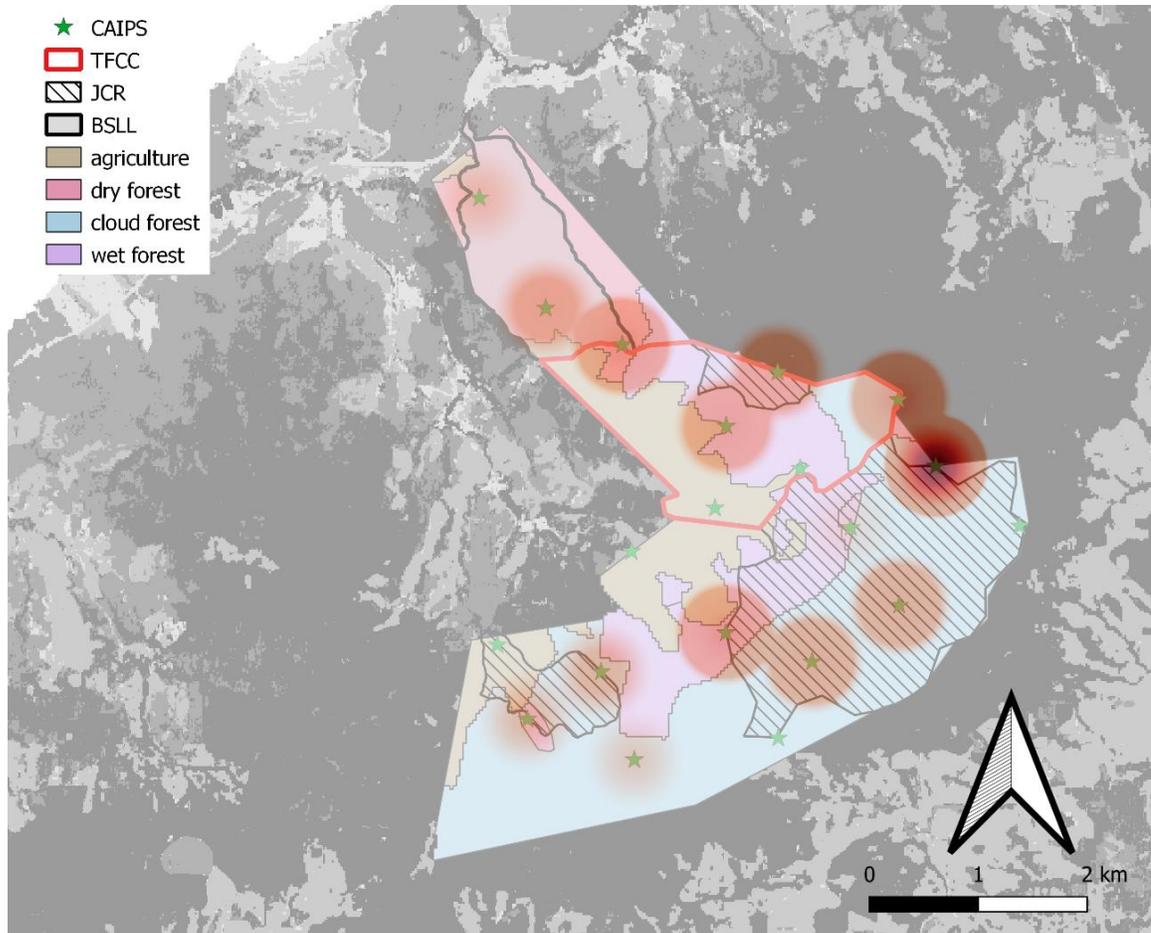


Figure 4: Heatmap of total Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) detections across the TFCA ($n = 20$) throughout the survey period. Darker red indicates a greater number of detections, whereas no shading indicates a lack of detections. The size of the heatmap shading was chosen for visibility. The green stars indicate the canopy stations, and the coloration within the outlined corridor indicates habitat type (blue = cloud forest, purple = wet forest, pink = dry forest, light brown = agriculture), the grey outlines indicate the protected properties (JCR and BSLL) and the red outline indicates the TFCC, while the light and dark shading outside of the colored corridor indicates fragmentation in the region (dark = tree cover, light = no tree cover).

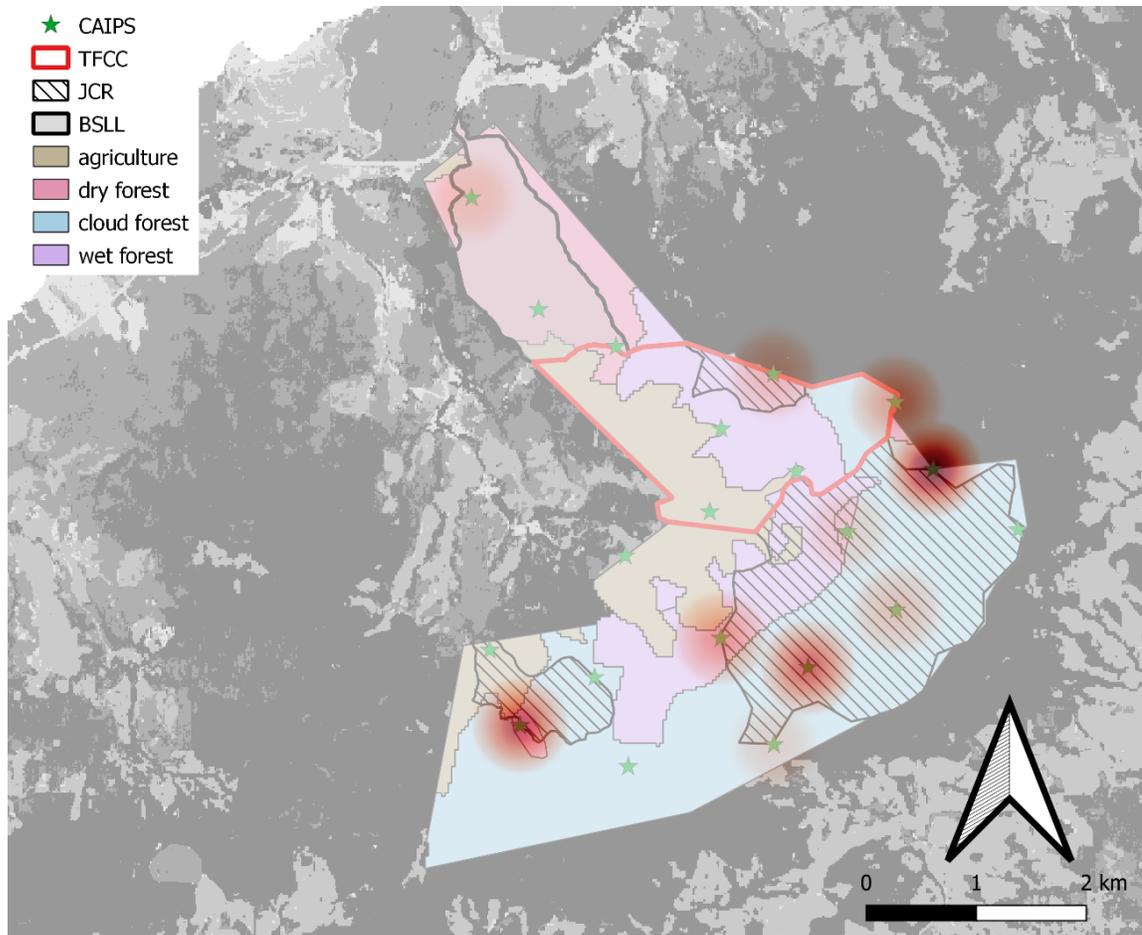


Figure 5: Heatmap of total Ecuadorian capuchin (*Cebus aequatorialis*) detections across the TFCA ($n = 20$) throughout the survey period. Darker red indicates a greater number of detections, whereas no shading indicates a lack of detections. The size of the heatmap shading was chosen for visibility. The green stars indicate the canopy stations, and the coloration within the outlined corridor indicates habitat type (blue = cloud forest, purple = wet forest, pink = dry forest, light brown = agriculture), the grey outlines indicate the protected properties (JCR and BSLL) and the red outline indicates the TFCC, while the light and dark shading outside of the colored corridor indicates fragmentation in the region (dark = tree cover, light = no tree cover).

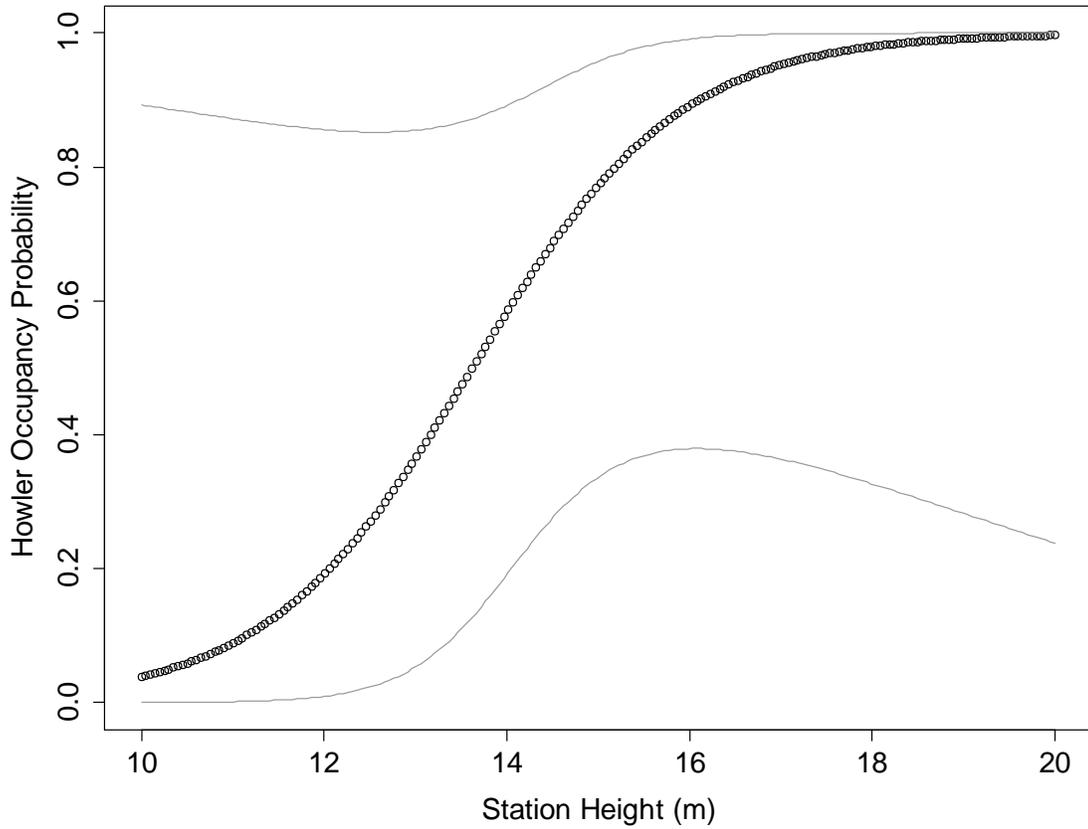


Figure 6: Occupancy probability of Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) across the TFCA ($n = 20$) based on canopy station height measured in meters, with 95% confidence envelope.

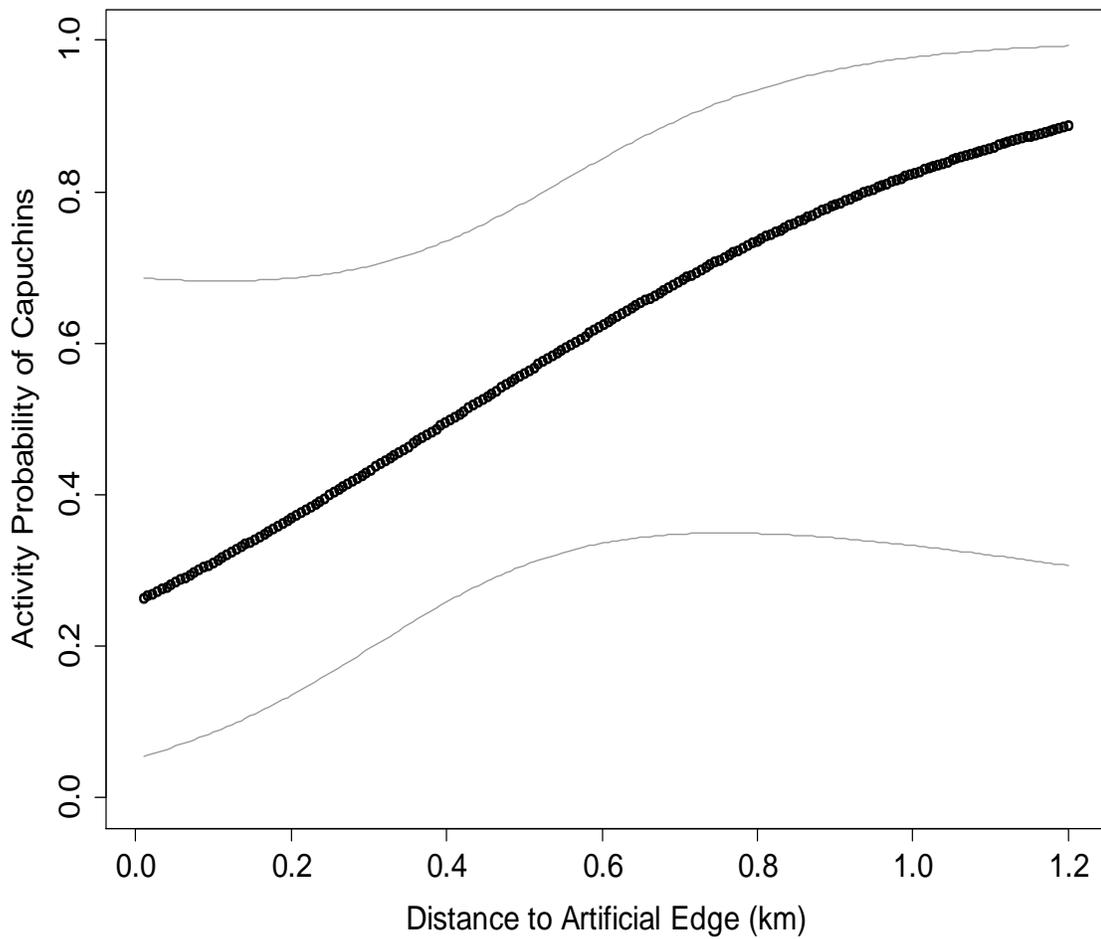


Figure 7: Local presence probability of Ecuadorian capuchin (*Cebus aequatorialis*) throughout the TFCA ($n = 20$) based on the distance to an artificial edge measured in kilometers with 95% confidence envelope.



Figure 8: Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) consuming the seedpod of *Inga edulis* at Jama-Coaque Reserve. Photo credit: Euan Ferguson

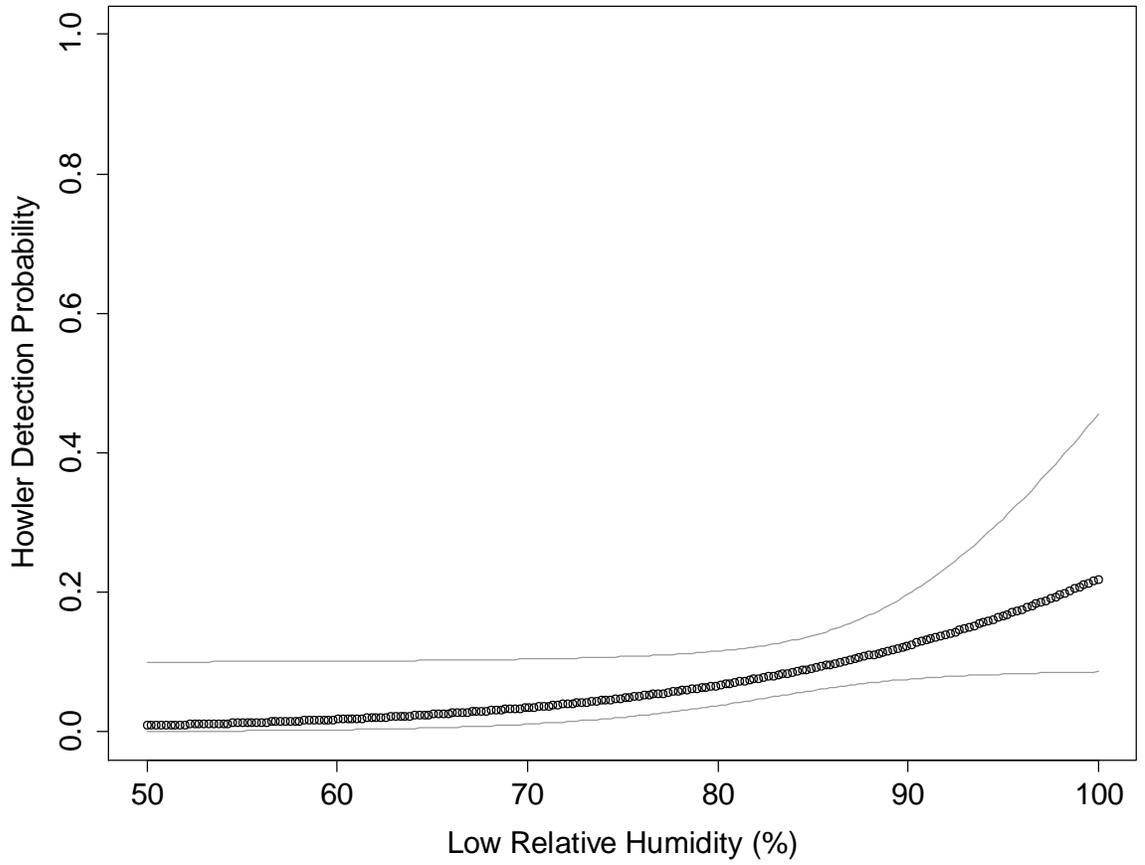


Figure 9: Detection probability of Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) across the TFCA ($n = 19$) during the dry season (Oct. – Nov.) based on the daily low relative humidity (%) with 95% confidence envelope.

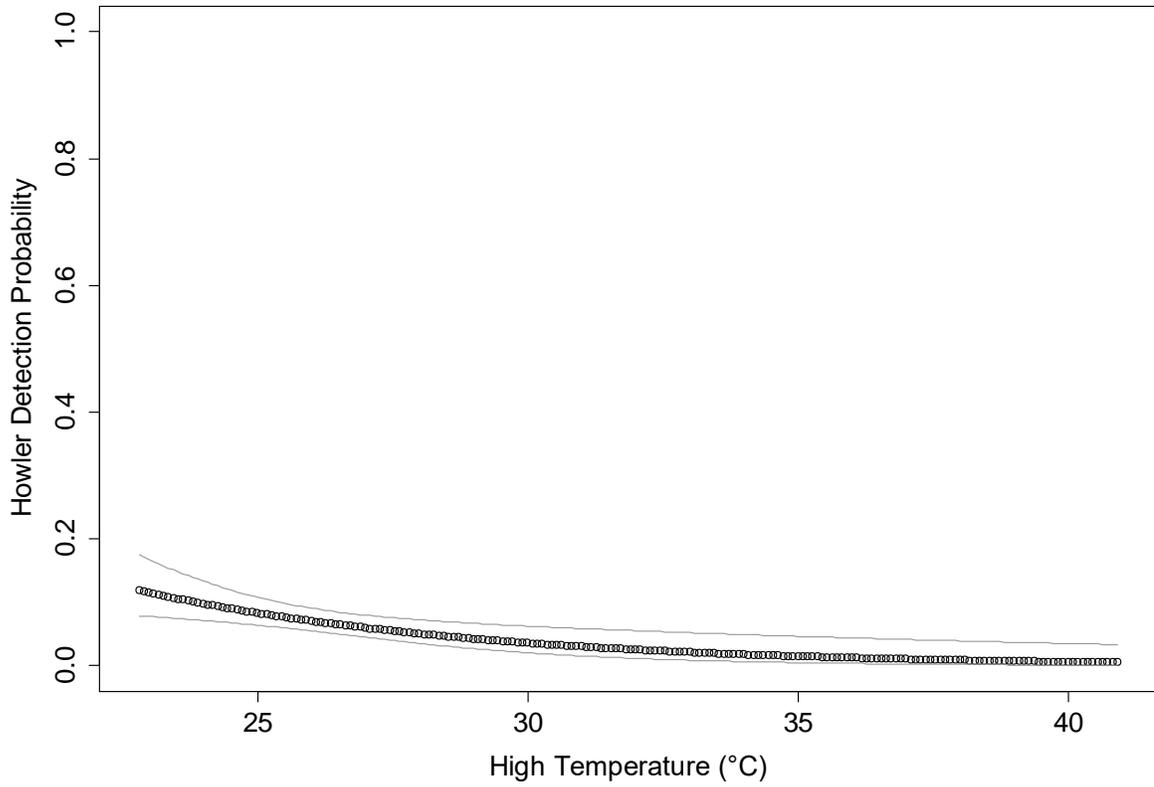


Figure 10: Detection probability of Ecuadorian mantled howler (*Alouatta palliata aequatorialis*) across the TFCA ($n = 20$) during the rainy season (Jan. – Mar.) based on the daily high temperature (°C) with 95% confidence envelope.

REFERENCES

- Albuja, M., P. Moreno, and M. Solorzano. 2018. Aspectos taxonómicos y ecológicos del capuchino ecuatoriano *Cebus albifrons aequatorialis* (Primates: Cebidae) en el Ecuador. Pages 411-426 in B. Urbani, M. Kowalewski, R. Cunha, et al., editors. La primatología en Latinoamérica. Ediciones IVIC. Instituto Venezolano de Investigaciones Científicas, Caracas.
- Albuja Viteri, L. H. and R. Arcos. 2007. Evaluación de las poblaciones de *Cebus albifrons cf. aequatorialis* en los bosques suroccidentales Ecuatorianos. *Politécnica Biología* 27:58-67.
- Aristizabal, J. F., L. Lévêque, C. A. Chapman, and J. C. Serio-Silva. 2018. Impacts of temperature on behaviour of the Mexican endangered black howler monkey *Alouatta pigra* Lawrence, 1933 (Primates: Atelidae) in a fragmented landscape. *Acta Zool Bugarica* 70:377-382.
- Arroyo-Rodríguez, V., and P. A. D. Dias. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. *American Journal of Primatology* 72:1–16.
- Arroyo-Rodríguez, V., and S. Mandujano. 2006. Forest fragmentation modifies habitat quality for *Alouatta palliata*. *International Journal of Primatology* 27:1079–1096.
- Bailey, L. L., D. I. MacKenzie, and J. D. Nichols. 2014. Advances and applications of occupancy models. *Methods in Ecology and Evolution* 5:1269-1279.
- Beier, P., and R. F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12:1241–1252.

- Bergman, T. J., L. Cortés-Ortiz, P. A. D. Dias, L. Ho, D. Adams, D. Canales-Espinosa, and D. M. Kitchen. 2016. Striking differences in the loud calls of howler monkey sister species (*Alouatta pigra* and *A. palliata*). *American Journal of Primatology* 78:755–766.
- Bicca-Marques, J. C. 2003. How do howler monkeys cope with habitat fragmentation? Pages 283-303 in L. Marsh, editor. *Primates in fragments*. Springer, Boston, MA.
- Butchart, S. H., M. Walpole, B. Collen, A. Van Strien, J. P. Scharlemann, R. E. Almond, J. E. M. Baillie, B. Bomhard, C. Brown, J. Bruno, et al. 2010. Global biodiversity: indicators of recent declines. *Science* 328:1164-1168.
- Campos, F. A., and K. M. Jack. 2013. A potential distribution model and conservation plan for the critically endangered Ecuadorian capuchin, *Cebus albifrons aequatorialis*. *International Journal of Primatology* 34:899-916.
- Caro, T., T. Jones, and T. R. Davenport. 2009. Realities of documenting wildlife corridors in tropical countries. *Biological Conservation* 142:2807-2811.
- Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. *Conservation Biology* 13:805-814.
- Cervera, L., D. J. Lizcano, D. G. Tirira, and G. Donati. 2015. Surveying two endangered primate species (*Alouatta palliata aequatorialis* and *Cebus aequatorialis*) in the Pacoche Marine and Coastal Wildlife Refuge, west Ecuador. *International Journal of Primatology* 36:933-947.

- Cervera, L., S. de la Torre, G. Zapata-Ríos, F. A. Cortés, S. Álvarez Solas, O. Crowe, R. Cueva, A. de la Torre, I. Dutch-Latorre, M. Fernanda-Solórzano, et al. 2018. Working together towards one goal: results of the first primate census in western Ecuador. *Primate Conservation* 32:1-8.
- Clare, J. D., E. M. Anderson, and D. M. Macfarland. 2015. Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. *The Journal of Wildlife Management* 79:469-480.
- Coley, P. D. (1980). Effects of leaf age and plant life history patterns on herbivory. *Nature* 284:545-546.
- Cove, M., R. M. Spínola, V. L. Jackson, J. C. Sáenz, and O. Chassot. 2013. Integrating occupancy modeling and camera-trap data to estimate medium and large mammal detection and richness in a Central American biological corridor. *Tropical Conservation Science* 6:781-795.
- Cristóbal-Azkarate, J., and V. Arroyo-Rodríguez. 2007. Diet and activity pattern of howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: effects of habitat fragmentation and implications for conservation. *American Journal of Primatology: Official Journal of the American Society of Primatologists* 69:1013-1029.
- Cuarón, A. D., A. Shedden, E. Rodríguez-Luna, P. C. de Grammont, and A. Link. 2008. *Alouatta palliata ssp. aequatorialis*. In IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <http://www.iucnredlist.org>.

- Dertien, J. S., P. F. Doherty Jr, C. F. Bagley, J. A. Haddix, A. R. Brinkman, and E. S. Neipert. (2017). Evaluating dall's sheep habitat use via camera traps. *The Journal of Wildlife Management* 81:1457-1467.
- Dodson, C. H., and A. H. Gentry. 1991. Biological extinction in western Ecuador. *Annals of the Missouri Botanical Garden* 78:273-295.
- Fedigan, L. M., L. M. Rose, and R. M. Avila. 1998. Growth of mantled howler groups in a regenerating Costa Rican dry forest. *International Journal of Primatology* 19: 405-432.
- Fiske, I., and R. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:1–23.
- Freire Filho, R., and J. M. Palmeirim. 2019. Potential distribution of and priority conservation areas for the Endangered Caatinga howler monkey *Alouatta ululata* in north-eastern Brazil. *Oryx* 54:794-802.
- Garstang, M. 2004. Long-distance, low-frequency elephant communication. *Journal of Comparative Physiology* 190:791-805.
- Goujon, A. 2019. Human population growth. *Encyclopedia of Ecology* 4:344-351.
- Gros-Louis, J. 2006. Acoustic analysis and contextual description of food-associated calls in white-faced capuchin monkeys (*Cebus capucinus*). *International Journal of Primatology* 27:273-294.
- Guerrero-Casado, J., R. I. Cedeño, J. C. Johnston, and M. S. Gunther. 2020. New records of the critically endangered Ecuadorian white-fronted capuchin (*Cebus aequatorialis*) detected by remote cameras. *Primates* 61:175-179.

- Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, et al. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342:850-853.
- Haro-Carrión, X., and J. Southworth. 2018. Understanding land cover change in a fragmented forest landscape in a biodiversity hotspot of coastal Ecuador. *Remote Sensing* 10:1-21
- Heywood, V. H., and R. T. Watson. 1995. Global biodiversity assessment. University Press for United Nations Environment Programme, Cambridge.
- Hilário, R. R., L. Jerusalinsky, S. Santos, R. Beltrão-Mendes, and S. F. Ferrari. 2017. A primate at risk in Northeast Brazil: local extinctions of Coimbra Filho's titi (*Callicebus coimbrai*). *Primates*, 58:343-352.
- IUCN. 2020. The IUCN Red List of Threatened Species. Version 2020. <https://www.iucnredlist.org>. Downloaded on 23 June 2020
- Jack, K. M., and F. A. Campos. 2012. Distribution, abundance, and spatial ecology of the critically endangered Ecuadorian capuchin (*Cebus albifrons aequatorialis*). *Tropical Conservation Science* 5:173-191.
- Johns, A. G. 1997. Timber production and biodiversity conservation in tropical rain forests. Cambridge University Press.
- Karunos, C., S. Barney, and M. Ellis. 2017. Habitat preference of two Ecuadorian primate species. Poster presented at Association of Tropical Biology.
- Kenney, J., F. W. Allendorf, C. McDougal, and J. L. Smith. 2014. How much gene flow is needed to avoid inbreeding depression in wild tiger populations? *Proceedings of the Royal Society B: Biological Sciences* 281:20133337.

- Kéry, M., G. Guillera-Arroita, and J. J. Lahoz-Monfort. 2013. Analysing and mapping species range dynamics using occupancy models. *Journal of Biogeography* 40:1463-1474.
- Kindlmann, P., and F. Burel. 2008. Connectivity measures: a review. *Landscape Ecology* 23:879-890.
- Lambert, J. E. 2011. Primate seed dispersers as umbrella species: a case study from Kibale National Park, Uganda, with implications for Afrotropical forest conservation. *American Journal of Primatology* 73: 9-24.
- Laurance, W. F., and R. O. Bierregaard. 1997. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago, Illinois.
- Laurance, S. G., and W. F. Laurance. 1999. Tropical wildlife corridors: use of linear rainforest remnants by arboreal mammals. *Biological Conservation* 91:231-239.
- Lenz, B. B., K. M. Jack, and W. R. Spironello. 2014. Edge effects in the primate community of the biological dynamics of forest fragments project, Amazonas, Brazil. *American Journal of Physical Anthropology* 155: 436-446.
- Lim, T. K. 2012. *Inga edulis*. Pages 715-719 in *Edible Medicinal and Non-Medicinal Plants*. Springer, Dordrecht.
- Lizcano, D. J., L. Cervera, S. Espinoza-Moreira, D. Poaquiza-Alava, V. Parés-Jiménez, and P. J. Ramírez-Barajas. 2015. Medium and large mammal richness from the marine and coastal wildlife refuge of Pacoche, Ecuador. *Therya* 7:135-145.

- Lovejoy, T. E., R. O. Bierregaard, A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown Jr., A. H. Powell, G. V. Powell, H. O. Schubart HO, et al. 1986. Edge and other effects of isolation on Amazon forest fragments.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, A. J. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248-2255.
- Merchant, N. D., K. M. Fristrup, M. P. Johnson, P. L. Tyack, M. J. Witt, P. Blondel, and S. E. Parks. 2015. Measuring acoustic habitats. *Methods in Ecology and Evolution* 6:257-265.
- McCann, C., K. Williams-Guillén, F. Koontz, A. A. R. Espinoza, J. C. M. Sánchez, and C. Koontz. 2003. Shade coffee plantations as wildlife refuge for mantled howler monkeys (*Alouatta palliata*) in Nicaragua. Pages 321-341 *in* *Primates in Fragments*. Springer, Boston, MA.
- Neam, K. D., and T. E. Lacher Jr. 2018. Multi-scale effects of habitat structure and landscape context on a vertebrate with limited dispersal ability (the brown-throated sloth, *Bradypus variegatus*). *Biotropica* 50: 684-693.
- Neville, M. K., K. E. Glander, F. Braza, and A. B. Rylands. 1988, The howling monkeys, genus *Alouatta*. Pages 349-453 *in* *Ecology and Behavior of Neotropical Primates*. R. A. Mittermeier, A. B. Rylands, A. F. Coimbra Filho, and G. A. B. Fonseca, editors. World Wildlife Fund, Washington, D.C.

- Papworth, S., and M. Mejia. 2015. Population density of Ecuadorian mantled howler monkeys (*Alouatta palliata aequatorialis*) in a tropical dry forest, with information on habitat selection, calling behavior and cluster sizes. *Studies on Neotropical Fauna and Environment* 50:65-72.
- Peterson, G. D., and M. Heemskerk. 2001. Deforestation and forest regeneration following small-scale gold mining in the Amazon: the case of Suriname. *Environmental Conservation* 28:117-126.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rich, L. N., D. A. Miller, H. S. Robinson, J. W. McNutt, and M. J. Kelly. 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. *Journal of Applied Ecology* 53:1225-1235.
- Ries, L., R. J. Fletcher Jr, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35:491-522.
- Schwitzer, C., R. A. Mittermeier, A. B. Rylands, F. Chiozza, E. A. Williamson, D. Byler, S. Wich, T. Humle, C. Johnson, H. Mynott, and G. McCabe. 2019. *Primates in Peril: The World's 25 Most Endangered Primates 2018–2020*. IUCN SSC Primate Specialist Group, International Primatological Society, Global Wildlife Conservation and Bristol Zoological Society, Washington, DC.

- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103-113.
- Smith, A., and G. Seyfang. 2013. Constructing grassroots innovations for sustainability. *Global Environmental Change* 23:827-829.
- Terborgh, J. 1992. Diversity and the tropical rain forest. *Scientific American Library*.
- Tirira, D. G. 2017. Guía de campo de los mamíferos del Ecuador. Murciélago Blanco, Quito
- Tirira, D. G. 2011. Red Book of the mammals of Ecuador (2nd Edition). Quito, Ecuador: Mammals and Conservation Foundation, Pontificia Universidad Católica del Ecuador and Ministry of Ambiente. Special Publication on the Mammals of Ecuador.
- Tobler, M. W., A. Z. Hartley, S. E. Carrillo-Percestequi, and G. V. N. Powell. 2015. Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *Journal of Applied Ecology* 52:413-421.
- Van Noordwijk, M. A., and C. P. Van Schaik. 1988. Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour* 105:77-98.
- Vera Barahona, J. 1993. Zonification y ecología del cultivo. Manual del cultivo de cacao, 2nd edition. Quevedo, Ecuador.
- Whitehead, J. M. 1989. The effect of the location of a simulated intruder on responses to long-distance vocalizations of mantled howling monkeys, *Alouatta palliata palliata*. *Behaviour* 108:73-103.

- Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. *Conservation Biology* 6:237-256.
- Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *The Journal of Ecology* 78:356-373.
- Yaap, E. A. 2018. Maintaining connectivity for tropical rainforest mammals in agricultural landscapes. Dissertation, James Cook University, North Queensland, Australia.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3-14.