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Billy Allen
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Demography and behavior of critically endangered *Alouatta coibensis trabeata* troops in forest fragments in and around Mata Oscura, Veraguas on the Azuero Peninsula of Panamá



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SIT Panama: Tropical Ecology, Marine Ecosystems, and
Biodiversity Conservation
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Abstract

The endemic Azuero howler monkey, *Alouatta coibensis trabeata*, was studied in three sites in and around the Mata Oscura community in Veraguas, Panamá in the western region of the Azuero Peninsula. *A. coibensis trabeata* is a critically endangered subspecies of *A. coibensis* that is threatened by continued habitat destruction and human encroachment throughout its entire distribution on the Azuero Peninsula. Sites included the Mata Oscura community (site 1), the Arenas community periphery (site 2), and the Cerro Hoya National Park (site 3). Demography, behavior, and habitat were assessed over 9 days of study in November. Troops were encountered in sites 1 and 2, but not in site 3. Troops had an average size of 9.43 individuals, with an average distribution of 4 females, 2.57 males, and 2.86 juveniles. The population density of the immediate study area was estimated at 0.15 individuals per hectare, which is fairly consistent with previous approximations of the subspecies' distribution. The majority of behaviors that were observed fell into the categories of either foraging or rearing young (or both). Adult females spent significantly more time interacting with juveniles than did adult males. Time spent foraging was consistent across the sexes within troops, but varied significantly across sites 1 and 2. Size of forest fragments also varied considerably between sites 1 and 2. Further research is needed into the habitat fragmentation that continues on the Azuero Peninsula and the inevitable impact it has on the demography, behavior, and population of *Alouatta coibensis trabeata*.

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Many thanks to the incredible Mata Oscura community who were so welcoming and helpful at every step. Thank you, Castro and Diego, for bringing me to the monkeys and sharing your wisdom along the way. Thank you Tomás and Jacinto for all of your logistical help and for directing me to my incredible guides.

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Introduction

The Azuero Peninsula

The Azuero Peninsula is located in southwest Panama on the Pacific coast and covers approximately 11,200 square kilometers. The peninsula is made up of regions in the Herrera, Los Santos, and Veraguas provinces. The region has been famously deforested for agricultural purposes, specifically cattle ranching. It is described as a fine-grained mosaic with small primary and secondary forest fragments interspersed between large areas of crops and cattle pasture (Mendez 2005). Abundant hunting, mining, crop spraying, teak plantations, and real estate development are also major contributors to wildlife threats. Historically, the Spanish developed the area as an agricultural production center for cattle primarily, but also rice, sugar cane, corn, and pineapple (Méndez 2013). Tourism is a major industry in the region, with beaches and multiple national parks including Coiba Island National Park, located off the Pacific coast of Veraguas.

The Mariato district makes up all of the land allocated to Veraguas in the western Azuero Peninsula. Within this district, the Mata Oscura community is located along the Rio Quebro in the greater Morrillo area. Vegetation in the area consists of secondary dry forest, live fences, and gallery forests, including mangroves. Average temperature in the region is 34°C, average rainfall is 1,400 millimeters annually, and elevation ranges from sea level to approximately 500 meters. Forest cover of the region was about 65% as of 2013 (Méndez 2013). Much of the area is dedicated to small scale cattle ranching and agriculture. However, several large privately-owned forest fragments still exist intermittently in and around the community. Much of the coast line in Mata Oscura is protected, although the immediate forested areas surrounding it are not, with the exception of a small patch of mangrove forest. At the edge of the beach are thin stretches of primarily black mangrove forest, much of the fringes of which have been converted to cattle ranching land as well. A single main road runs parallel to the coast approximately 1 kilometer inland, with nearly all of the mangrove forest residing between the road and the beach.

The Cerro Hoya National Park in the Veraguas and Los Santos provinces, is a protected area covering 32,557 hectares made up of primarily low montane forests on its higher peaks and humid tropical forests in more coastal areas. The park, along with the forest and mangrove fragments in and around the Mata Oscura community, are home to a population of the critically endangered Azuero howler monkey, *Alouatta coibensis trabeata*.

Genus *Alouatta*

The howler monkey is a subfamily of new world primates found in Central and South America. Currently 20 species and subspecies of the genus *Alouatta* have been identified with various distributions across Central and South America. All species of the genus *Alouatta* consist of large bodied folivore-frugivores. Two frequently studied species *Alouatta pigra*, found in southeastern Mexico, and *Alouatta palliata*, found further south in Central America, occupy evergreen broad-leafed forests, deciduous broad-leafed forests, mangroves, and swamps. *A. pigra* has been documented at elevations up to 3,350 meters, while *A. palliata* are found only below 2,000 meters (Baumgarten and Williamson 2007). The *Alouatta* genus as a whole has the widest range of habitats of any neotropical primate genus, ranging from sea level to 3,200 meters elevation. They occupy habitats from wet evergreen forests to seasonal deciduous and semi-deciduous forests, and some species occupy mangrove forests. These habitats are not limited by a need for proximity to a water source as *Alouatta* are able to absorb sufficient water from their diet (Crockett 1997).

Alouatta tree size preference can become problematic when populations live in fragmented forest habitats. Typically, *Alouatta* prefer to dwell in larger trees, with a DBH greater than 60 centimeters (Arroyo-Rodriguez et al. 2007). Fragmentation can alter vegetative structure and make a habitat suboptimal as vegetative structure strongly influences whether or not an area can be inhabited by *Alouatta*. A fragment is considered “small” when it is 10 hectares or less. These small fragments can be occupied by *Alouatta* troops; however, the living situation is not optimal (Arroyo-Rodriguez et al. 2007). For comparison, black howlers (*Alouatta pigra*) have been documented occupying home ranges as small as 1.21 hectares, but the average home range of *Alouatta palliata*, the species with the largest home range, is 28 hectares (Wyman et al. 2011). When the home range has a suboptimal size or vegetative structure, *Alouatta* practice landscape supplementation, where they leave the home range in search of resources. Common destinations of howlers practicing landscape supplementation are isolated trees, lives fences, and neighboring forest fragments (Asensio et al. 2009). Supplementation has only been documented in pursuit of fruits and flowers (but not leaves) as a food source, suggesting it is a method used for diet optimization (Asensio et al. 2009). This speaks to the importance of large forest fragments and fragments with high connectivity for *Alouatta* habitats.

Species of *Alouatta* eat primarily canopy leaves and fruits and are essential contributors to forest floral diversity through seed dispersal. These seed dispersal patterns differ across howler monkey species (Amato and Estrada 2010), and thus a wide range of howler monkey species could be indicative of a highly variable forest distribution. Generally, howlers consume some pioneer plant species, but rely more consistently on persistent forest species in their diets (Arroyo-Rodriguez et al. 2007). The foraging behavior of *Alouatta palliata* (the mantled howler monkey), the most commonly found howler in Panama, involves feeding on canopy leaves roughly 50% of the time while feeding on fruit only 28% of the time (Chapman 1988). The structure of *Alouatta* troops can sometimes be impacted by food patch size, with the size of the patch of fruit limiting the size of the feeding aggregate (Leighton and Leighton 1982). This is consistent with the tendency of *Alouatta* troops to split up for sometimes days at a time for foraging purposes (Chapman 1988). Due to this low-energy, leaf-heavy diet, *Alouatta* are fairly inactive throughout the day and typically travel little for foraging purposes. The exception to this occurs when particular fruits, specifically of the *Moraceae*, *Cecropiaceae*, *Combretaceae*, *Annonaceae*, *Anacardiaceae*, and *Burseraceae* families, are available (Arroyo-Rodriguez et al. 2007). Research has suggested that *Alouatta palliata* possess powerful spatial memories which they use to maximize the efficiency of their route and minimize energy consumption when foraging for faraway fruit (Hopkins et al. 2015).

Alouatta palliata travel in troops between 10 and 40 individuals where genetic relatedness between mature individuals is low. Group demography typically consists of 7-8 adult males and 16-18 adult females. Multiple infants and juveniles from multiple females are typically present as well (Chapman 1988). Mature monkeys are polygamous and practice bisexual dispersal, meaning both males and females leave their native troop for a new troop when they reach sexual maturity. Common social behaviors include grooming, embracing, biting, and slapping, although only a small portion of energy is allocated to social interaction. Howling is a common behavior in males, thought to be used to define the troop’s territory. Females and juveniles, while incapable of howling, often make softer grunting vocalizations (Milton et al. 2016).

Multi-male groups are less common in other *Alouatta* species than they are in *A. palliata*, however overcrowding in forest fragments seems to be making it a more common occurrence in

threatened species like *A. pigra* and *A. coibensis*. All *Alouatta* troops have a single alpha male. In multi-male *A. palliata* troops, however, there is no discernable hierarchy of adult males below the alpha. Interindividual aggression between adult males within a single group is documented but uncommon. In fact, males of a group often participate in cooperative howling when they come in contact with an outside group or individual (Wang and Milton 2003). This howling is thought to define territory and protect resources. Little is known about how the dynamics of multi-male groups in *A. palliata* relate to multi-male group dynamics in *Alouatta* species where its occurrence is uncommon.

Pressures and Conservation of *Alouatta*

Considering all species of *Alouatta* rely on tropical forest trees for both diet and habitat, it is important to evaluate the impacts human activities have on these species. Deforestation specifically can be devastating to *Alouatta* populations. Forest fragmentation can lead to anthropogenic edge effects where a species is impacted by its proximity to non-forested area. *Alouatta palliata* in forest fragments tend to show high adaptability and neutral edge effects, meaning their populations are minimally impacted by proximity to human-altered land. It has been proposed that this could be in part due to their preference for younger leaves, as they are typically more protein rich (Bolt 2018). A greater abundance of these types of growth in edge areas could be related to the observed neutral edge effects. Although, they found in this particular study no significant differences in tree density between the forest edge and interior. This same neutrality has been observed in other large bodied Central American primates like *Cebus capucinus* and *Ateles geoffroyi*, which is interesting given that negative edge effects are often found in large bodied mammals, specifically large bodied frugivores (Bolt 2018). This finding should not be misinterpreted as *Alouatta palliata* being impervious to large-scale deforestation.

Of the 20 observed *Alouatta* species and subspecies, 7 are considered threatened, meaning they have a conservation status of vulnerable, endangered, or critically endangered. While they are quite resilient to partial deforestation, total deforestation and flooding from dam building are major threats. Although *Alouatta* can often adapt to fragmentation, the increased hunting pressure from humans and dogs that correlates with fragmentation threatens populations. Despite this pressure, many species of *Alouatta* occupy forest patches in the immediate periphery of cattle ranching land (Crockett 1997). Although occupying a fragmented, but connected habitat is possible for *Alouatta* species; this inevitably will lead to pressures in terms of food, security, and health.

While anthropogenic proximity doesn't show negative edge effects in *Alouatta palliata* within the parameters of the research previously discussed, a relationship seems to exist between high exposure to human activity and botfly parasitism of howler monkeys. The botfly *Alouattomyia baeri* is a parasite that lays its larvae in the skin of the *Alouatta* genus. Individual instances of botfly parasitism seem to manifest in a commensalist relationship. Nevertheless, incidences of high botfly larval burden in individuals correlates with unusual mortality, suggesting that a high larval load can be detrimental to *Alouatta* health (Milton 1996). While botfly larvae don't seem to attack the body of *Alouatta* directly, the lesions they produce on the surface of the skin leave the monkey prone to secondary infection and screwworm fly infestation, which can be fatal. The higher incidence of botfly infection in *Alouatta* compared to other new world monkeys could be due to the comparatively low grooming rate of the genus (Crockett 1997). A fair amount of behaviors during resting time consist of slapping for

individual pest avoidance. Symptoms associated with high botfly larval load include fever, weight loss, organ damage, anemia, and death (Dudley and Milton 1990). Furthermore, *Alouatta* that reside in areas of high tourism tend to show significantly more botfly lesions per individual and more individuals with lesions per troop than do monkeys of the same species in lower impact areas (Treves and Carlson 2012). Therefore, while proximity to anthropogenic development and activity doesn't seem to affect *Alouatta* populations negatively in direct ways, it could have subtler, yet significant, consequences to their overall health.

While *Alouatta* populations cannot be supported in fully deforested areas, various species of monkey have been documented in regenerating tropical dry forests. Importantly, the density of any new world monkey population (howler monkeys, capuchins, spider monkeys) has been found to correlate strongly with the age of the forest inhabited (Sorensen and Fedigan 2000). Studies find that the return of *Alouatta palliata* to regenerating forests is limited in part by the monkey's preference for large trees, found more frequently in primary forest. In fact, the preference for high canopy environments seems to be considered by *Alouatta* alongside the availability of appropriate food sources (Bolt 2018). Despite this limitation, one particular study found that in a 28-year time period, a significant *Alouatta* population was able to be reestablished in a regenerating forest at a faster rate than that of *Cebus capucinus* (Fedigan and Jack 2001). This could perhaps be related to the relative flexibility of the *Alouatta* diet compared to that of *C. capucinus*. The bisexual dispersal pattern of *Alouatta* has also been proposed as a contributor to the genus's strong capacity for population recovery and ability to populate regenerating habitats. This is because genetic diversity can be introduced by both males and females as they enter a new troop. In a similar vein, human translocation of isolated or otherwise threatened *Alouatta* populations for the purpose of increasing gene flow or occupying suitable but unused habitats have been successful (Crockett 1997).

Much of the research surrounding the conservation of the black howler monkey, *Alouatta pigra*, focuses on the habitat loss they have faced and the ways they have succeed and failed in adapting to these losses. Their diet has been observed to be extremely flexible when preferred food sources are scarce. *A. pigra* is able to modify its consumption of fruit, young leaves, and older leaves to meet nutritional requirements of sugar, protein, and fiber (Behie and Pavelka 2012). This modification has been postulated to be responsible for some rather counterintuitive trends seen in *A. pigra* conservation in recent years. A study of a community primate reserve in Belize found that population density of *A. pigra* increased significantly from 1985 to 2004. Population was estimated at 1130 in 1985 and increased to approximately 5162 individuals, while population density increased from an estimated 31.9 individuals per square kilometer to 178 individuals per square kilometer. During this same time period, total forest cover of the area decreased significantly, while fragment connectivity increased marginally (Wyman et al. 2011). This suggests that perhaps forest cover is not as suitable a metric to predict *Alouatta* habitat security as is forest connectivity. With regards to the sizable increases seen in population density, there could be negative implications as well given that overcrowding has been linked to demographic changes including territory overlap and higher instances of socially unstable multi-male troops (Wyman et al. 2011).

Alouatta Coibensis – The Coiba and Azuero Howler Monkeys

The island of Coiba (Coiba National Park) just off the western coast of the Azuero Peninsula is completely uninhabited by humans and is home to its own endemic species of

howler monkey, *Alouatta coibensis* (Méndez 2012). *A. coibensis* was thought to be a subspecies of *A. palliata* (*Alouatta palliata coibensis*), however recent genetic analyses have concluded that *A. coibensis* is in fact a standalone species of the *Alouatta* genus (Méndez 2005). These genetic analyses along with theories of evolutionary divergence suggest that *A. coibensis* is more closely related to *A. palliata* than it is to any other howler species. Comparison of these evolutionary cousins could provide valuable insights as to where and how this divergence occurred, and what consequences it had. The *A. coibensis* population distribution is notably small compared to those of other *Alouatta* species, as they are confined to only the Azuero Peninsula and the island of Coiba. Despite a small distribution, *A. coibensis* occupy a wide range of forest types including mangrove forests. The population has been found to be most dense in the central and northern regions of Azuero, specifically the northern Herrera lowlands (Méndez 2013).

Closely related evolutionarily to the Coiba howler, *Alouatta coibensis coibensis*, is the subspecies *Alouatta coibensis trabeata*. Commonly known as the Azuero Howler Monkey, it is found only on the Azuero Peninsula. *Alouatta coibensis trabeata* has been named a critically endangered species primarily as a result of habitat destruction by humans. As of 2013, it was estimated that roughly 3,092 individuals remained of the entire subspecies (Méndez 2013). While research has gone into community-based conservation and regeneration practices on the Azuero Peninsula (Méndez et al. 2013), little has been studied on the impact of this large-scale deforestation on *Alouatta coibensis trabeata*'s behavior, health, and troop demographics. Hunting and deforestation are obvious dangers to the howler monkey and their habitats. However, human activities like feeding and general close contact could present threats to the monkey's behavior as well that are currently underestimated. Feeding from humans could impact the howler's diet and foraging strategies and consequently alter seed dispersal in the area, which the howler contributes to. Additionally, human encroachment in the territory of *Alouatta coibensis trabeata* could impact the animal's territorial and social behaviors. These alterations could have serious implications for the health of not only the *Alouatta coibensis trabeata* species, but also the health of the forest ecosystems they contribute to.

The purpose of this research is to evaluate the troop demography and behavioral patterns of *Alouatta coibensis trabeata* in forest fragments in and around the Mata Oscura community in the Veraguas province of the Azuero Peninsula. These data will be used to approximate the population density of the area. Comparisons will also be drawn to existing literature on these population and behavioral patterns in *Alouatta coibensis coibensis* and *Alouatta palliata*. This research was conducted with the goal of expanding the knowledge on how this critically endangered subspecies is managing in the face of the numerous anthropogenic pressures it faces.

Research Question

What are the troop demography and behavioral patterns of *Alouatta coibensis trabeata* in forest fragments on the Azuero Peninsula, and how do these compare to existing data on *Alouatta coibensis coibensis* of Coiba Island, and other howler monkey species?

Methods

Study Sites

Nine days of data collection were completed across three different sites in the greater Morrillo area. Each day consisted of data collection from approximately 6am-12am, when *Alouatta* are most active (Méndez 2013). Standardized transects were not utilized as it was expected that *Alouatta coibensis trabeata* would be scarce. Rather, opportunistic walking and

following the sound of vocalizations heard was used to maximize the chance of encounters (Méndez 2005). The smell of feces and presence of chewed leaves on the forest floor were also used to locate troops.

Six of the nine days of data collection were spent in the Mata Oscura community (site 1). The area was immediately off the coast of the Pacific Ocean in a small bay and was transected by a single main road that ran parallel to the coastline. The inland side of the road consisted primarily of cattle pasture on steeply sloped hills with small intermittent secondary forest fragments. Houses were few and far between, and real estate development was fairly minimal with the exception of a collection of 15 houses built for tourist use. The coastal side of the road tended to have a greater density of houses but less cattle pasture, as much of the forested area was mangrove.

Two days of data collection were spent at a site about 5 kilometers south of Mata Oscura near the community of Arenas (site 2). This site was notably less developed, both in terms of cattle pasture and real estate. Fragments were a blend of forest and mangrove as no point in the site was ever more than 1 kilometer from the coast. The site was also considerably less hilly than site A.

One day of data collection was spent in the forested mountains of Cerro Hoya National Park (Site 3). The site was approximately 24 kilometers south from the Mata Oscura community. The park was accessed through a series of small farms, however the site itself was protected and fully undeveloped. The trail used appeared to be accessed very infrequently as there was lots of growth in the path. The entirety of the trail followed a very steep elevation gain.

Demographic Observation

Upon finding a troop of *Alouatta coibensis trabeata*, the time and GPS waypoint were recorded. A viewfinder was used to record the approximate height in the canopy at which the troop was located. If individuals were at very different heights, multiple heights were recorded and averaged. A densiometer was used to calculate the percent cover underneath where the population was most dense. After assessing the entire troop, a rapid observation of each individual in the troop was performed. Sex was determined by the presence of testicles in males or vulva in females. Relative age was determined by body size, with individuals being classified as either juvenile or adult (Mendez 2012). Botfly lesions, when visible from a distance, were counted on each individual (Treves and Carlson 2012). Finally, trees that were densely populated by *Alouatta coibensis trabeata* were identified using a dichotomous key and a guide.

Behavioral Observation

After demographic observation of the entire troop was completed, each individual was observed for exactly 10 minutes. In this time, the amount of time allotted to foraging, social behaviors, or any other activity was distinguished. The food consumed was identified as was possible. Socializing behaviors were described in detail and categorized according to the executor and the recipient (Wang and Milton 2003). Sex of the recipient of the behavior was noted. Vocalizations made in the observation period were also noted. Behavioral assessment was only completed for individuals that were fully visible. Some assessments were also incomplete as individuals moved out of site during observation. After 10 minutes of observation was completed for each visible individual the troop was left to search for others.

Data Analysis

Aspects of troop demography were averaged using the entire data set. Averages of demographic percentages and ratios per troop were used to statistically analyze differences across sites using t-tests. Linear regressions were also used to determine if any relationships existed between demographic assays.

Behavioral data was analyzed and compared both across sexes and across sites. T-tests were used to evaluate the statistical significance of differences observed in foraging behavior, interactions with juveniles, and vocalizations.

Garmin GPS data and the BaseCamp software were used to approximate the areas of forest fragments. The software was also used to measure the distance from the road at which each troop was found. Fragment data were used to draw comparisons across sites 1 and 2. The relationship between distance from road and various demographic variables was assessed using linear regressions and t-tests.

Ethics

This study was conducted with the understanding that *Alouatta coibensis trabeata* is a critically endangered species. I never called at or antagonized the animals and certainly did not feed or touch them. Throughout data collection I was conscious to leave as minimal impact as possible on the study site.

Results

Data was collected over nine days across three sites. Each site was walked from approximately 6am-12am. Site 1, the Mata Oscura community, was walked 6 days in total. Site 2, the Arenas community exterior, was walked 2 days (Figure 1). Site 3, Cerro Hoya National Park, was walked one day. In total, 66 *Alouatta coibensis trabeata* individuals were observed across 7 troops and 1 individual was seen in isolation. Four troops totaling in 34 individuals were observed in site 1. One troop of 7 individuals was observed twice on separate days in separate areas of site 1. Three troops totaling in 32 individuals were observed in site 2, as well as the lone individual. No *A. coibensis trabeata* were observed in site 3, although, howling was heard from what was presumed to be a single, multi-male troop.

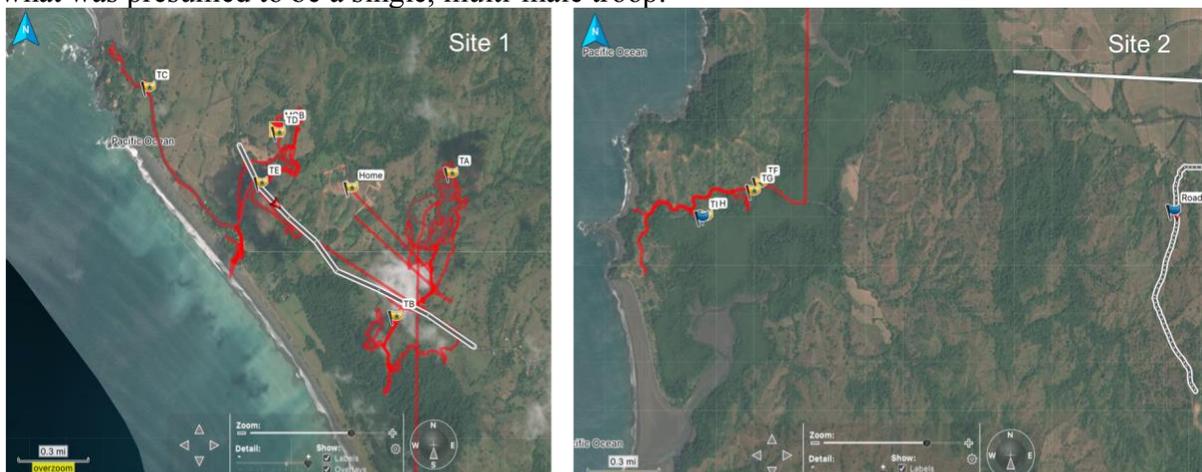


Figure 1. Birdseye™ Imagery from the Garmin GPS of data collection sites 1 and 2. GPS data on site 3 was not available. The main road is marked by grey lines. Trails walked are marked in red and waypoints where troops were encountered are marked with flags.

Demographics

Each troop of *Alouatta coibensis trabeata* encountered consisted of at least one adult male, three adult females, and two juveniles. Sex of adults was determined by the presence of testes or vulva; however, identification of juveniles was unsuccessful due to a lack of secondary sex characteristics. Average troop size was 8.2 individuals in site 1 and 10.67 in site 2 (the lone individual was not considered a troop and was excluded from statistical analyses of troops). The overall average troop size was 9.43 individuals. The range of troop sizes observed was 6 individuals to 14. The average troop consisted of 4 females, 2.57 males, and 2.86 juveniles. Averages were also calculated for the percentage of individuals in a troop who were adult males, adult females, and juveniles, as well as the ratio of adult males to adult females and juveniles to adults (Table 1). Two sample t-tests assuming unequal variances were run to determine if statistically significant differences existed in any of these demographic assays across sites 1 and 2. None showed any significant difference, although, the two assays closest to significance were percentage of males and troop size, both with one-tailed p-values of 0.18. The average troop had a demographic breakdown of approximately 24.9% adult males, 41.4% adult females, and 31.5% juveniles (Figure 2).

Table 1. Troop demographic averages across sites and for the entire data set

	Avg. Troop Size	Avg. %Adult Males	Avg. %Adult Females	Avg. %Juveniles	Avg. Adult M:F	Avg. Juv:Adult
Site 1	8.2	25.4	41	33.2	0.652	0.563
Site 2	10.67	25.3	42.7	32.3	0.61	0.477
Site 3	NA	NA	NA	NA	NA	NA
Total	9.43	24.9	41.4	31.5	0.593	0.488

The full range of adult male to adult female ratios observed was large with a standard deviation of 0.22. Little correlation was found between percent adult females and percent juveniles per troop ($R^2=0.1366$), although a slight negative correlation was found between percent adult males and percent juveniles ($R^2=0.4972$) (Figure 3).

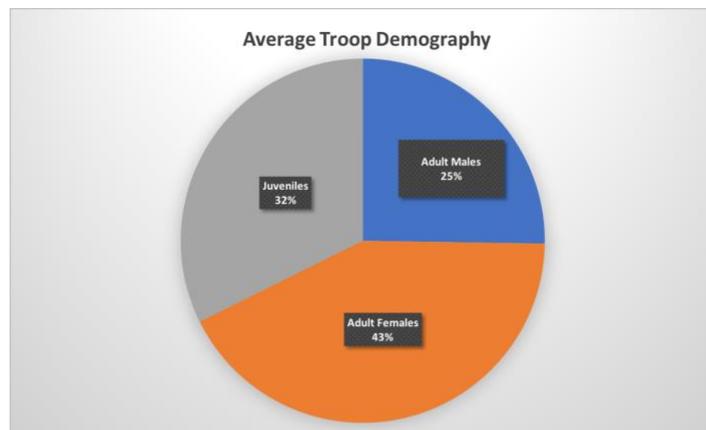


Figure 2. Average sex and age distribution across all troops. Juveniles are presumed to be both males and females.

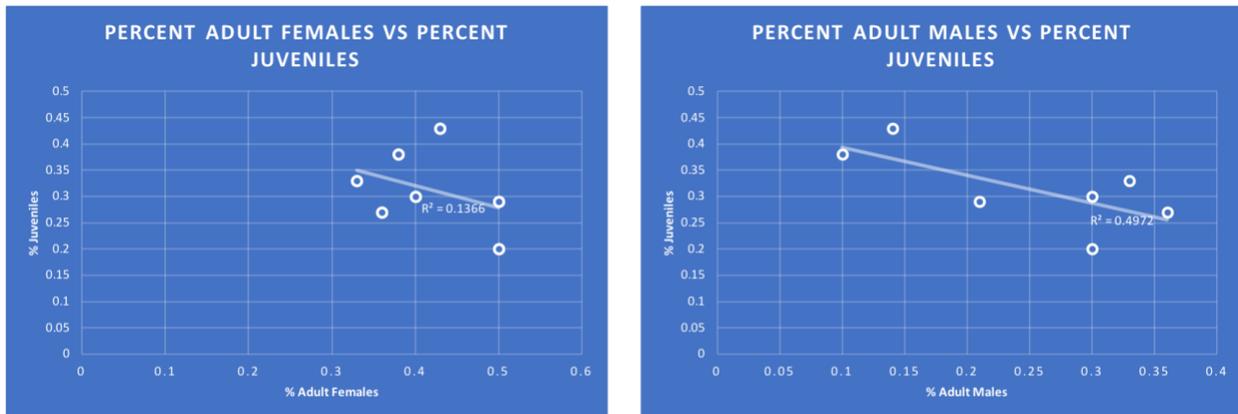


Figure 3. Linear regressions of percent adult females (A) or percent adult males (B) versus percent juveniles for all troops. $R^2 = 0.1366$ (A), 0.4972 (B).

Analyses of botfly lesion occurrence were not carried out at the troop level because visibility was not sufficient to fully assess each individual. Fourteen individuals were identified as having botfly lesions. Of the individuals that had lesions, the average number of lesions was 1.43. Notably more females had lesions (9) than did males (5), however there were a far greater number of females observed. No one troop had a considerably different number of individuals with lesions.

Approximately 393.7 hectares were covered in site 1, where 34 individuals were found. With this, the low approximation of the population density of *Alouatta coibensis trabeata* in site 1 is 0.0864 individuals per hectare. Approximately 49.21 hectares were covered in site 2, where 33 individuals were found. The low approximation of the population density of *Alouatta coibensis trabeata* in site 2 is 0.67 individuals per hectare. The total population density estimate across the two sites is 0.15 individuals per hectare. There is not sufficient data to make an informed high approximation of the population density at either site.

Behavior

The only behavioral assay found to have a significant difference across the sexes was time spent interacting with juveniles. Analysis of the time spent interacting (defined as being in direct contact with or directly engaging with at a close distance) with juveniles within the 10-minute individual observation period of each adult was carried out. On average, adult females spent 2.62 minutes of 10 minutes interacting with juveniles while adult males spent an average of 0.875 minutes with juveniles. Notably, only a single male spent any time interacting with juveniles, so this average is skewed. A two-sample t-test assuming equal variance for the average time spent with juveniles in each troop across the sexes (Figure 4) produced significant results (one tail $p=0.005$). Common interactions included playful pushing and slapping, carrying the juvenile on the back, embracing from the front, and grooming. Juveniles would often follow adults that they interacted with, especially when the adult was foraging.

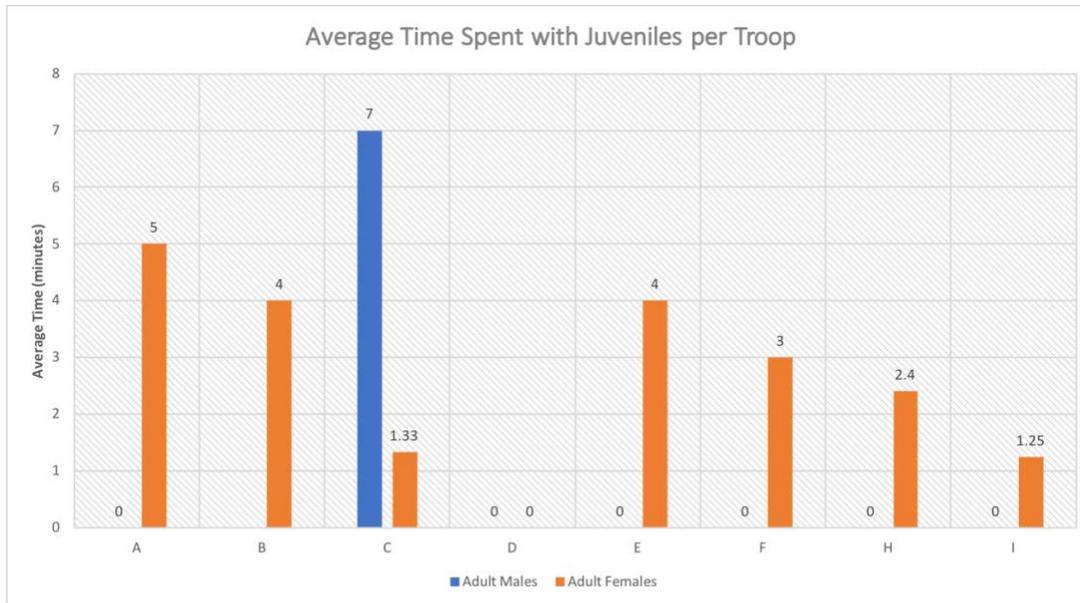


Figure 4. Average time spent interacting with juveniles in a ten minute period in adult males and females across each troop. Two-sample one-tailed t-test assuming equal variance, $p=0.005$ ($p<0.05$).

Foraging behavior was generally similar across males, females, and juveniles. Typically, individuals were observed eating leaves, although it was often difficult to distinguish what exactly was being eaten, only that something was in fact being eaten. Trees that were frequently identified as a food source include fig trees of the *Moraceae* family and the guayacan tree, *Tabebuia chrysantha*. Average time spent foraging across all individuals was 0.95 minutes per 10-minute period. Average time spent foraging in site 1 was 1.24 minutes, while the average in site 2 was 0.36 minutes. Analysis of the average time spent foraging for each troop across sites 1 and 2 revealed a statistically significant difference between the sites with a one-tailed p -value $p=0.008$ (Figure 5).

Little social behavior was observed aside from the interactions between females and juveniles and the instance of a single male interacting with two juveniles. Almost no clear social interactions were observed between adult males and adult females or adult females and other adult females. One behavior that was observed that seemed to have a social aspect was cooperative howling between males. Of the 6 multi-male groups observed, 3 exhibited cooperative howling, where the howling of one male almost immediately led to the howling of all other males. Of the 3 multi-male troops that did not exhibit cooperative howling, 2 did not exhibit any howling. One male in a multi-male troop howled approximately every 15 seconds for 2 minutes. This did not initiate any howling in the other male in the troop.

Average Time Spent Foraging in Ten Minute Periods per Troop Across Sites

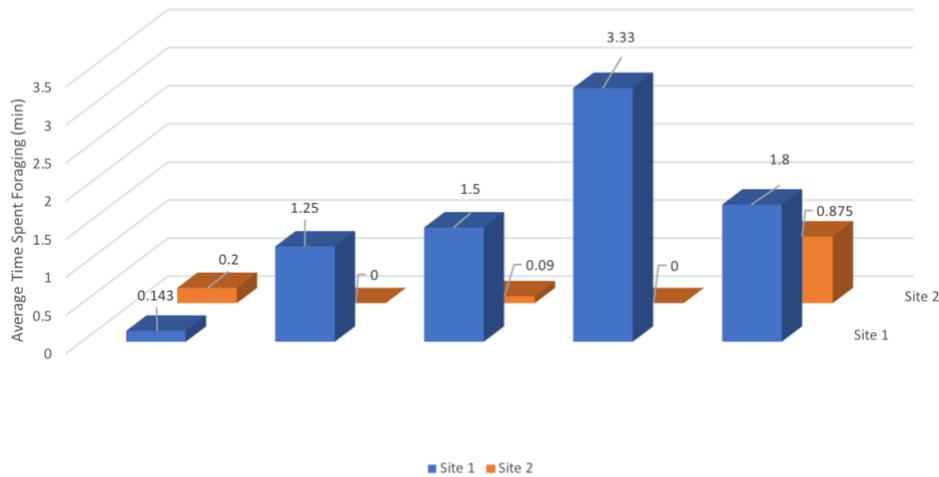


Figure 5. Average time spent foraging in minutes in ten minute periods in each troop across sites 1 (blue) and 2 (orange). Two sample one-tailed t-test assuming equal variance, $p=0.008$ ($p<0.05$).

Habitat

Alouatta coibensis trabeata troops were found as close as 10 meters to the main road and as far as 3701.5 meters from it. Distance from road correlated weakly with troop size ($R^2=0.2941$), although a t-test comparison of troop sizes that were found less than 1000 meters from the road versus greater than 1000 meters from the road did not produce significant results ($p=0.07$). Troops were found at elevations ranging from 8 meters to 107 meters above sea-level. Other habitat parameters compared across sites include percent cover and height of troop, both of which did not show significant differences.

Statistical analysis of fragment sizes was not possible as troops in site 2 were all found in a single large forest fragment. The site 2 fragment was approximately 235.7 hectares, while fragments where troops were found in site 1 ranged from 0.5-10 hectares. All troops were found in terrestrial trees, although 3 troops were found at the fringe of a mangrove and terrestrial forest.

Discussion

Demographic trends in western Azuero, Coiba Island, and the entire Azuero Peninsula

More *Alouatta coibensis trabeata* individuals were encountered than expected, given the estimations that approximately 3,092 individuals remain of the subspecies on the entire Azuero Peninsula (Méndez 2013).

Trends in group demography were fairly consistent with the limited existing literature on *A. coibensis trabeata* populations. Average troop size in this study was 9.43. This is comparable with the average of 9.6 individuals per troop across the entire Azuero Peninsula. The same study that calculated this overall average, however, also found that troop size varied regionally within the peninsula. Average troop size in western Azuero specifically was 12.2 (Méndez 2013). The 2.77 individual difference in the troop average found in this study of western Azuero could be

due to this study's relatively small sample size. Additionally, the average of 12.2 individuals per troop was calculated for the entirety of western Azuero while this study only surveyed a small portion of this region. Perhaps average troop size in *A. coibensis trabeata* varies more finely within regions than has been previously suggested in the literature. This is conceivable considering how variable forest cover and connectivity is within the region. Across the two sites of this study alone, average fragment area where howlers were found ranged from 3.33 hectares in site 1 to 235.7 hectares in site 2, which was only 5 kilometers away. This could impact variability in troop size considering average troop size has been positively correlated to habitat size in Azuero (Méndez 2013). The similarity of this study's average troop size with the overall average found for the peninsula suggests that the difference in forest structure across sites 1 and 2 could have accounted in part for the variation seen across the greater region.

Estimations of population density were similarly comparable to literature values. Population density was calculated by dividing the number of individuals encountered by the area covered (calculated in BaseCamp using Garmin GPS data). The population density value was considered a "low" estimation because it assumed that the individuals encountered were the only *A. coibensis trabeata* in the area covered. There was not sufficient data or background to make a "high" estimation of population density. The overall population density across sites 1 and 2 of 0.15 individuals per hectare was similar to a population density estimation of 0.17 individuals per hectare for the western region of the Azuero Peninsula (Méndez 2013). The slightly lower estimation of this study could be related to the fact that only low estimations were calculated. Notable also is the variation seen in population density across sites 1 and 2. Site 2 had a population density of 0.67 individuals per hectare, almost 8 times as dense as site 1's 0.0864 individual per hectare. This sizeable difference could be related to the notably larger forest fragments in site 2 compared to site 1. It is logical to suggest that a fully intact fragment of 235.7 hectares has a greater carrying capacity for a denser *A. coibensis trabeata* population than a fragment of 10 hectares, even if that fragment is well connected to other fragments. The population density of site 1 (0.0864 individuals per hectare) is similar to the population density of the entire peninsula of 0.05 individuals per hectare (Méndez 2013), which could suggest that site 1 is more representative of the forest conditions and *A. coibensis trabeata* populations of the entire peninsula than is site 2.

An important demographic assay to the status of *A. coibensis trabeata* as a species is the ratio of adults to juveniles in a troop. This study found the average troop to consist of 24.9% adult males, 41.4% adult females, and 31.5% juveniles. This translates to approximately 2.57 males, 4 females, and 2.86 juveniles per troop. This corresponds somewhat to Méndez's findings of troops across the Azuero Peninsula averaging 2.5 males, 4.3 females, and 3.8 juveniles per troop (Méndez 2013). The disparity among juvenile populations in this study could be telling of the status of population growth of *A. coibensis trabeata* in the area of study. Across the *Alouatta* genus, somewhat intuitively, higher birth rates correlate strongly with higher population growth rates. Additionally, female to infant ratio correlates strongly with population growth in *Alouatta*, however juveniles were not distinguished from infants in this study, so that metric was unable to be calculated (Crockett 1997). Still, this correlation is interesting when considered alongside the stronger correlation seen between percent adult males and percent juveniles than was seen between percent adult females and percent juveniles (Figure 3). The generally lower incidence of juveniles in the troop, however, could be indicative of a habitat that is unsuitable for significant population growth. If the case, this could have major implications for the conservation of this critically endangered subspecies, especially considering population estimates dropped from

4,214 in 2008 to 3,092 in 2013 (Méndez 2013). Importantly, the average distribution of site 2 alone is 2.66 males, 4.33 females, and 3.33 juveniles, values far more similar to those found across the full population distribution in the Méndez study. The ratio of females to juveniles is also far higher in this case than it was across sites 1 and 2, suggesting that site 2 may have a greater capacity for population growth than does site 1. It is possible that this proposed greater capacity for population growth is a consequence of the larger forest fragments found in site 2. In opposition to what was found regarding population density, site 2 seems to be more representative of the entire *A. coibensis trabeata* population demography than is site 1.

Despite technically being the same species, *Alouatta coibensis trabeata* (the Azuero howler monkey) and *Alouatta coibensis coibensis* (the Coiba howler monkey) have notably different troop demography. *A. coibensis coibensis* has a 4.3 individual per troop average, which is about half the average troop size found in this study (9.43 individuals per troop). The variation in troop size is likely not due to insufficient habitat area, as the population density of *A. coibensis coibensis* on Coiba is 0.0008 individuals per hectare, which is far less than the density of *A. coibensis trabeata* found in this study of 0.15 individuals per hectare (Méndez 2012). Some other factor either in the biology of *A. coibensis coibensis*, or in the habitat of Coiba, must be influencing this dramatic difference in demography. More research is needed in order to understand this dissonance.

Behavior – rearing, communicating, and foraging

Minimal social interactions were observed between adults with the exception of cooperative howling among males. This is fairly consistent with existing literature on the energy budget of the adult *Alouatta palliata*, who tends to spend less than 2% of its daily activity on direct social interactions with other adults (Milton et al. 2016). Aggression between adult males in multi-male troops is well documented in *Alouatta palliata*, however, none such behaviors were observed in any of the *A. coibensis trabeata* encountered. Cooperative howling, however, was a common male-male social interaction. In *Alouatta palliata*, the cooperative howl is most often observed during intergroup interactions, when territory or food sources are being defined or perhaps disputed (Wang and Milton 2003). Somewhat contrastingly, none of the three instances of cooperative howling observed in the *A. coibensis trabeata* troops were followed by any audible response from a distant troop. This could suggest that the cooperative howl serves a different function in *A. coibensis trabeata*, perhaps of simple intragroup communication between males. It is also possible that what was thought to be cooperative howling was in fact not, or that the out-group that was being howled at was not in fact another howler troop but me, a strange encroaching primate.

By far the most commonly observed behaviors were parenting behaviors. The significant difference in time spent interacting with juveniles across adult males and females, with females spending significantly more time, follows previous understanding of parenting tendencies in non-monogamous primates. *Alouatta palliata* are raised almost exclusively by their mothers, who typically nurse them up to 22 months and stay with them up to three years (Cancelliere 2012). Some variation does occur across the *Alouatta* genus, though, as male *Alouatta pigra* have been documented playing parental roles (Bolin 1981). Little research exists currently on the rearing strategies of *Alouatta coibensis*, however the data from this study suggests that child rearing is primarily maternal. Seven out of eight troops showed some form of adult female interaction with a juvenile whether through direct contact such as grooming or embracing, or indirect interaction such as shared foraging. The data could also suggest that paternal behaviors in male *Alouatta*

coibensis trabeata do occur, albeit infrequently, however considering only a single instance of a male interacting with juveniles was observed, further study would be needed to fully reach this conclusion.

Time spent foraging varied within sites and varied significantly between sites. Sufficient research does not exist, both in this study and in the literature, to paint of full picture of the typical energy budgeting that goes into foraging in *Alouatta coibensis trabeata*. Research has been conducted, however, on the foraging patterns of *Alouatta palliata*, who on average spend 4.57% of their daily activity budget on foraging (Hopkins 2015). This statistic was found in both males and females, which is consistent with the lack of significant difference found in the foraging patterns of male and female *A. coibensis trabeata*. The significant difference observed in time spent foraging across sites 1 and 2 can be interpreted in a multitude of ways. It could be argued that less foraging was seen in site 2 because less food was available, however this seems unlikely since the vegetative structures of the two sites were not notably different and the forest fragment in site 2 was considerably larger than all fragments found in site 1. Given this, the exact opposite could be argued, that less foraging was observed in site 2 because food was *more* abundant. It is also very possible that not enough observation time was logged to get a truly representative idea of the foraging time of *Alouatta coibensis trabeata*, and for that reason alone statistically significant differences were seen.

An important note on the behavioral data of this study is that the monkeys were very much aware of my presence at all times. Howling and the occasional feces throwing were very clearly directed at me at times. This could be a sizable source of error as there is no way to know for sure how the extended presence of a human in their habitat may impact the “natural” behaviors I was hoping to observe. Also, the occasional presence of dogs that followed me into my sites could have similarly contributed to error.

Variation in Habitat

Troops of *Alouatta coibensis trabeata* were found at elevations ranging from 8 meters to 107 meters above sea-level. The distance of each troop from the main road was measured and ranged from 10 meters to 3,701.5 meters. A t-test analyzing the size of troops found either greater than or less than 1,000 meters from the main road gave a p-value of $p=0.07$. While this result is technically insignificant, it is in proximity to significance which suggests that some relationship between proximity to a main road and troop size could exist. More data would be needed as well as more information on the home range of *Alouatta coibensis trabeata* to determine if this relationship exists. The trend of larger troops being encountered farther from the main road seen in this study could suggest that forested area that is more removed from human development could have a greater carrying capacity for *A. coibensis trabeata*. Howler monkeys generally prefer to reside in mature trees and high canopy environments, which may be less abundant in close proximity to a main road. Conversely, if a relationship between troop size and proximity to road truly does not exist, this could be an example of the neutral anthropogenic edge effects studied in *Alouatta palliata* (Bolt 2018).

The various sizes of forest fragments where *A. coibensis trabeata* were encountered could suggest flexibility in the habitat needs of the species. Three separate troops were encountered in a fragment of 235.7 hectares in site 2, the largest of which was 14 individuals. In site 1, however, a troop of 11 individuals was found in a fragment of only 2.2 hectares. This is somewhat consistent with findings of habitat size in *A. pigra*, who tend to prefer fragments of area 10 hectares or larger, but who have been documented surviving in fragments as small as

1.21 hectares (Wyman et al. 2011). It is possible also that the fragments where troops were encountered do not make up the entirety of their home range. Troops B and C, found on days 3 and 4 of data collection, respectively, were presumed to be the same troop as they were the same size and had the same demographic breakdown. Under this assumption, the troop traveled approximately 2.8 kilometers in one day, well outside the range of the 0.5-hectare fragment they were originally found in. Satellite images show that no broad corridors exist between the two locations in which they were found, which suggests that the troop utilized live fences, which were abundant in the Mata Oscura community, and possibly other means to relocate. This is consistent with Méndez's findings of *Alouatta coibensis trabeata* utilizing live fences to travel between forest fragments (Méndez 2013). It could also be an example of landscape supplementation if the troop's home range is in fact insufficient (Asensio et al. 2009). More research is needed into the home range required for a healthy *A. coibensis trabeata* troop, and the effectiveness of live fences in making accessible potential habitats.

Conclusion

A somewhat scarce, although seemingly otherwise sustained, population of *Alouatta coibensis trabeata* was found in the small region of western Azuero that was studied. Estimations of population density and demography were fairly consistent with recent literature on *A. coibensis trabeata*, although fairly divergent from literature on *A. coibensis coibensis*. More research is needed into these demographical and behavioral trends across the entire species distribution. Just about every population faces some degree of anthropogenic impact, so the true "healthy" ranges are still unknown. Although forest fragment size was quite small in much of the studied area, troops seemed to have some degree of mobility, as each encounter site was revisited at least once and no troop was encountered in the same general area twice. This suggests that the howlers successfully use the multitude of live fences as a mode of habitat connectivity in the fine-grained mosaic of western Azuero. Given this, future conservation efforts should focus not only on regeneration of lost habitat for *A. coibensis trabeata*, but also on the reinforcement of the connectivity of already existing fragments through live fence keeping and other methods. *Alouatta coibensis trabeata* are still very much threatened by the development of the Azuero Peninsula. This being said, they are an incredibly flexible and resilient species with the potential to repopulate and rebound if only given the chance.

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