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### Troop composition and behavior of mantled howler monkeys (*Alouatta palliata*) in mangroves and forested islands south of David, Panama

Slate Hyacinthe  
*SIT Study Abroad*

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**Troop composition and behavior of mantled howler monkeys (*Alouatta palliata*) in mangroves and forested islands south of David, Panama**

**Slate Hyacinthe  
SIT Panama: Tropical Ecology, Marine Ecosystems, and Biodiversity Conservation  
Spring 2023**

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### **Abstract**

The mantled howler monkey, *Alouatta palliata*, is one of the most commonly studied and widely distributed primate species in Central America. They have been reported to inhabit mangrove environments in Panama, but few studies have undertaken to describe their demography and behavior in these particular ecosystems. For my study, I spent 12 days studying *A. palliata* populations in both the mangrove and forested island ecosystems (Isla Parida and Isla Boca Brava) south of David. Seven groups were found in the mangrove environments, and 11 groups were found on the island environments. The mangrove groups were significantly smaller and at a lower population density than in the islands. They also spent significantly less time foraging and ate less fruit than in the islands. Reasons for these differences may be connected to the low species diversity and nutrient quality of food in mangrove environments, which could present an ecological constraint on *A. palliata* troop size and behavior. This was a preliminary study into the previously undescribed populations of the region, and more research is needed. It is important to understand the ways that primates utilize coastal mangroves, particularly because these ecosystems face threats of habitat destruction.

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## Introduction

### *Study species*

*Alouatta palliata*, or the mantled howler monkey, is one of the most widespread Mesoamerican primate species (Ceccarelli et al., 2006). They are a member of the genus *Alouatta*, a group of neotropical primates which are all characterized by their distinctive howling behavior (Cortes-Ortiz et al., 2002). The *Alouatta* genus is distinguished amongst neotropical primates for having the widest range of all neotropical primate genera, from southern Mexico to northeastern Argentina (Ruiz-Garcia et al., 2016; Crockett and Eisenberg, 1987). They are also known for their flexibility and adaptation to many different habitats and fragment sizes (Pope, 1992).

*A. palliata* is the only species of the 12 in the genus to form large, stable social groups with consistent male and female representation (Bezanson et al., 2008). In continuous forest, troop sizes can range from 6 to over 20 individuals (Milton, 1998), but fragmentation of habitat has been shown to lead to lower group sizes (Bridgeman, 2012; Sutherland and Jaqadeesh, 2017). *A. palliata* are bisexual dispersers, meaning that the majority of both males and females leave their natal group as juveniles (Bezanson et al., 2008). These emigrations to other groups can be voluntary, or due to aggression and harassment forcing a juvenile to leave (Glander, 1992). As a result, groups are typically composed of unrelated adult members (Milton, 2016). While social groups tend to be stable and cohesive, there is occasional group fragmentation, where smaller subgroups split off for a short time (Chapman, 1989; Leighton and Leighton, 1982). Social behaviors are relatively uncommon amongst *A. palliata*, comprising less than 2% of their daily activity budget (Milton, 2016). Relations between adult *A. palliata* are generally amicable, and agonistic behaviors are rare (Wang and Milton, 2003).

The diet of *A. palliata* is primarily folivorous, and they also are known to consume fruits and flowers as important sources of energy acquisition (Espinosa-Gomez et al., 2013). Primarily folivorous diets are known to pose an energetic challenge to organisms, as leaves typically have low nutrient and sugar concentrations and high amounts of difficult-to-digest fiber (Cork and Foley, 1991). One way that *A. palliata* deal with this challenge is through the flexibility and diversity of their diets, which can vary widely based on seasonality and location (Crockett, 1998; Glander, 1978). They are thus able to select for different nutritionally adequate foods during different seasons, making up for what the leaves lack (Milton, 1998). In a continuous forest environment such as Barro Colorado Island in Panama, *A. palliata* have been determined to eat, on average, 1.7 species of fruit, 5.1 species of leaf, and 0.8 species of flower per day (Milton 1980).

Perhaps due to their low-energy folivorous diet, *A. palliata* spend the majority of the day resting (Milton, 1980). When they do move between resource sites, it has been documented that they move in relatively straight lines, and reuse pathways multiple times (McLean et al., 2016;

Hopkins, 2011). They have been shown to have strong spatial memories that help them maximize energy conservation during foraging (Hopkins, 2016). Howling behaviors are also used to convey spatial information, such as where the troops are located and where resources are abundant (Hopkins, 2013; Bolt et al., 2019).

Currently, *A. palliata* is threatened by deforestation and habitat fragmentation. Worldwide forests are disappearing at a rate of over  $1.3 \times 10^7$  hectares per year (Boyle et al., 2008). The size of remaining habitable land for animals is rapidly reducing and fragmenting, threatening biodiversity at a global scale (Fahrig, 2003). In the face of these threats, *A. palliata* has managed to maintain healthy enough population numbers to be considered a Species of Least Concern (IUCN, 2023). *A. palliata* are particularly adaptable to fragmented habitats and have even been shown to permanently occupy agricultural areas (Lagunes et al., 2016). Despite this demonstrated resilience, more monitoring is needed to understand the long-term impacts of deforestation and habitat fragmentation in the species.

### ***Mangroves and the primates that inhabit them***

Mangrove forests are mixed wetland, coastal ecosystems that are currently being threatened worldwide by habitat destruction (Friess et al., 2019). Between the 1970s and the 2000s, it has been estimated that over half of the world's mangrove ecosystems were lost (Hamilton, 2013). Panama has over 165,000 hectares of mangroves which are threatened by deforestation, and it is estimated that 50% of Panamanian mangroves have been lost since 1972 (STRI, 2021). Mangroves support human livelihoods by providing timber, fish, and coastal protection to communities (Chamberland-Fontaine, 2021). In the region of Chiriqui in Panama, it is estimated that mangroves provide over 27 million dollars a year in environmental goods and services (UNDP, 2017). Other services that mangroves provide include improving water quality in coastal ecosystems, mitigating climate change by serving as a climate sink, and preventing coastal erosion (ARAP and ANAM, 2013). They also provide habitat to other organisms, such as primates.

In a worldwide survey, Nowak and Coles (2018) were able to gather data on 36 different primate species confirmed to inhabit mangroves. The species found represented a range of taxa and locations, with the largest number of species living in Africa (17), followed by the Americas (12) and Asia (7). Many of the species reported only had one published paper about their presence in mangroves, providing evidence to support the authors' claim that primate populations in mangroves are generally understudied compared to terrestrial forest habitats. Amongst the global group of confirmed species, only one species, *Nasalis larvatus* (proboscis monkey) is believed to be an obligate mangrove user (Salter and MacKenzie, 1985). Different primate species have adapted to and utilize mangrove habitats in different ways, for travel, foraging, or other purposes. *Cebus capucinus* (white-faced capuchin) is a noted mangrove specialist, the only primate species in the neotropics to feed on the crabs and mollusks that

inhabit mangroves (Nowak and Coles, 2018). For many primate species, mangroves serve as a place of refuge when other, more desirable habitat has been destroyed or fragmented (Galat-Luong et al., 2019). In Mexico, a population of *Alouatta pigra* (Yucatan black howler) were forced into mangrove forests as a result of lowland forest destruction for cattle farming. They now live solely in the mangroves, despite it not being their endemic environment (Bridgeman 2012).

In Central America, only four primate species have been recorded in mangroves: *Alouatta palliata*, *Alouatta pigra*, *Ateles geoffroyi* (Geoffroy's spider monkey), and *C. capucinus* (Dos Santos and Bridgeman, 2019). *A. palliata*, in particular, lacks extensive research on their distribution and behavior in mangroves. Snarr (2006), who performed one of the only in-depth studies on *A. palliata* in the mangroves of Honduras, found that group sizes were smaller than average in mangrove environments. In Panama, *A. palliata* have been reported in mangrove environments on Coiba island (Milton and Mittermeier, 1977), but either very few or no in-depth studies have been performed on their usage and behavior in mangroves. More research is needed to understand the potential of mangrove ecosystems to serve as primate habitat refuges in the neotropics, as well as the potential impacts of mangrove destruction on primate species.

### ***Study site***

This study takes place in the David region of the Gulf of Chiriqui. This gulf is on the Pacific side of Panama, and stretches from the Costa Rican border to the west, to the beginning of the Veraguas peninsula to the east. Of the 11 principal mangrove zones which have been designated by the Autoridad de los Recursos Acuáticos de Panama (ARAP), the Gulf of Chiriqui comprises the largest concentration of mangroves at 501.33 km<sup>2</sup> (ARAP, 2007). Major industries amongst the mangrove communities of the Gulf of Chiriqui include black conch harvesting, fishing, and tourism (MarViva, 2022). Threatened by deforestation, the mangroves located south of David were declared a protected area in 2007 (MiAmbiente, 2022). A 2022 monitoring report by MiAmbiente Panama reported that the David mangrove area is currently in a good state of conservation, and hasn't had significant deforestation since they were protected.

The study area comprises three different protected areas: the central mangroves of David (including Isla Boca Brava), the Refugio de Silvestre Playa La Barqueta, and the Gulf of Chiriqui Marine National Park. While the central mangroves were protected in 2007, Refugio de Silvestre La Barqueta and the Gulf of Chiriqui Marine National Park were both declared protected by the Autoridad Nacional del Ambiente (ANAM) in 1994 (MarViva, 2022). The Gulf of Chiriqui Marine National park comprises 44 islands scattered around the Pacific coast, the largest of which is Isla Parida. The Refugio de Silvestre Playa La Barqueta is to the east of David, and serves as a turtle nesting site and mangrove conservation area (MiAmbiente, 2022). In 2022, a mangrove reforestation initiative began in Playa La Barqueta, where propagules of *Rhizophora mangle* and *Rhizophora racemosa* have been cultivated in the degraded, sandy habitat (MiAmbiente, 2022). All three of the protected areas have tourist development. Hiking



trails are present in Playa La Barqueta, kayak tours are offered in the David mangroves, and Isla Parida has a hotel and beach catering to visitors (MarViva, 2022).

In the study area, *A. palliata* have been reported by the Panamanian Ministerio de Ambiente (2021), as well as anecdotally by hotels and tourism agencies (Cala Mia Island Resort, 2019). However, no extensive studies have been published on *A. palliata* distribution and behavior in the region.

## **Research Question**

How does *Alouatta palliata* troop composition (troop size, sex, age) and foraging behavior (foraging times and diets) differ between mangrove environments and forested island environments (Isla Parida and Boca Brava) south of David in the Gulf of Chiriqui, Panama?

## **Methods**

### ***Roaming transect***

Data collection took place for 12 days between April 15th and April 27th, 2023. The first 6 days were spent in the mangroves just south of David, Panama, and the last 6 days were spent between Isla Boca Brava and Isla Parida. The mangrove region was split up into 3 different sections, Mangrove 1, 2, and 3. The sections were studied for 2 days each, from 6:00am-12:00pm. This time period was chosen as it corresponds with peak howling hours of *A. palliata* (Bernstein, 1962), making the tracking and discovery of the groups easier.

Mangrove 1 (57.26 km<sup>2</sup>) comprises the region directly south of the port of Pedregal, as well as the river channel that extends west into the Refugio de Vida Silvestre Playa. Mangrove 2 (44.75 km<sup>2</sup>) is just east of this region, comprising the main river channels between Isla Chalapa and the agricultural mainland to the north. Mangrove 3 (59.54 km<sup>2</sup>) comprises the region east of Isla Chalapa and extends to the coastal towns of Boca Chica and Horoncitos. For a map outlining the borders of these regions, see Appendix A, Figure 1. Each section was initially accessed by a motor boat, and then a kayak was utilized during the study period in order to minimize sound and environmental disturbance (Barnett et al., 2019). A roaming transect method was utilized (Lehner, 1992), where the major and minor river channels of the section were traversed, opportunistically following the audible howler calls. When a group was identified, behavioral observation began, and the groups were followed on-foot through the mangroves if necessary.

In the islands, 3 days were spent on Isla Boca Brava and 3 days on Isla Parida. The study period was also 6:00am-12:00pm, utilizing a roaming transect method. The islands were traversed on foot on loop trails. I opportunistically sought to follow the howler calls, and went off trail in pursuit of howler groups when necessary.

### ***Troop composition, behavior, and habitat data***

Once a group was found, I marked and labeled the longitude and latitude with a Garmin GPSMap 64s device. Then, the first instantaneous scan would commence (Amato, 2013). This scan was a full-group assessment that recorded the number of individuals, demographic composition of the group (adult male, adult female, juvenile, or newborn), general group behavior (moving, foraging, resting, or socializing), location (a by-eye estimation of upper, middle, or lower canopy), and type of food being eaten if applicable (leaf, fruit, or flower). Behavioral observation was aided by the use of Bushnell 10x25mm binoculars. If the species of tree that the groups were located on was identifiable, that information was recorded as well, but the recording was inconsistent due to equipment constraints. Adult females and adult males were distinguished by the presence of testes or vulva. Juveniles were not able to be sex-distinguished due to lack of developed secondary sex characteristics. This instantaneous scan occurred within a minute, and reoccurred every 5 minutes based on a timer. Between these instantaneous scans, there was a focal study (Lehner, 1992) of one individual in the group for 5 minutes each, taking care to keep the individuals distinct. During each period of focal study, the following information was recorded for the focal individual: their behavior (moving, foraging, resting, or socializing) and what they are foraging on if applicable (leaf, fruit, or flower). The expression and duration of howling behavior was recorded throughout both the instantaneous and focal scans.

Once all individuals were observed by the scans, the sequence was repeated until the group was no longer in sight. After the behavioral observation ended, canopy density was recorded at the initial encounter site with a spherical densiometer. Then, the roaming scan recommenced, looking for a new group. This continued until the allotted study time for the day was complete.

### ***Methods of data analysis***

Population density of the study areas were determined using the help of the Google Maps measuring tool. The borders of the mangroves and island areas were defined using the measuring tool, which provided the km<sup>2</sup> of the area. Then, the total number of individuals found were divided by the km<sup>2</sup> to determine the estimated population density. Average percent of behavior recorded was calculated for all behavior types, including moving, foraging, resting, socializing, and howling. Mann-Whitney statistical tests were used to compare all averages between island and mangrove environments. Because sample sizes were small, the Mann-Whitney test was chosen for statistical analysis because it does not require the assumption of a normal distribution (Gibbons and Chakraborti, 1991). Significance is indicated as ( $p < 0.05$ ). Linear regressions for canopy density and group sizes were performed using Google Sheets.

### **Ethics**

The primary ethical concerns of this research were potential disturbance of *A. palliata* and potential disturbance of the study environment. Efforts were taken to disturb howlers to the least extent, by remaining quiet and concealed, though some disturbance was to be expected as the howlers monkeys likely detected my presence. As for the study environment, kayak access was the less-invasive method for traversing the mangroves, as it is a quiet and non-motorized form of transport. When moving through the mangroves on foot, I took care to move in a way that minimizes mangrove damage, especially to young seedlings. On the islands, there was less concern about habitat damage as I was primarily moving through designated trails, though I did need to go off trail from time to time. No seedlings or brush were cut down when moving off-trail; I simply pushed through the brush gently and took care not to step on seedlings.

This study also underwent and was approved by the Institutional Review Board process at the School for International Training. A form was filled out about the project scope, methods, and location, which was then sent for external approval. This IRB process ensures that there is ethical oversight on student research projects.

## Results

### *Group distribution and composition*

Over the span of 12 days of study, including 6 days roaming the mangroves of David, 3 days roaming Isla Parida, and 3 days roaming Isla Boca Brava, a total of 18 separate *A. palliata* group encounters were recorded. One hundred and eighty seven individuals were recorded and monitored in total, and 969 minutes (16.15 hours) of active observation occurred. The majority of encounters occurred closest to dawn, between 6:30am-8:00am (8/18 encounters), and the second highest amount occurred between 8:00am-9:30am (4/18 encounters).

In the mangroves, 303 minutes of observation and 51 instantaneous scans occurred over 6 days. A total of 7 individual groups were found, with group sizes that ranged from the smallest of 3 members to the largest of 9 members. Two groups with identical group numbers and demographic composition were encountered on different days, and may be the same group encountered twice. The average group size in the mangroves was  $6.14 \pm 1.95$ . Across the three different mangrove study areas, 1 group was found in Mangrove 1 (western), 3 groups were found in Mangrove 2 (center), and 4 groups were found in Mangrove 3 (eastern) (Appendix A, Figure 1). Calculating density for the mangrove areas yielded results of 0.1 ind./km<sup>2</sup> in Mangrove 1, 0.4 ind./km<sup>2</sup> in Mangrove 2, and 0.3 ind./km<sup>2</sup> in Mangrove 3. Every group found in the mangroves had at least 1 adult male and at least 2 adult females. Four groups had between 1 and 2 juvenile members, and only 2 groups had a single newborn member. On average, the groups were composed of  $22.07 \pm 8.02\%$  adult males,  $65.71 \pm 9.07\%$  adult females,  $10.14 \pm 9.55\%$  juveniles, and  $3.36 \pm 5.75\%$  newborns (Appendix B, Figure 2).

Across the two islands of Isla Parida and Isla Boca Brava, 669 minutes of observation and 130 focal scans occurred over 6 days. Five groups were found on Isla Boca Brava and 6

groups were found on Isla Parida, for a total of 11 groups across the two islands. On Isla Parida, two groups with identical group numbers and demographic composition were encountered on different days, and may be the same group encountered twice. Troop sizes ranged from the smallest of 6 members to the largest of 13 members. Density calculations for the two islands yielded 1.3 ind./km<sup>2</sup> for Isla Boca Brava, and 3.7 ind./km<sup>2</sup> for Isla Parida (Appendix A, Figure 1). Across both islands, the average group size was  $9.18 \pm 2.14$ . Every group in the islands had at least 2 adult males, at least 3 adult females, and at least 1 juvenile. Three out of 11 of the groups had a newborn. On average, the demographic composition of the island groups were  $21.73 \pm 4.36\%$  adult males,  $54.82 \pm 3.76\%$  adult females,  $19.45 \pm 7.83\%$  juveniles, and  $2.64 \pm 4.52\%$  newborns (Appendix B, Figure 2).

Comparing the islands and the mangrove groups, the average troop sizes were significantly different with a p-value of 0.0076. None of the average troop composition data (% adult male, % adult female, % juvenile, % newborn) yielded statistically significant differences between the islands and mangrove groups.

### ***Behavior***

During the periodic instantaneous scans, howler monkeys in the mangroves were found, on average, to be resting  $73.57 \pm 7.35\%$  of the time, moving  $10.29 \pm 3.59\%$  of the time, foraging  $8.37 \pm 3.75\%$  of the time, and socializing  $3.03 \pm 3.06\%$  of the time (Appendix B, Figure 3). Foraging behaviors included searching for food, picking food, as well as eating. Social behaviors that were recorded in the mangroves are embracing from the front/carrying and grooming, and were exhibited exclusively from adult female to juvenile. Four out of 7, or 57%, of the mangrove groups exhibited social behaviors. When present, newborns were carried by the adult females for the duration of the observational period, and this was excluded as a social behavior from total calculations. During the 5 minute focal scans, individuals were found to be foraging on average  $7.14 \pm 3.84\%$  of the time (21.42 seconds per focal scan). There were no significant differences in average foraging time between the demographics of adult male, adult female, and juvenile. Newborns were not seen foraging. On average, howling behavior occurred  $4.35 \pm 2.33\%$  of total observation time across the groups, occurring in all of the groups except the smallest group of 3. Based on a linear regression analysis, there was little to no correlation detected between percent of time spent howling and group size ( $R^2=0.089$ ).

For the groups located on the islands, they were found, on average, to be resting  $69.91 \pm 8.47\%$  of the time, moving  $9.91 \pm 3.42\%$  of the time, foraging  $18.82 \pm 6.45\%$  of the time, and socializing  $2.73 \pm 3.45\%$  of the time (Appendix B, Figure 3). Foraging behaviors included looking for food, picking food, and eating. Social behaviors included front embracing, grooming recorded, and one instance of playful slapping. All social behavior was recorded from adult female to juvenile. Five out of 11, or 45%, of the island groups exhibited social behavior. During the 5 minute focal scans, individuals were found to be foraging on average  $14.23 \pm 2.39\%$  of the time (42.69 seconds per focal scan). Similarly to the mangrove environment, there were no

significant differences in average foraging time between the demographics of adult male, adult female, and juveniles, and newborns were not seen foraging. On average, howling behavior occurred  $8.6\% \pm 3.4\%$  of total observation time across the groups, occurring in 9 out of 11 groups. There was little to no correlation detected between percent of time spent howling and group size ( $R^2 = 0.0045$ ).

Percent of time spent foraging was found to be significantly different between the mangrove and island environments, during both the instantaneous scans ( $p=0.005$ ) and the focal scans ( $p=0.024$ ). Percent of time spent howling was also significantly different between the mangrove and island environments ( $p=0.043$ ). None of the other behaviors were significantly different between the environments.

### ***Foraging diet***

In the mangroves, amongst the instances of foraging recorded, groups were found on average to eat  $76.43 \pm 14.69\%$  leaves,  $23.57 \pm 13.51\%$  flowers and  $1.85\% \pm 3.29\%$  fruit (Appendix C, Figure 4). One group was found to eat 100% leaves. Only 2 groups were found eating fruit, and it was identified as the fruit of *R. mangle*. Detailed dietary information was not able to be recorded due to difficulties with identification and visibility, but the author was able to qualitatively identify consumption of the leaves and flowers of both *R. mangle* and *L. racemosa* by the howler monkeys.

In the island environments, groups were found to eat on average  $70.09 \pm 9.07\%$  leaves,  $9.09 \pm 6.38\%$  flowers, and  $20.82 \pm 9.08\%$  fruit (Appendix C, Figure 4). Similarly to the mangrove environment, observational constraints prevented the positive identification of most of the food types beyond these three categories, though some were able to be identified. Identified plants include the fruits and flowers of *G. superbia*, *G. madruno*, and the leaves of *C. brasiliense* and *M. staminodella*. These plants were found on both Isla Parida and Isla Boca Brava.

The only significant difference in average % diet category consumed between the islands and mangrove environment is in fruit percentage ( $p=0.00058$ ).

### ***Habitat:***

The average canopy cover where the groups were found in the mangroves was  $52.54 \pm 20.12\%$ , and in the islands it was  $71.18 \pm 8.85\%$ . The canopy coverage is not found to be significantly different between the environments.

In the mangroves, *A. palliata* was most commonly first encountered on *L. racemosa* (4/7 groups). Primary species that were identified in the mangrove areas studied were *R. mangle*, *L. racemosa*, and *A. germinans*. Groups were found, on average, to be  $3.02 \pm 1.70\text{km}$  away from the nearest deforested area. They were encountered most often on the upper canopy (5/7 groups) or middle canopy (2/7 groups). Groups were not witnessed moving between canopy levels.

In the islands, *A. palliata* was first encountered on the species *M. staminodella* (2/11 groups), *C. bate* (3/11), and *C. salvadorensis* (1/11), as well as 5 encounters on unidentified trees. Other trees on the islands that were identified are *G. madruno*, *G. superba*, and *L. seemannii*. Groups were found, on average, to be  $1.11 \pm 0.40$  km away from the nearest deforested area. They were encountered most frequently on the upper canopy (7/11 groups) middle canopy (3/11 groups), and less commonly on the lower canopy (1/11). Two of the groups were seen moving between the upper, middle, and lower canopies to retrieve food from lower strata.

Average canopy coverage for mangrove and island environments were not found to be statistically different. Linear regressions plotting canopy coverage vs. group size found that in the mangroves, there was little to no correlation detected between the two variables ( $R^2=0.009$ ) (Appendix D, Figure 5). In the island environment, however, there was a moderate correlation detected between the two ( $R^2=0.664$ ) (Appendix D, Figure 6).

## Discussion

### *Group distribution and composition*

In both the mangrove and the island environments, total group sizes were found to be on the lower end of the typical range for *A. palliata*, at average group sizes of  $6.14 \pm 1.95$  and  $9.18 \pm 2.14$ , respectively. In continuous forested environments, *A. palliata* groups are typically much larger, greater than 10 individuals and averaging around 19 individuals per group (Milton, 1998). However, when there are lower amounts of food resources available, such as in fragmented habitats, it has been found that *A. palliata* have smaller group sizes than are typically recorded (Chapman, 1988). This follows the “ecological constraints model” in primates, which posits that as group members increase, the need to travel to access adequate food resources increases. If the environment is not large or continuous enough to accommodate this travel, then the number of group members will be reduced in order to ensure that enough resources are available for continued reproductive success (Ganas and Robbins, 2005). Both the mangroves of David and the western islands of this study have nearby disturbed and deforested habitat, stemming from timber extraction, agriculture, and, to a lesser extent, tourism development (MarViva, 2022). Based on GPS satellite data estimations, approximately 24% of Boca Brava is deforested, and 14% of Isla Parida is deforested. In the mangrove areas, most of the deforestation and disturbance happens to the north of the bay, around the major metropolitan area of David. With both of these environments facing fragmentation and deforestation, resource availability is reduced and thus may contribute to the smaller group sizes. Sample sizes are limited in this study, however, so strong conclusions cannot be drawn from the data.

While both environments had smaller than the typical *A. palliata* troop size, the mangrove environment had a significantly smaller troop size than the islands. For this, there may be contributing factors besides habitat fragmentation and deforestation. The mangrove

environment, though isolated by surrounding deforestation on the mainland to the north, is nearly 3 times larger than the islands overall (approx. 151.55 km<sup>2</sup> as opposed to 49.36 km<sup>2</sup>), and is more continuous. *A. palliata* groups that were found on the mangroves were also located almost three times further away from the closest deforested area than in the islands on average ( $3.02 \pm 1.70$  km as opposed to  $1.11 \pm 0.40$  km). Yet, in the mangroves, both the group sizes and the estimated population density were smaller. This is evidence to suggest that mangrove environments can't support as large of group sizes or as dense of population distribution as in forested environments.

This finding is fairly congruent with the two other research projects that have been performed on howler monkeys in neotropical mangroves. Both Snarr (2006) and Bridgeman (2012) found that howler monkey group sizes were smaller in mangrove environments than non-mangrove environments. With only 12 plant species recorded in the mangroves in the region, as opposed to the 213 species recorded in Isla Parida and Isla Boca Brava (ANAM, 2010), species diversity and richness is clearly much lower in the mangroves. For a species like *A. palliata* who typically relies on a diverse array of food sources ranging from leaves, fruit, flowers, and seeds (Milton, 1998), the lower diversity of food sources in mangrove environments may contribute to the ecological constraints on their group size and density. Despite knowing that *A. palliata* typically enjoys a diverse diet, it is important to mention that they have still been found to thrive on limited, leaf-only diets, for example during the wet season on Barro Colorado Island (Milton, 2016). Therefore, reduced food diversity may not be a fully comprehensive explanation for why group sizes are significantly smaller in mangroves.

Another potential explanation for the lower average group sizes in mangrove environments is due to reduced nutrient quality in mangroves. Bridgeman (2012) pursued this line of inquiry in her research, performing phytochemical analyses of mangrove and non-mangrove plant species that were consumed by her study species of *A. pigra*. She found that mangrove fruits were significantly lower in sugar, calcium, and protein, as well as higher in lignin, which is a digestion deterrent. *A. pigra* in her study were not found to consume any fruit at all, similarly to this study where significantly less fruit consumption was found within the mangroves of David ( $1.87 \pm 3.29\%$ ) than in the islands ( $20.82 \pm 9.08\%$ ). Fruit has been shown to be a nutritionally important part of the *A. palliata* diet (Dunn et al. 2009), but unlike some primate species like the *Ateles* genus (spider monkeys), *A. palliata* are not dependent on it (Eisenberg, 1989). Reduced or eliminated access to high-quality fruit over the long term, may be a sufficient enough stressor to constrain both group sizes and population density.

It is also important to note that *C. capucinus* groups were recorded on two instances in the western mangrove portion. While *A. palliata* and *C. capucinus* have been recorded sharing habitat with one another (Aguiar et al., 2011), the presence of *C. capucinus* may exacerbate resource and territorial scarcity issues. More research would need to be done on the distribution and resource use of *C. capucinus* in the region before solid conclusions can be drawn.

In terms of the gender and age composition of the groups found in the study, they were found to be consistent with the ranges of other studies of *A. palliata*. For example, both males and females were represented in all the groups, and the ratio of females to males did not exceed

the benchmark of 4:1 (Milton, 1998, Conaster, 2016). The most notable observation is that, while the average gender and age compositions were overall not significantly different between the mangrove and island environments, the average percentage of juveniles in the island groups (19.45%) was nearly double the average percentage of juveniles in the mangrove groups (10.14%). This difference is not statistically significant, but it may suggest that upon further inquiry, differences in reproductive rates may be found between the mangrove and the island environments.

### **Behaviors**

The percent of instantaneous scans where foraging occurred were found to be significantly different between the mangrove and island environments, at  $8.37 \pm 3.75\%$  vs.  $18.82 \pm 6.45\%$ , respectively. Lower foraging rates in mangroves were also found by Bridgeman (2012) in her study on *A. pigra*. Similarly to the proposed explanations as to why the group sizes and population density were smaller in the mangroves, decreased foraging behavior could be due to lower nutritional density, diversity, and lack of available food resources in mangroves. In this case, they may simply not be able to access enough high-quality food to spend the same amount of time foraging as they do on the islands where diverse food, and especially fruit, are more plentiful. A potential oversight with this explanation, however, is that if the food resources are of lower quality in the mangroves, one might expect *A. palliata* to instead forage *more* frequently to make up for the lower nutrient quality and energy gained from their diet. Without more extensive data, however, strong conclusions cannot be drawn.

Another explanation for the decreased amount of foraging behavior seen in the mangroves as opposed to the islands is that *A. palliata* may not be solely foraging within the mangroves. Because the mangroves of David are also connected to mainland and island forest fragments, it is possible that the groups are moving in-between forest and mangrove, gleaning more resources from the forest and decreasing the necessity of foraging in the mangroves. This behavior has been recorded in *N. lavartus* (proboscis monkeys), who are primarily folivorous and move into mangroves when shelter is needed, but gather most of their diet from forests nearby (Bennett and Sebastian, 1988).

One last potential explanation for this behavior is due to where the majority of troop encounters took place. Because I was accessing the mangroves by boat and kayak for my research, the majority of troop encounters occurred on the edges of the mangroves, whereas in the islands I was able to roam more freely amongst different forest types. It is possible that the preferred foraging region for mangrove-dwelling *A. palliata* is deeper into the interior of the mangroves, as opposed to the edges closer to the water. More in-depth data would be needed to answer this question, such as transect data on the mangrove distribution from edge to interior.

The other behaviors of resting, moving, and socializing were not significantly different between mangrove and island, and correspond with the existing literature on *A. palliata* (Nagy and Milton, 1979). For example, social behaviors were scarce and limited to adult females and



juveniles, at an average of  $3.03 \pm 3.06\%$  in the mangroves and  $2.73 \pm 3.44\%$  in the islands, which is similar to previous findings that *A. palliata* only spends about 2% of its daily activity budget socializing (Milton et al., 2016). Percentage of time spent howling, however, did significantly differ between the mangrove and island environments, at  $4.35 \pm 2.33\%$  and  $8.6\% \pm 3.4\%$ , respectively. A likely reason for this difference is due to the lower density of groups in the mangroves than in the islands. The function of howling in *A. palliata* is most principally for inter-group communication, establishing territory, dominance, and resource use (Hopkins et al., 2013). It is suggested by existing research that *A. palliata* howls more frequently in areas of denser group populations and richer resources (Bolt et al., 2019). With less dense populations in the mangroves, there is less of a motivation for the howling behavior to be expressed. It should be noted, as well, that I likely instigated or influenced the howling behavior by my presence once the groups noticed me. For a more conclusive analysis on howling behavior in this region, a study would have to be done where researcher presence is entirely concealed, or using tools such as audio-traps (Lynne and Bidner, 2016).

### ***Habitat***

As previously mentioned, detailed information on forest composition, canopy height, and species diversity for the different environments were not able to be achieved for this study due to time and equipment constraints. The species that were identified and reported in the results are consistent with previously reported forest data and no novel species were identified (ANAM, 2010). One notable finding regarding habitat and location of the groups is that while groups were not found moving between canopy levels in the mangroves, they were found moving between canopy levels in the islands. This is possibly due to foraging purposes, as some of their diet on the islands are located in the lower canopy levels, including the identified fruits of *G. superbia* and *G. madruno*. Generally, *A. palliata* seek to conserve energy and move little, a species known for its high quantities of daily rest (Milton, 1998), however, if sufficiently motivated they will seek resource opportunities on the lower canopy levels (McLean et al., 2016). This finding could be interpreted as more evidence for the comparative resource richness of the islands as opposed to the mangroves. It is also possible that the shorter canopy height of the mangrove environment as compared to the islands, which have mature forest canopy between 35 and 50 meters (ANAM, 2010), de-incentivizes *A. palliata* from moving to lower levels.

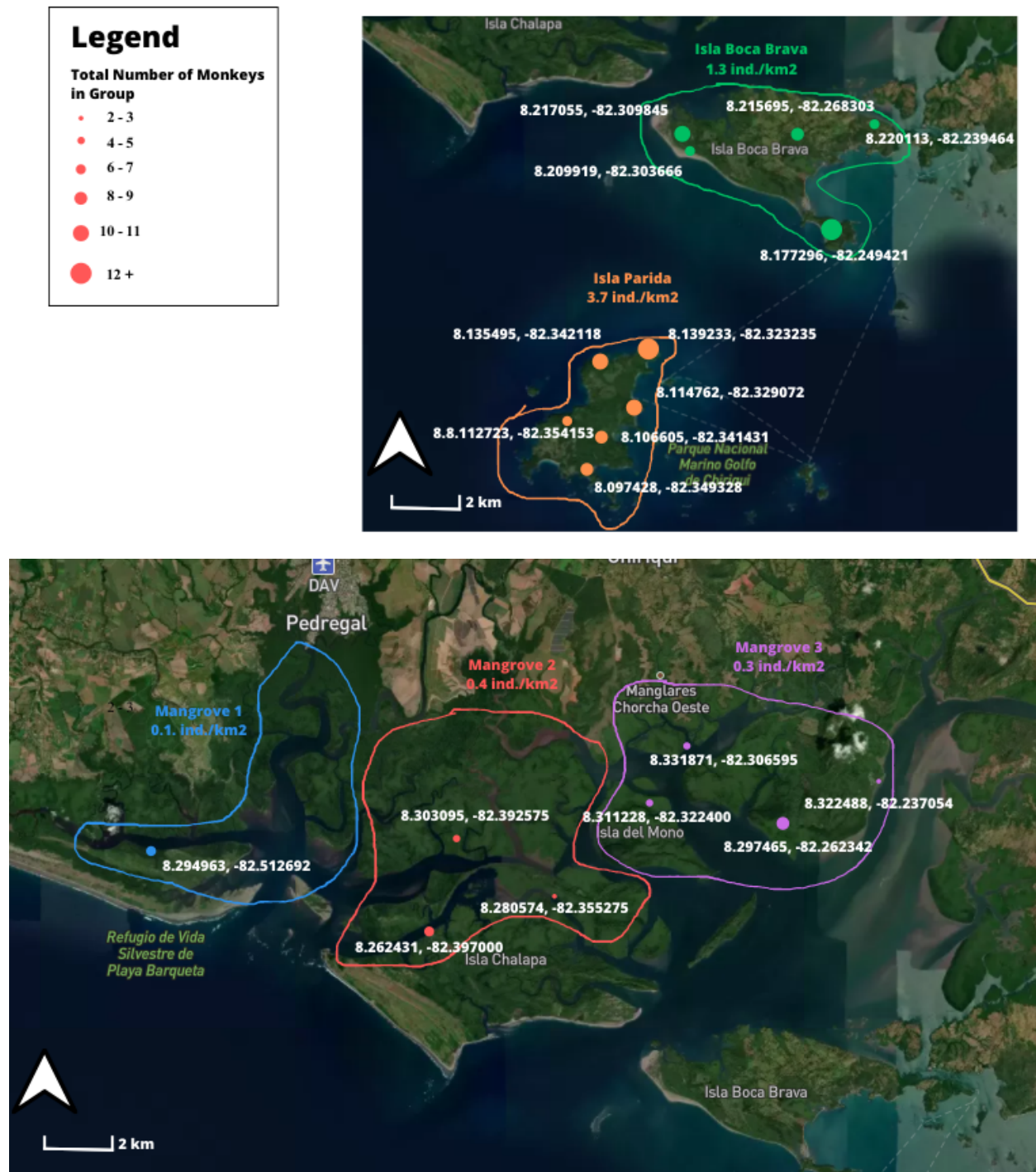
Another finding related to habitat is the correlation between canopy cover and group size encountered. These variables were not correlated in the mangrove environment, but they were moderately correlated in the island environment. One potential reason for this is that in the island environments, the areas with the lowest canopy cover were closer to the areas of deforestation and human disturbance. It is possible that larger *A. palliata* troops are actively avoiding areas that humans may frequent, either due to the actual presence of humans on the island or due to the fact that these areas are very wide-open and clear cut. *A. palliata* tends to avoid edges near wide-open, deforested areas (Bolt et al., 2019), but correlations between edge habitation and

group size were not found in the literature. There aren't many wide-open, clear-cut areas close to the mangrove environments, so this may explain why canopy density didn't correlate to group size. However, without more detailed information, these suggestions are highly conjectory.

## Conclusion

Studying the *Alouatta palliata* populations amongst the mangroves and islands south of David was, overall, an exploration into a largely unstudied corner of primatology in Panama. This is true both for the study region, which has no published studies on the local primates, and the mangrove habitat, which has very little research regarding the neotropical primates that live in these environments. Where *A. palliata* were found in the mangroves, groups were significantly smaller, less densely distributed, spent less time foraging, and were observed to eat nearly no fruit in their diet. Reasons for these differences may include limited resource availability, low nutrient values, limited species diversity, and the presence of other primate species in mangrove environments. While we can make some conclusions that, broadly, mangrove environments likely have effects on the troop composition and behavior of *A. palliata*, we can't say for sure why this is without further research and larger sample sizes. However, this is a good start toward discovering more about *A. palliata* in the mangroves and forested islands south of David. Despite the potential challenges faced by primates living in mangrove environments, it is a testament to the resiliency and flexibility of *A. palliata* that they are still able to occupy these low-diversity ecosystems at all, as well as fragmented ecosystems in general. It is important to study primate distribution in threatened ecosystems such as mangroves and islands, so that we can better develop conservation strategies on the behalf of both the primates and the environment. In an age of increasing deforestation and destruction of tropical coastal environments, primates such as *A. palliata* may be useful for helping us monitor mangrove ecosystem health and animal resiliency.

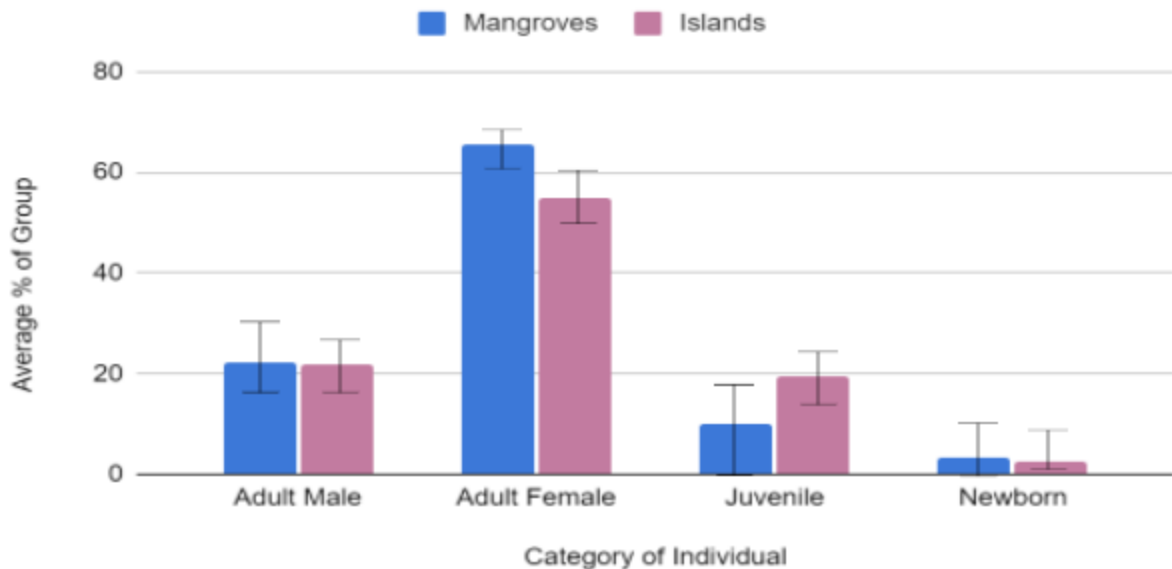
## Appendix A



**Figure 1.** Map of study area in Isla Parida and Isla Boca Brava (top right) and Mangroves of David (bottom), in Panama. Within the different colored boundary markings are circles which indicate the *A. palliata* groups that were found within the boundaries. The sizes of these circles correspond to the size of the group found (see Legend, top left). Longitude and latitude marking of group location are noted.

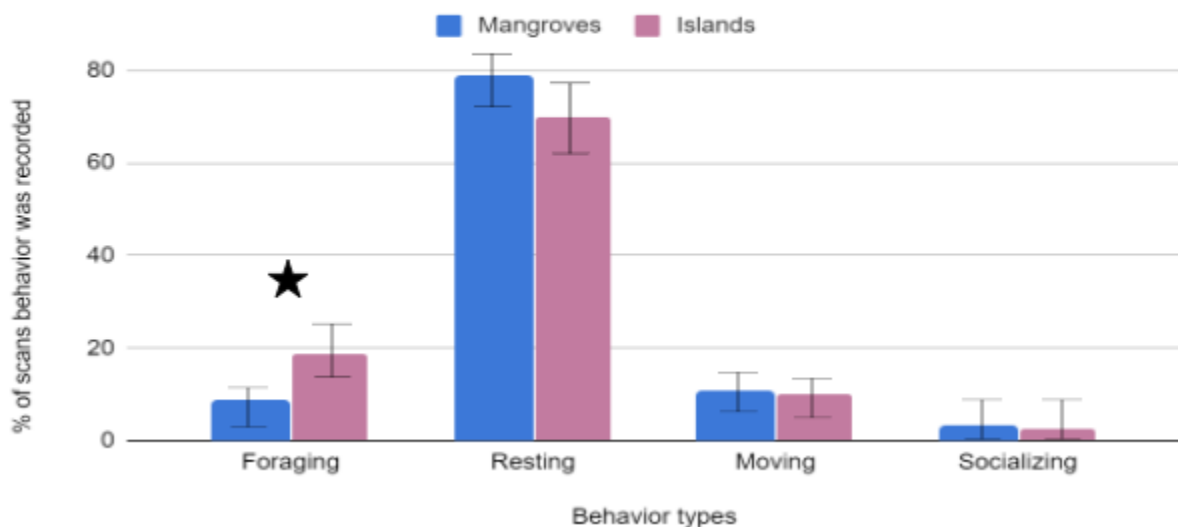
## Appendix B

### Comparing average group demographics between mangrove and island environments



**Figure 2:** Column chart comparing the average % of group total demographics for mangrove and island conditions. Error bars indicate standard deviation from the mean. No statistically significant differences between island and mangrove results were found ( $p > 0.05$ ). Mangrove  $n=7$ , Islands  $n=11$

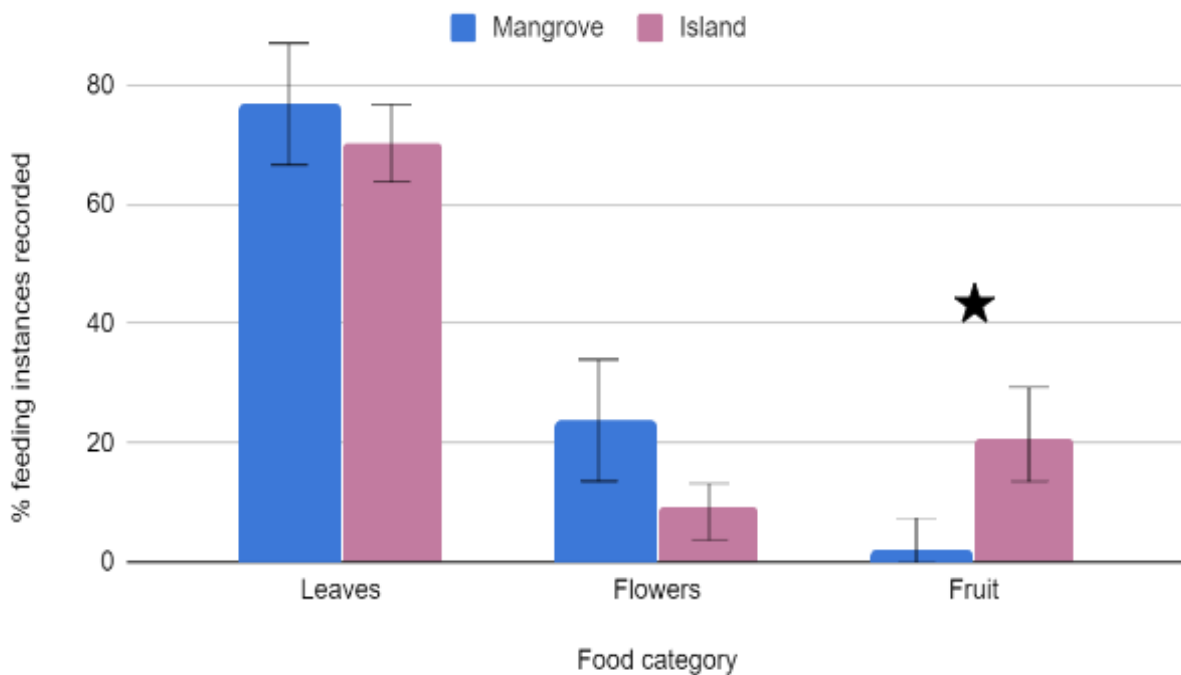
### Comparing average % recorded behavior between mangrove and island environments



**Figure 3:** Column chart comparing the average % of recorded behavior between mangrove and island environments. Data is from instantaneous scans occurring once every 5 minutes. Error bars indicate standard deviation from the mean. Star indicates significant difference in average foraging instances between mangroves and islands ( $p=0.00496$ ,  $p < 0.05$ ). Mangrove  $n=7$ , Islands  $n=11$ .

## Appendix C

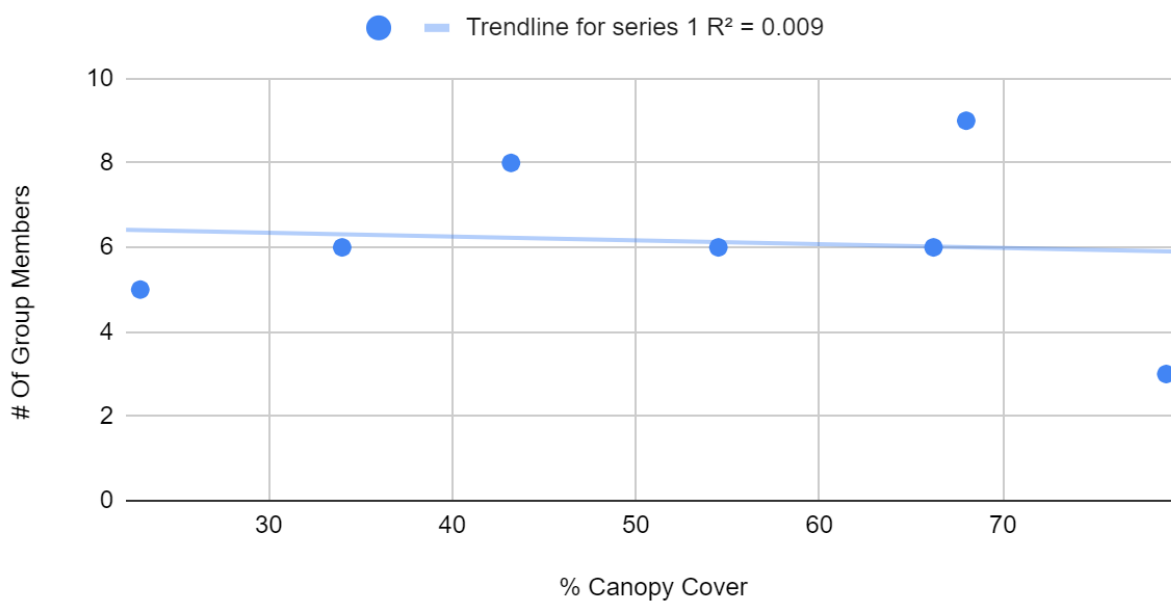
Comparing average % food type consumed between mangrove and island environments



**Figure 4:** Column chart comparing the average % of food type consumed between mangrove and island environments. Data is from the total number of feeding incidents recorded. Error bars represent standard deviation from the mean. Star indicates significant difference in average % fruit consumed between mangroves and islands ( $p=0.00058$ ,  $p<0.05$ ). Mangrove  $n=7$ , Islands  $n=11$ .

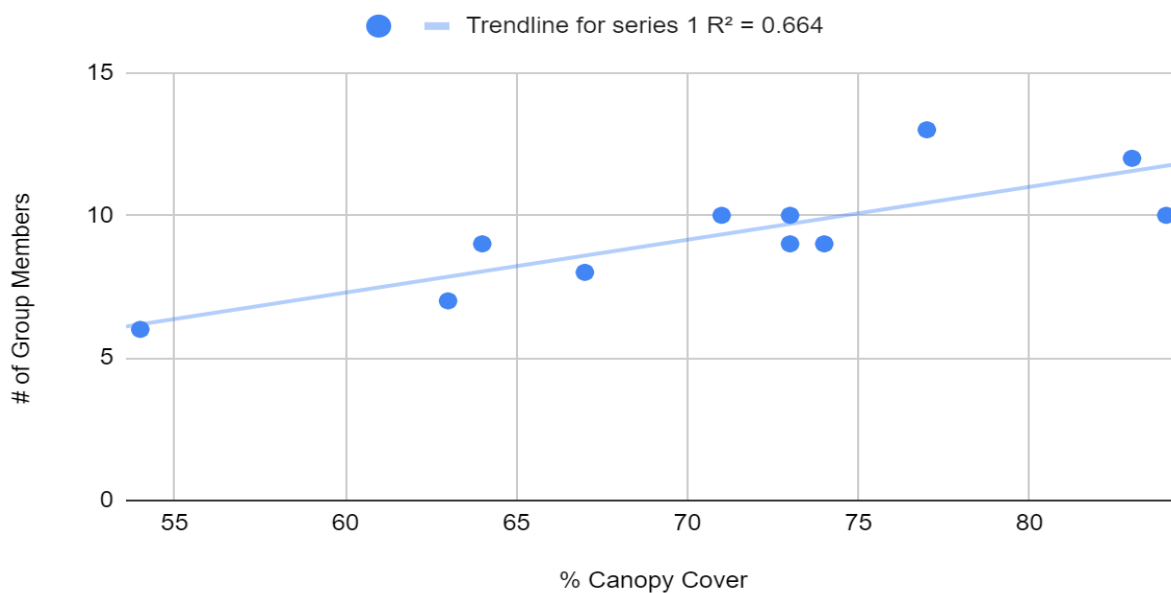
## Appendix D

### Percent canopy cover vs number of group members (mangroves)



**Figure 5:** Linear regression for # of group members within the troops found in the mangrove environments vs. the % canopy cover recorded at the troop location. R2 value for trendline: 0.009.

### Percent canopy cover vs. number of group members (islands)



**Figure 6:** Linear regression for # of group members within the troops found in the mangrove environments vs. the % canopy cover recorded at the troop location. R2 value for trendline: 0.664.

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