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Habitat Stratification of *Pithecia* Species in the Área de Conservación Regional Comunal Tamshiyacu Tahuayo in the Northeastern Peruvian Amazon

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April, 2016

To the Dean of the Graduate School:

We are submitting a thesis written by Richard L. Jackson, Jr. entitled “Habitat Stratification of *Pithecia* Species in the Área de Conservación Regional Comunal Tamshiyacu Tahuayo in the Northeastern Peruvian Amazon”

We recommend acceptance in partial fulfillment of the requirements for the degree of Masters of Science in Biology.

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HABITAT STRATIFICATION OF *PITHECIA* SPECIES IN THE ÁREA DE CONSERVACIÓN REGIONAL COMUNAL TAMSHIYACU TAHUAYO IN THE NORTHEASTERN PERUVIAN AMAZON

A Thesis

Presented to the Faculty

Of the

College of Arts and Sciences

In Partial Fulfillment

Of the

Requirements for the Degree

Of

Master of Science

In Biology

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April, 2016

By

Richard L. Jackson, Jr.

ABSTRACT

Researchers previously reporting equatorial and monk sakis (*Pithecia aequatorialis* and *P. monachus*) occurring sympatrically north of the Amazon River in Peru raised the question of whether the two species were syntopic or separated by habitat. I encountered both species of saki south of the Amazon in Peru in the Área de Conservación Regional Comunal Tamshiyacu Tahuayo (ACRCTT). Initial observations and local lore suggested that in this area equatorial sakis occur predominantly in flooded forests and monk sakis in terra firme. I conducted a six-week survey (324 hours effort, a minimum of 18 groups observed) to test this hypothesis, collecting data on location and habitat preference of the two species using both terrestrial line transect surveys and canoe-based sampling. My findings indicate that the two species are syntopic, with both species occurring in igapó forest adjacent to rivers, but only equatorial sakis observed in terra firme forest. These results indicate that if the two species segregate by habitat, it is based on features other than a simple dichotomy between igapó and terra firme forest. In my study area, equatorial sakis significantly outnumber monk sakis (x^2=10.889, d.f.=1, p=0.0010), despite previous surveys that only reported monk sakis in the reserve. My census data also confirmed the presence of atypically colored adult females in some equatorial saki groups, supporting earlier suggestions that the two species may be hybridizing.

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DISCUSSION

BACKGROUND

The Amazonian basin of Peru is one of the most biologically diverse areas of the world. Western Amazonia, including Peru, contains some of the most species-rich primate assemblages anywhere, with as many as 14 sympatric primate species occurring in some locations (Peres and Janson 1999; Haugaasen and Peres 2009). This study looks at the habitat distribution of two species of saki monkeys, equatorial sakis (*Pithecia aequatorialis*) and monk sakis (*P. monachus*), in the Amazon basin of Northeastern Peru. The study took place in the communal reserve Área de Conservación Regional Comunal Tamshiyacu Tahuayo (ACRCTT) in Loreto Department.

The Pitheciids

Pitheciidae is a family-rank clade of New World monkeys (Infraorder Platyrrhini). While there is ongoing debate regarding the evolutionary history of playtyrrhines, recent work suggests a separation of the pitheciids from other extant platyrrhine families in the Early Miocene, approximately 20.1 mya (Kay et al. 2013). The Pitheciidae family is made up of four genera - titis (*Callicebus*), uakaris (*Cacajao*), bearded sakis (*Chiropotes*) and sakis (*Pithecia*).

The geographic range of pitheciids is limited to South America (de Sousa e Silva Júnior et al. 2013). They are able to occupy a diverse range of habitats including terra firme, flooded forests, sand-ridge forests, coastal swamp forests, upper lowland forests, tropical dry forests surrounded by savanna, montane forests and secondary growth (Setz et al. 2013, Sussman 2003).

Pitheciids are arboreal monkeys and range in size from 850g to 3,500g (Norconk 2007, Norconk & Setz 2013). The defining characteristic that separates pitheciids from other platyrrhine families is that they are highly adapted for predation on seeds (Kay et al. 2013). When eating fruit, most platyrhhines will ingest the seeds whole allowing the seeds to pass through the digestive tract or discard the seeds before eating the fruit, making the seeds available for future germination. Pitheciids are known as "seed predators" as they extract seeds from tough-rinded fruit and masticate them before ingesting them. This process destroys the seeds and effectively removes them from any future germination (Kay et al. 2013, Norconk & Veres 2011, Norconk et al. 2013). The multi-step process of extracting seeds using anterior dentition and hands followed by mastication of the seeds using the molars is known as "sclerocarpic foraging" (Norconk et al. 2013).

Saki Monkeys (*Pithecia*)

Saki monkeys (genus *Pithecia*) are found in a wide range of habitats throughout northern South America and the Amazon Basin. Sakis can be found in lowland tropical rainforests (both in terra firme and flooded forest), montane forests, dry tropical forests, sandy plains, upland forests, and refugia islands created by damming in Venezuela (Norconk & Setz 2013, Setz et al. 2013).

Hershkovitz divided the *Pithecia* genus into sakis of the Guianan Region, which included *P. pithecia*, and of the Amazonian Region, which included *P. aequatorialis*, *P. monachus*, *P. albicans* and *P. irrorata* (Hershkovitz 1987).

P. aequatorialis, *P. monachus* and *P. irrorata* are all found in Peru (Porter et al. 2013). For years, researchers have relied on Hershkovitz' taxonomy in identifying saki species. However, the uncertainty of the geographic origin of specimens used to establish species and phenotypic variations within the genus has led to confusion in the taxonomy of *Pithecia* (Aquino and Encarnación 1994). Recently, Marsh published a new taxonomy of *Pithecia* based on reviewing the morphology of specimens in thirty-six museums and increased the number of saki species from Hershkovitz' five species to now sixteen distinct saki species (Marsh 2014).

Studying saki monkeys is inherently difficult because of their cryptic behavior and, often, cryptic coloration. Sakis have relatively short daily activity periods, and may enter their sleeping trees by early afternoon. Sakis also have a habit of staying completely still for periods of thirty minutes or more (Pinto et al. 2013). Their propensity to remain motionless, combined with their cryptic coloring, makes it easy to mistake a saki for a similarly colored and shaped termite nest, thus making them harder to locate and observe (personal observation).

Because of the difficulty in finding sakis and keeping contact with a group once it is found, sakis are some of the least studied New World monkeys. There have been very few, if any, long-term studies on *Pithecia* and our understanding of saki social behavior is limited (Norconk 2007). Of the published research on sakis, most is focused on white-faced sakis (*P. pithecia*). Comparatively, very little research has been done on equatorial sakis (*P.* aequatorialis) and monk sakis (*P. monachus*), the subjects of this study.

The traditional view of saki mating systems has been described as monogamous with an adult pair and offspring (Robinson et al. 1987). Aquino et al. (2009) report that equatorial saki groups in Peru are usually comprised of an adult pair with one or two offspring. However, other studies have reported saki groups containing multiple adult females and/or multiple males, which could indicate that cooperative breeding is occurring (Norconk & Setz 2013). Norconk and Setz (2013) hypothesize that both male and female sakis disperse, and dispersers may fill open breeding positions created by death or disappearance of an adult.

Sakis are heavily frugivorous with fruit comprising between 80-98% of their diet. Within the category of fruit, seeds account for between 26-64% of their diet (Norconk & Setz 2013). Sakis are dentally adapted to open mechanically protected (tough-rinded) fruit (Norconk 2007). The dentition of sakis allows them to breach hard fruits and their molars' decussated enamel (crossing of rods of the enamel in an x-shaped pattern) prevents it from cracking under the pressure required to do this (Norconk and Veres 2011). Thus, sakis are able to consume seeds with both hard and soft pericarps. This dental adaptation allows sakis to feed on fruit and seeds in various stages of ripeness throughout the year. Sakis' seed-rich diet may compensate for seasonal fruit shortages since seeds compose a higher proportion of their diet in the dry season (Norconk 2007; Norconk & Setz 2013). Sakis supplement their fruigovrous diet with young leaves, flowers from trees, shrubs, lianas and hemiparasitic plants, and insects (Norconk & Setz 2013).

Monk Sakis (*Pithecia monachus*)

Monk sakis are found in upper Amazon basin within the borders of Brazil, Columbia, Ecuador and Peru (see Fig. 3; March & Veiga 2008a). Monk sakis are widely distributed and common in Peru and have been reported in the departments of Amazonas, Huánuco, Pasco, Loreto and Ucayali (Aquino and Encarnación 1994, Hershkovitz 1987). Monk sakis have been found to occur sympatrically with equatorial sakis in most areas where equatorial sakis are found (Aquino et al. 2009).

Sakis, in general, are threatened by habitat loss, hunting, capturing of infants as pets and use of their tails and teeth in local handicrafts (Aquino and Encarnación 1994, Marsh and Viega 2008a). The IUCN Red List of Threatened Species categorizes monk sakis as of least concern (Marsh and Viega 2008a), although there are few studies of monk sakis that would support actual population numbers. Monk sakis are afforded refuge in three protected areas in Peru, Tingo Maria National Park, Pacaya-Samiria National Reserve and the Área de Conservación Regional Comunal Tamshiyacu Tahuayo (Porter et al. 2013).

Monk sakis are only minimally sexually dimorphic (Hershkovitz 1987), making identification of adults in groups challenging. Both males and females have similar body coloration consisting of dark brown to black fur on the back and limbs, brown to black fur on the chest and belly, and pale hands and feet (Hershkovitz 1987; Aquino and Encarnación 1994; Emmons 1997). The differences between male and female monk sakis are observable in their faces and crowns. Males have creamy to yellow malar stripes, crown fur that hangs over the face and is the same color as their back and body, and short, pale fur around the face (see Fig. 1; Hershkovitz 1987; Aquino and Encarnación 1994). In contrast, females have more consistent, less distinct, smaller malar stripes and thicker facial pelage that hides the skin on the face (see Fig. 2; Hershkovitz 1987; Aquino and Encarnación 1994).

Figure 1. Photo of an adult male monk saki taken during the study on July 16, 2015 in the ACRCTT.

Figure 2. Photo of an adult female monk saki taken during the study on July 16, 2015 in the ACRCTT.

Equatorial Sakis (*Pithecia aequatorialis*)

Equatorial sakis are found in the upper Amazon basin within the borders of Ecuador and Peru (see Fig. 3; Marsh & Veiga 2008b). Compared with monk sakis, equatorial sakis are reported to have a much narrower range in Peru. According to a prior study on the geographic distribution of equatorial sakis in Peru, their range is delimited by the Marañón, Amazon, Corrientes, Tigre, Curaray and Napo rivers (Aquino et al. 2009). There are no published reports of equatorial sakis south of the Amazon River. During a rapid biological inventory of the Yavarí River area (included in the ACRCTT), monk sakis were observed, but no equatorial sakis were found (Pitman et al. 2003). However, even though no equatorial sakis were reported during the rapid biological inventory, it could be easy to overlook them or confuse them with monk sakis given their cryptic behavior and similar morphology. Chism et al. (in review) do report equatorial sakis as inhabiting the ACRCTT, which is located south of the Amazon River.

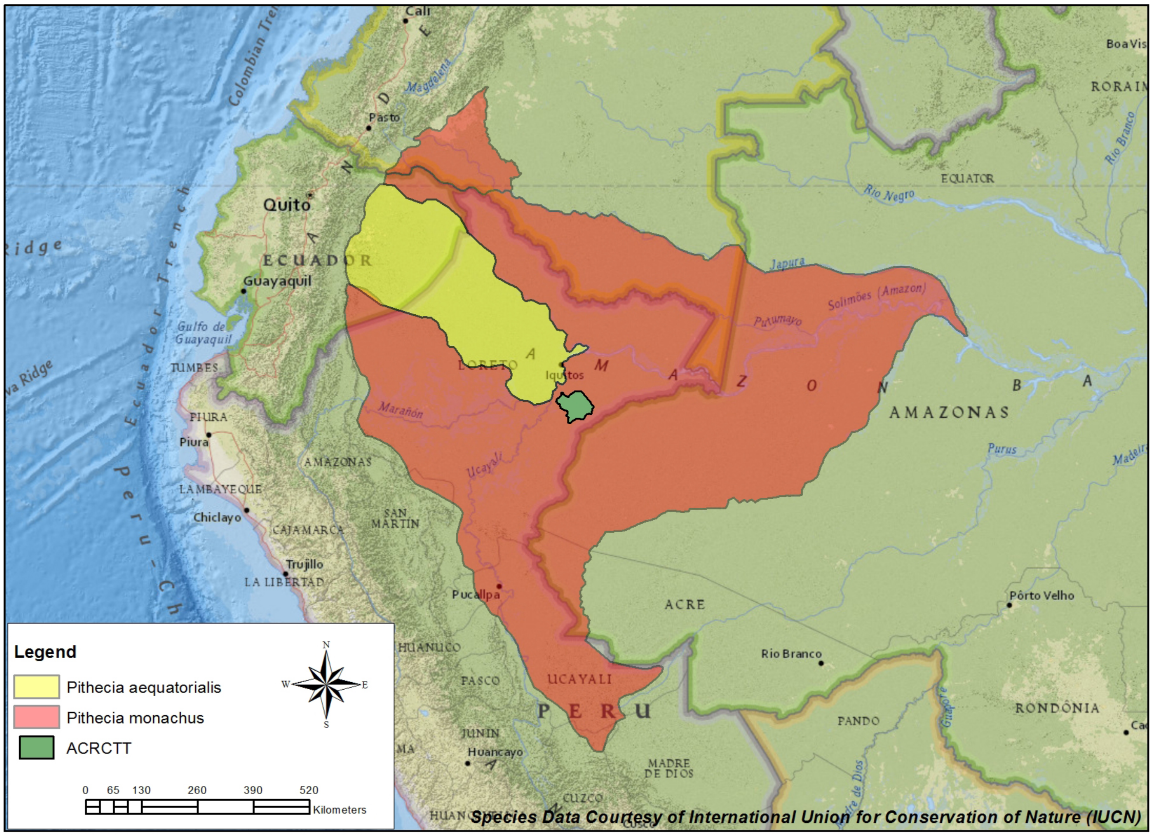

Figure 3. Map showing the range of equatorial sakis (yellow) and monk sakis (red), along with the boundaries of the ACRCTT (green). Species distribution data used by permission of the International Union for Conservation of Nature (IUCN).

Equatorial sakis are one of the least studied neotropical primates (Aquino et al. 2009). Part of this is due to their cryptic behavior and part is because they are very susceptible to hunting pressure, which is increasing in many areas (Aquino and Encarnación 1994). Equatorial sakis are categorized as of least concern on the IUCN Red List, although Marsh and Veiga (2008b) emphasize that the distribution of the species is not well known. Porter et al. (2013) state equatorial sakis are afforded no official protection in Peru. However, confirmation of equatorial sakis living within the ACRCTT (Chism et al. in review) would mean that at least one protected area in Peru contains a population of equatorial sakis.

There are some variations between the morphological descriptions of equatorial sakis by Hershkovitz (1987), Aquino and Encarnación (1994), and Emmons (1997), most notably in the description of color of fur on the heads of males. Hershkovitz (1987) describes equatorial males having red fur on their heads, while Aquino and Encarnación (1994) and Emmons (1997) describe males with creamy to buffy fur on their heads. These disagreements about the species appearance could be a result of the limited amount of observations and lack of studies of equatorial sakis in the wild. It is also possible that populations experience enough isolation due to geographic barriers of rivers that they have developed into distinct subspecies or at least different morphs. Chism et al. (in review) suggest that the second saki morph in the ACRCTT is *P. aequatorialis*. Here, I will use the description by Chism et al. for identification of equatorial sakis in the ACRCTT.

In contrast with monk sakis, and as reported by Hershkovitz (1987), equatorial sakis are sexually dichromatic (Figure 4). Both males and females share the characteristics of white malar stripes, dark-brown to black fur on the back and limbs, patches of reddish-brown fur on the chest and shoulders and pale hands and feet. Males have short, reddish-brown to buffy fur above the brow, a triangular area of darker fur between the brows, pale cheek fur, and their faces appear muscular with well defined muzzles. Females lack the reddish-brown fur on their foreheads and instead have pale-grayish fur around the face; their faces lack the muscular look of the males (Chism et al. in review).

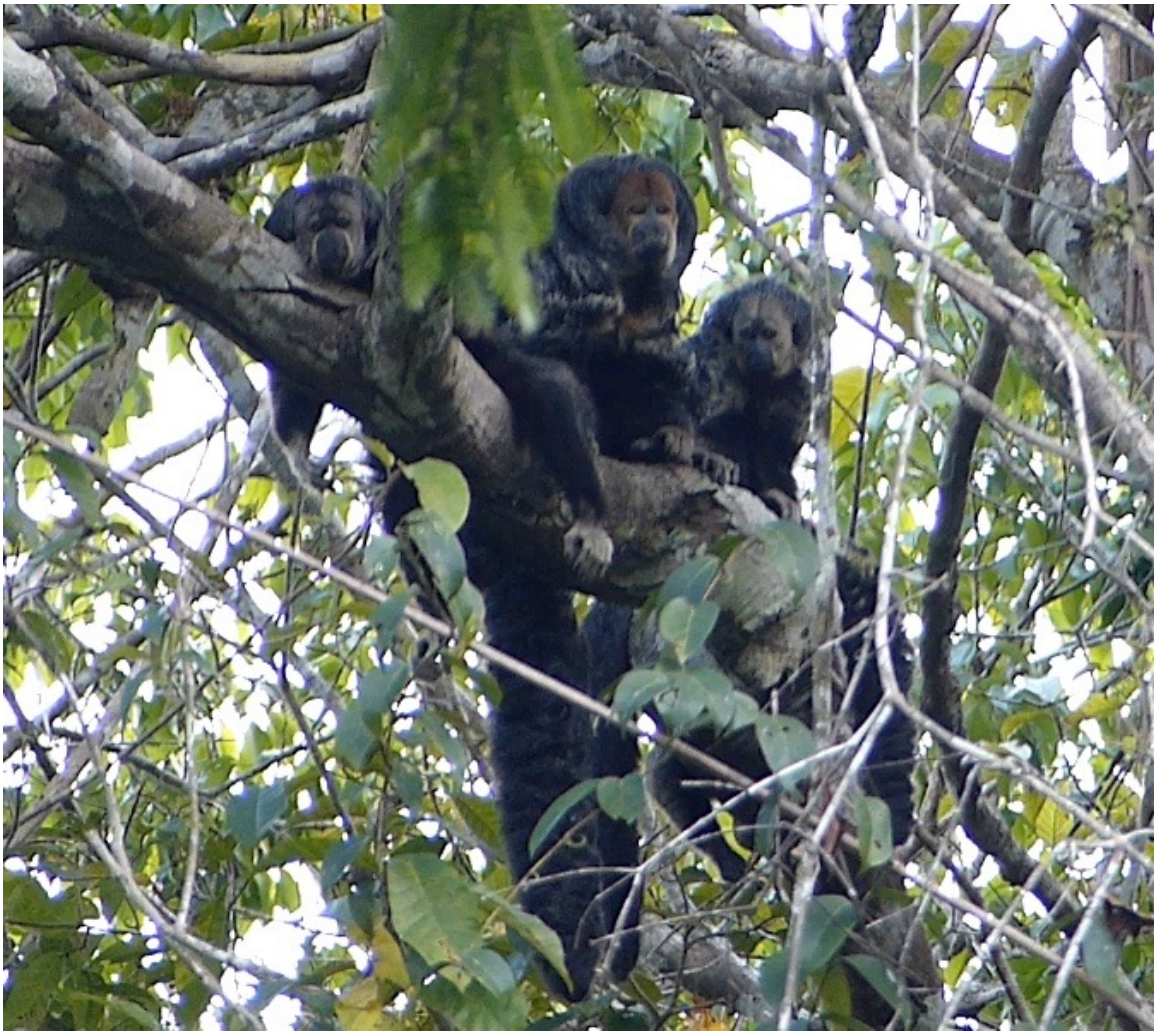

Figure 4. Photo of an adult female equatorial saki (left), adult male equatorial saki (middle) and juvenile equatorial saki (right) taken during the study on June 26, 2015 in the ACRCTT.

Habitat

The Amazon basin in Peru contains approximately 660,000 km^2 of tropical lowland rain forest of which approximately 20% is subject to annual monomodal flooding (Kvist & Nebel 2001). In Iquitos, the city nearest to the ACRCTT, a 10-year study showed the average peak flooding occurred between March-May and the lowest water levels occurred between August-October, with a difference of 8-10 meters between the high and the low water levels during this time period. (Kvist & Nebel 2001).

There are many different habitat types within the tropical lowland forest of the Peruvian Amazon basin, but they can generally be divided into flooded and unflooded forests. Unflooded forests, referred to hereafter as terra firme forest, are not subject to the seasonal flooding patterns, while flooded forests are subject to the seasonal flooding patterns. Kvist & Nebel (2001) estimate that during the average peak flooding, more than 90% of the forests subject to seasonal flooding are covered with water, while at the low water point, less than 10% of the flood plain remains as lakes, rivers and swamps. In years where the water rises 1-2m above the average peak, 100% of these forests will be inundated with water.

Flooded forests can be divided into two types based on the water type of the river they are associated with. The first, várzea forests, are forests seasonally flooded by white-water rivers that dominate the Peruvian Amazon basin. White-water rivers, which are turbid and are close to a neutral pH, carry a nutrient-rich alluvial suspension from the Andes (Prance 1979; Kvist and Nebel 2001). While called white-water rivers, they are actually muddy reddish-brown in color. The nutrient-rich soil of várzea affects the strategies of the resident flora that enjoy a more nutrient-rich growing environment as compared with the leached soil of terra firme or the sandy soil of igapó forests, and results in higher net primary production of vegetation cover compared to terra firme or igapó forests. Várzea has the highest species richness of flora of any floodplain forest in the world (Wittmann et al. 2010).

The second type of flooded forest in the Peruvian Amazon basin is igapó forest. Igapó forests are seasonally flooded by black-water rivers. Black-water rivers, which are a dark brown color and acidic due to colloidal suspension of plant compounds, originate in sandy areas and are therefore nutrient-poor (Prance 1979; Kvist and Nebel 2001). Igapó forests usually contain less-productive vegetation compared to várzea due to the absence of nutrient-rich alluvial suspensions that white-water rivers contain. Tree species richness is poorer in igapó forest compared to várzea forest (Wittmann et al. 2010). However, the igapó forests of Peru are often várzea-like in their vegetation, as their soil tends to be richer than igapó forests further down the Amazon River (Prance 1979). This appears to be the case at our study site where both igapó and várzea forests appeared visually very similar and rich in vegetation, as opposed to the poor vegetation described by Prance (1979) associated with typical igapó forest that can often be desert-like when it dries out. A compensatory strategy of igapó trees for growing in nutrient-poor soils of black-water rivers is to invest heavily in nutrient-rich seed mass (Parolin 2001). Large, well-protected, nutrient-rich seeds are a specialty of saki monkeys, so one would expect to find sakis in igapó forest.

The 80% of the tropical lowland rain forest in the Peruvian Amazon basin that is not subject to annual flooding is collectively referred to as terra firme. As terra firme does not benefit from the annual deposition of alluvial sediments, the soil of terra firme is typically leached and nutrient-poor (Haugaasen and Peres 2005). Nevertheless, tree species richness is higher in terra firme than in either várzea or igapó flooded forest because the soil in flooded forest is subjected to a periodic lack of oxygen during times of inundation with water. Despite the differences in species richness, representatives of almost all of the neotropical woody plant families can be found in flooded forests and terra firme (Wittmann et al. 2010).

Área de Conservación Regional Comunal Tamshiyacu Tahuayo

The Área de Conservación Regional Comunal Tamshiyacu Tahuayo (ACRCTT) is a communal reserve located in Loreto Department in northeastern Peru (Figures 5, 6). The reserve was established in 1991 as a unified response by local inhabitants, conservationists and researchers to loggers and hunters coming into the area from outside the region and extracting resources, and for the protection of the endangered red uakaris (*Cacajao calvus ucayalii)* (Meyer and Penn 2003, Newing and Wahl 2004). The ACRCTT was the first protected area in Peru to contain the vulnerable red uakaris (Veiga et al. 2008).

Communal reserves in Peru were established as a means to protect large areas of land wherein the resident populations were able to secure subsistence rights over resources while prohibiting any commercial use or settlement of the land. In the case of the ACRCTT, the reserve was created at the regional level with management responsibility of the reserve falling to the local communities (Newing and Bodmer 2003, Newing and Wahl 2004). The ACRCTT falls under the classification of a *Category VI Protected Area with Sustainable Use of Natural Resources* as defined by the International Union for the Conservation of Nature (IUCN 2012). The primary objective of a Category VI Protected Area is to protect a natural ecosystem while allowing limited, low-level, non-industrial resource use to local communities where conservation and sustainable use proves to be mutually beneficial. Secondary objectives of a Category VI Protected Area include protecting ecosystems and habitats, protecting threatened species and facilitating scientific research (IUCN 2012).

The reserve originally was comprised of 325,000 hectares of flooded forest and terra firme within the boundaries of the Tamshiyacu, Yarapa, Yavarí Mirí and Blanco rivers (Meyer and Penn 2003). In 2009, the reserve was upgraded to a state reserve and the size of the reserve was increased to 420,080 hectares (Penn 2009).

https://maps.google.com/?ll=-9.557417,-71.850586&spn=21.011257,33.815918&t=m&z=6

Figure 5. Map showing the location of the ACRCTT within Peru. Map downloaded from Google (https://maps.google.com).

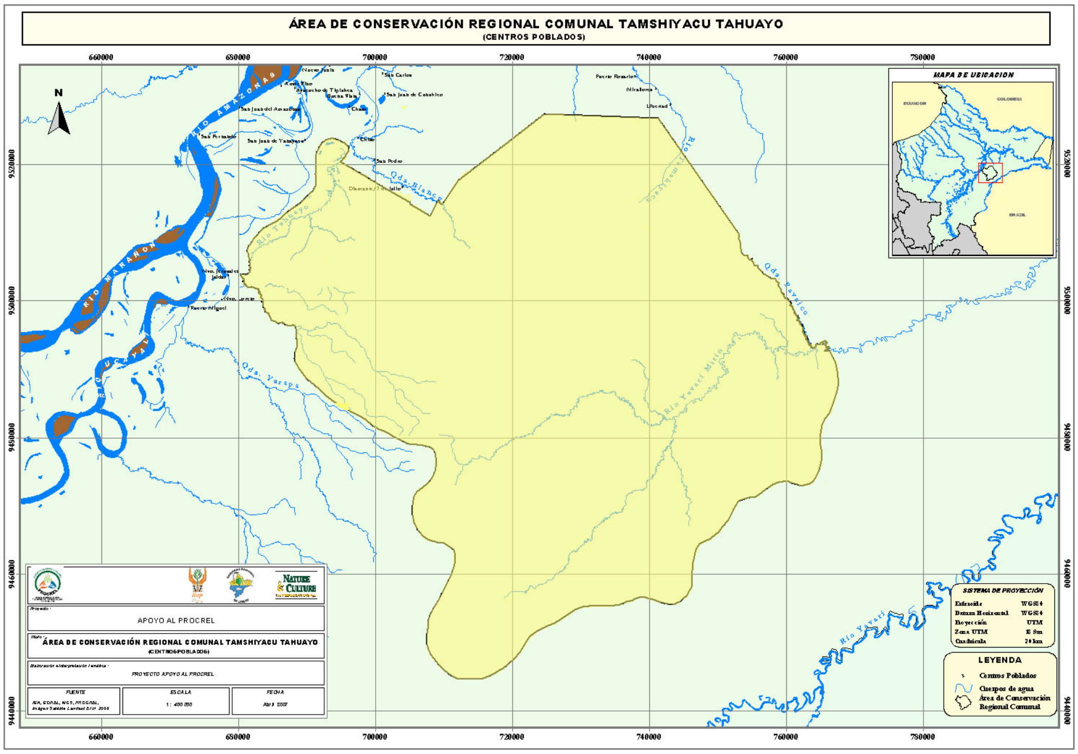

Figure 6. Map showing the ACRCTT and its boundaries. Map courtesy of Amazonian Expeditions (www.perujungle.com).

Primate Species Richness

Primate species richness, density and biomass vary by type of forest in the Amazon basin. Primate species richness is reported to be higher in terra firme, while primate density and biomass is reported to be higher in flooded forest (Haugaasen and Peres 2005). Haugaasen and Peres (2005) speculate this is due to the poorer plant species richness in flooded forest compared to terra firme and differences in flora composition. They do report that seasonal fruiting in flooded forest often results in an influx of primates into flooded forest. There are at least fourteen species of primates that have been reported to live sympatrically within the ACRCTT (see Table 1, Aquino and Encarnación 1994, Pittman et al. 2003, Puertas & Bodmer 1993, Chism et al. in review). Puertas and Bodmer (1993) also report a second species of squirrel monkey potentially occurring within the ACRCTT (*Saimiri bolvienis*), which would bring the count of sympatric primates up to fifteen, although that species has not been confirmed in the study area of this project.

Table 1. Primate species occurring in the study area within the ACRCTT (sources: Aquino and Encarnación 1994, Pittman et al. 2003, Puertas & Bodmer 1993, Chism et al. in review)

Scientific Name	**Common Name**
Alouatta seniculus	Red howler monkey
Aotus nancymaae	Owl monkey
Ateles paniscus	Black spider monkey
Cacajao calvus ucayalii	Red uakari
Callicebus cupreus	Coppery titi monkey
Cebuella pygmaea	Pygmy marmoset
Cebus albifrons	White-fronted capuchin
Cebus apella	Brown capuchin
Lagothrix lagotricha	Humbolt's woolly monkey
Pithecia aequatorialis	Equatorial saki
Pithecia monachus	Monk saki
Saimiri sciureus	Common squirrel monkey
Saguinus fusciollis	Saddleback tamarin
Saguinus mystax	Moustached tamarin

RATIONALE

As previously noted, there is very little research on saki monkeys in general and on monk and equatorial sakis in particular. To a great extent, the behavior and ecology of monk and equatorial sakis is still a mystery, including habitat partitioning. While monk and equatorial sakis are reported to be sympatric and syntopic (Aquino et al. 2009; Chism et al. in review), no studies were found that specifically look at habitat partitioning between these two species. Aquino and colleagues (2009) ask whether monk and equatorial sakis are separated by habitat type in areas where they occur sympatrically, and if hybridization occurs between the two species in those same areas?

While many studies have confirmed that monk sakis inhabit the ACRCTT (Puertas and Bodmer 1993; Aquino and Encarnación 1994; Porter et al. 2013), there is recent evidence that equatorial sakis also inhabit the ACRCTT (Frisoli 2009; Kieran 2012; Chism et al. in review). Thus the ACRCTT is an ideal location to test the habitat preferences of monk and equatorial sakis as both species have been reported to live sympatrically and syntopically within the reserve's boundaries. The ACRCTT also provides a good mixture of terra firme and igapó forests in which to conduct research on their habitat preferences.

Hardin, building on the work of Gause and others, describes the competitive exclusion principle as the idea that two species should not occupy the same ecological niche as one of the competitors will displace the other or drive it to extinction (Hardin 1960). The research described in this thesis hopes to shed light on whether and how these two sympatric saki species, that appear to occupy the same ecological niche of arboreal seed predators, actually partition their niches.

My first question was: Are monk and equatorial sakis separating themselves by habitat type in the ACRCTT? My hypothesis was that monk and equatorial sakis are separating themselves by forest type in the ACRCTT. My hypothesis led to two further predictions. First I predicted that monk sakis would be more likely to be found in terra firme forest than in igapó forest, as the genus *Pithecia* in general, and monk sakis in particular, have been described as preferring terra firme forest. In a three-year study of bald-faced sakis (*P. irrorata*) in Peru, Palminteri and Peres (2012) concluded they are terra firme specialists, but not obligates. Emmons (1997) suggested that while monk sakis can be found in flooded forest, they are usually found in terra firme.

On the other hand, there is some evidence that although they also can be found in terra firme, equatorial sakis may prefer flooded forest (Emmons 1997). Hunters who reside in the ACRCTT report that equatorial sakis are typically found in flooded forest, while they report seeing monk sakis most often in terra firme (Chism et al. in review). Thus, my second prediction was that equatorial sakis are more likely to be found in igapó forest than terra firme forest.

Earlier surveys reported that monk sakis are the more common saki species in the ACRCTT. A rapid biological inventory of the ACRCTT suggested that monk sakis were the only saki species living in the ACRCTT (Pitman et al. 2003). Aquino and Encarnación (1994) also reported monk sakis as the sole saki inhabitants of the ACRCTT, although they cautioned that previous inventories may have been incorrect in listing monk sakis as the only saki species when equatorial sakis may have also been present. Thus, my second question was: Are monk sakis the more common saki species in the ACRCTT as earlier surveys have suggested?

This study has important conservation implications with regard to protection of sakis in flooded forest habitat. Ecological pressure from human activity, such as hunting, and habitat disturbance from logging, agriculture and harvesting of resources (such as aguaje palm fruits, *Mauritia flexuosa*), is more concentrated in riverine forests, to which access is easier than to terra firme (Kvist and Nebel 2001). Understanding the habitat preference of both equatorial and monk sakis is of great conservation importance to both the sakis and the flooded forest habitat. Most of the area of the ACRCTT is terra firme forest, with only a small portion being protected flooded forest (Puertas & Bodmer 1993). So even if equatorial sakis are protected by being in the reserve, they are less protected by virtue of having more vulnerable habitat.

Finally, there have been reports of possible hybridization occurring between equatorial and monk sakis (Chism et al., in review). If this is occurring, then understanding equatorial and monk saki habitat partitioning could shed some light on this phenomenon and what is driving it.

MATERIALS AND METHODS

Field Sites

The Tahuayo River Amazon Research Center (TRARC) (S 04° 23.334’, W 073° 15.438’, Figure 7) is a research station located on the black-water Tahuayo River within the ACRCTT. I used the TRARC as a base of operations from which I collected data from five different locations within the ACRCTT. The first three locations were accessible from the TRARC. The last two locations required traveling by boat to reach the locations and camping overnight in the area.

My first study site consisted of a 400 ha. trail grid located at the TRARC and running southeast from the Tahuayo River. The trail grid consists of 42 intersecting trails spaced approximately 100m apart, creating a 2km x 2km grid (Figure 7). In addition, a trail starting behind the research station that runs between the trail grid and the river (known locally as the *River Trail*) was also included in this study site. This study site consisted of igapó forest.

The second study site was the igapó forest on either side of the Tahuayo River. Starting at the TRARC, both canoes and small johnboats were used to travel upriver and downriver from the TRARC. A flooded area known as the Colpayo adjacent to the Tahuayo River was also included in this study site (Figure 7). The range of this study site was approximately 5km upriver from the TRARC and 5km downriver from the TRARC.

The third study site was a series of trails in terra firme forest located east of the trail grid. This series of trails was accessed by hiking in approximately

800m beyond the end of the trail grid (S 04° 25.073’, W 073° 14.009’, Figure 7). These trails were cut in prior years for a red uakari research project and were not maintained. My surveys included approximately 6 km of trails in this location.

The fourth study site was in terra firme located adjacent to the Tangarana River, a tributary of the Tahuayo River (S 04° 26.226’, W 073° 15.038’, Figure 7). Unlike the Tahuayo River, the Tangarana River is a white-water river. There were no existing trails at this location. I hiked in approximately 5 km and then hiked out another 5km taking a slightly different route.

The last study site was a series of trails in terra firme located behind the village of Diamante along the Blanco River, a tributary of the Tahuayo River (S 04° 22.252’, W 073° 09.697’, Figure 7). The Blanco River is a white-water river. The inhabitants of Diamante created this trail system to extract resources from the forest and the local people use these trails on a regular basis. I surveyed approximately 13 km of trails at this site.

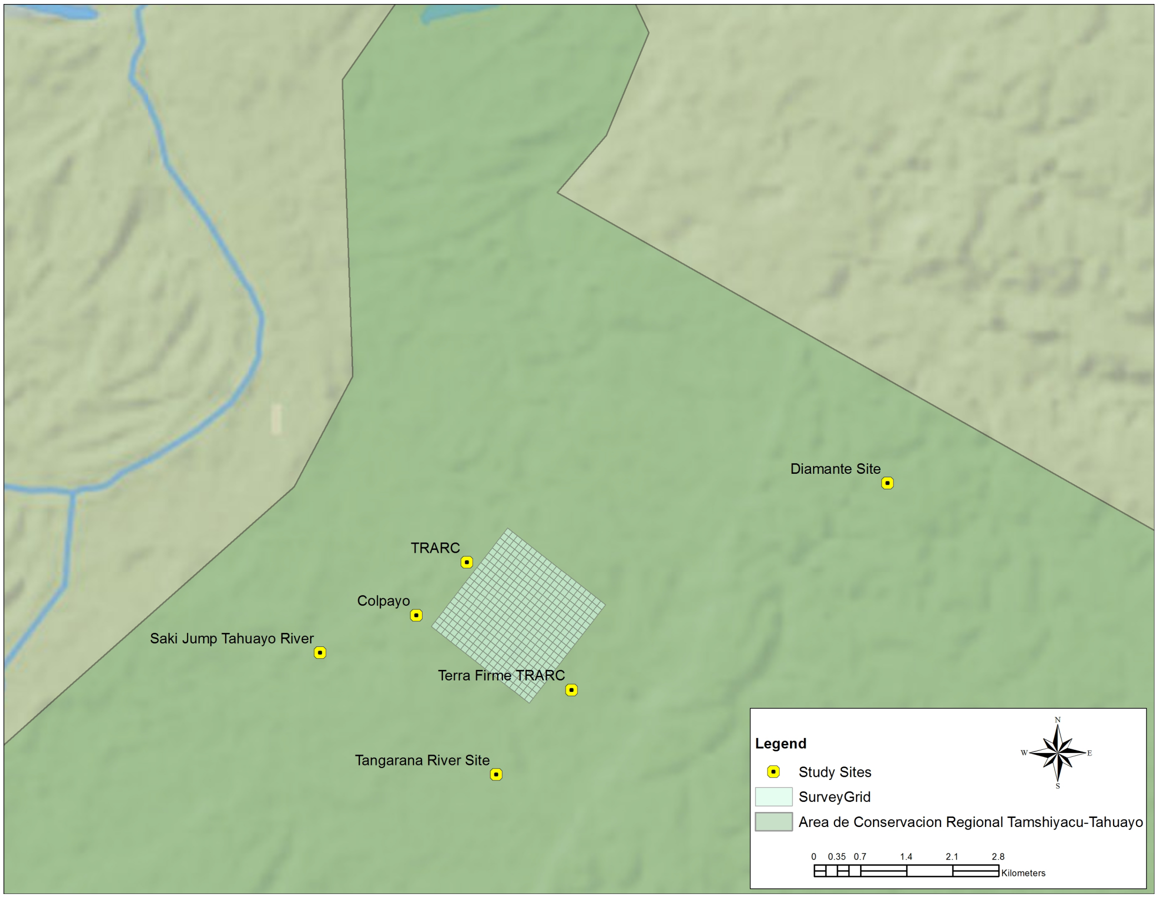

Figure 7. Map of study sites. The ACRCTT is shown in dark green and the trail grid is shown in light blue. The TRARC, Colpayo and Trail Grid are all within igapó flooded forest. The Terra Firme TRARC, Diamante Site and Tangarana River Site are all within terra firme forest. The location on the Tangarana River where I observed the male equatorial saki jumping the river is also shown on this map. Bryan McFadden at Winthrop University created this map.

Data Collection

Data were collected between June 17, 2015 and July 28, 2015. The start date was chosen in anticipation that by then I would be able to walk on the trail grid because the annual flooding would have receded such that the trail grid would be above water. The normal difference between the high and low water level at the TRARC is roughly 12m (personal comm. A. Dosantos Santillan). However, flooding in 2015 at the TRARC and the surrounding areas was higher and more prolonged than normal. I was able to walk the highest portions of the trail grid (reachable only by canoe) on June 20, but it was not until the first week of July that most of the trail grid could be reliably accessed on foot. During this prolonged period of flooding, I surveyed the trail grid by canoe. By the time the study was finished, the entire trail grid was accessible by foot.

The two flooded forest sites (Trail Grid and the Tahuayo River) were immediately accessible from the research station. Data collection in terra firme sites (Diamante and Tangarana River) required overnight trips or long hikes away from the research station (TRARC Terra Firme). This is the primary reason data were not collected evenly between flooded forest and terra firme.

Data Collection in Flooded Forest

Data were obtained in igapó forest both by walking transects and searching for saki monkeys from canoes and small johnboats. As conditions permitted, most mornings I would search a portion of the trail grid by canoe (on days when the grid was still inundated by water) or by waking (after the water had receded). Most afternoons I would search a portion of the igapó forest along the edges of the river by canoe or johnboat. At the beginning of the study, it was possible to take the canoes into the flooded forest on either side of the Tahuayo River. By the end of the study, the water had dropped approximately 10m and the forest on either side of the Tahuayo River could only be observed from a canoe or boat in the river. This schedule depended on the weather, as I did not attempt observations when it was raining, because saki monkeys are very hard to see and hear in the rain. If it started raining while I was out searching for sakis, I would wait fifteen minutes to see if the rain would stop so I could continue my search. If the rain did not stop in fifteen minutes, I would end that search period.

Data Collection by Walking Transects

I walked both the trail grid and the river trail at a pace of approximately 1.25-1.50 km per hour, pausing regularly to scan the trees for signs of sakis and to listen for saki calls. I used Nikon Monarch 5 8x42 binoculars to search for and observe sakis in the trees. At all times I had a local trained field assistant with me who assisted in locating and collecting data on saki groups.

When a saki group was located, I recorded the time detected, number of group members, identification of all group members by sex/age (male/female, adult, sub-adult, juvenile, infant), species, behavior observed, length of time observed, GPS coordinates (using a Garmin GPSmap 62s), grid coordinates (if applicable), estimate of the group's location in the canopy (visually dividing the canopy into upper, middle and lower thirds), habitat type (igapó vs. terra firme forest), and weather conditions. When conditions were favorable, I used a Panasonic Lumix FC200 digital camera to take pictures and record video and sound of the saki groups encountered.

As the purpose of this project was to locate and identify the species of as many saki groups within the study sites as possible, locations were chosen each day based on where I thought I would be most likely to encounter saki groups. Locations were often chosen based on reports of guides and tourists at the TRARC who had recently seen sakis. At the same time, I varied where I searched on the grid from day to day to cover as much of the grid as possible during my time of study. During a typical day I would chose an area of the grid to search and then walk in a zig-zag pattern using the grid trails to cover as much area as possible. When I encountered a saki group, I would stop the search and follow that group as long as visual or auditory contact could be maintained.

Data collection by Canoe and Johnboat

When searching by canoe, I had a field assistant who piloted the canoe while I observed the flooded forest. When canoes were not available, or if I wanted to travel farther up or down the Tahuayo River than could be done in a canoe, observations were made from small johnboats piloted by my field assistant. While I traveled at a slow pace in the johnboat, the pace was faster than in a canoe. Even though the johnboats' gasoline engines made noise, that did not seem to impede finding saki groups along the river. My assumption is the sakis have become habituated to the sound of boats on the river. When a group was located we stopped the engine and were able to conduct observations of the saki groups using a paddle to hold our place in the river. The same kinds of data recorded while walking transects were recorded while observing from canoes and johnboats.

Additional Participants in Data Collection

Dr. Janice Chism participated in the data collection from 17-28 June. During this time Dr. Chism instructed me in observation techniques. All observations from 17-28 June where made by both myself and Dr. Chism working together except for 24-26 June when I was in terra firme and Dr. Chism remained at the TRARC to continue searching for sakis and collecting data.

I also had the assistance of two interns who assisted with the collection of data from 2 July to 28 July. The first few days they accompanied me during data collection as I trained them and their field assistants in observation techniques. From 11 July until the study ended, the interns conducted separate observations on the trail grid and along the Tahuayo River in canoes. The interns were always accompanied by field assistants and followed the same methods as I did. Having the interns searching for saki groups in different locations from where I was working increased the sample size of groups encountered and helped give a better idea of how many groups were in the area.

Data Collection in Terra Firme

Data were collected in terra firme using the same methods as walking transects in flooded forest. Existing trails were used in terra firme habitat located beyond the TRARC trail grid and in terra firme habitat adjacent to the village of Diamanté. There were no existing trails in terra firme habitat at the Tangarana River site, thus the field assistants cut our own trail at this location as needed.

Data Analysis

Two sets of data were collected in igapó habitat, a large data set by me and a smaller data set by the interns. Similarly, the interns and I collected two data sets in terra firme habitat. In each case, the two sets of data were collected using the same methods. I used the Kruskal-Wallis test (Dythem 2011) to determine whether the two sets of data collected in igapó habitat could be combined into one homogenous set and to determine whether the two sets of data collected in terra firme habitat could be combined into one homogenous set.

In order to determine whether equatorial sakis were more likely to be found in igapó habitat than in terra firme habitat, I first calculated the average number of equatorial sakis encountered per hour of search effort for each individual search excursion both in igapó and terra firme. I then used the Rank Sum Test based on the White modification of the Wilcoxon Rank Sum Test (Ambrose and Ambrose 1987) to see whether there was a significant difference in encounter rates between the two habitats. The Rank Sum Test is a non-parametric test of differences between means of two samples of unequal size, and this test allowed me to compare the results between my unequal efforts in igapó and terra firme habitats.

All of the effort in searching for saki groups consisted of searching for both equatorial and monk saki groups simultaneously. In order to determine whether monk sakis are the more common saki species in the ACRCTT, I used the chi-squared goodness of fit test (Dytham 2011) to compare the number of equatorial saki groups and monk sakis groups found in all habitats. In order to determine whether equatorial sakis are more likely than monk sakis to be found in igapó habitat, I used the chi square goodness of fit test (Dytham 2011).

RESULTS

Combination of Data Sets

I searched for sakis for a total of 215.22 hours in igapó habitat and found 14 groups of equatorial sakis and 1 group of monk sakis. The interns searched a total of 80.06 hours in igapó habitat and found 7 groups of equatorial sakis and no monk saki groups (Table 2). As I had one large data set and one smaller data set of equatorial sakis in igapó habitat and I wanted to know whether I could combine them or whether they had to be analyzed separately, I performed a Kruskal-Wallace test to determine the homogeneity of the two data sets of equatorial sakis in igapó habitat. The results of the Kruskal-Wallace test affirmed the null hypothesis and indicated the combined data of the igapó habitat searches was one homogenous data set (n=97, x^2=1.510, p=0.219, d.f.=1).

I searched for sakis for a total of 20.45 hours in terra firme habitat and found 3 groups of equatorial sakis and no groups of monk sakis. The interns searched a total of 8.0 hours in terra firme habitat and found no groups of either equatorial or monk sakis (Table 2). As I had one large data set and one smaller data set of equatorial sakis in terra firme habitat and I wanted to know whether I could combine them or whether they had to be analyzed separately, I performed a Kruskal-Wallace test to determine the homogeneity of the two data sets of equatorial sakis in terra firme habitat. The results of the Kruskal-Wallace test affirmed the null hypothesis and indicated the combined data of the terra firme habitat searches was one homogenous data set (n=7, x^2=0.933, p=0.334, d.f.=1).

Table 2. Search effort and saki groups observed.

	Total Search Effort	Number of Equatorial Saki Groups Observed	Number of Monk Saki Groups Observed
Igapó Habitat	295.28 hours	21	1
Terra Firme Habitat	28.45 hours	3	0
Totals	323.73 hours	24	1

Equatorial Saki Habitat Distribution

In a combined effort of searching for sakis in igapó habitat for 295.28 hours, a total of 21 groups of equatorial sakis were observed for a mean encounter rate of 0.071 groups of equatorial sakis encountered per search hour. In a combined effort of searching for sakis in terra firme habitat for 28.45 hours, a total of 3 groups of equatorial sakis were observed for a mean encounter rate of 0.105 groups of equatorial sakis encountered per search hour (Figure 8). The Rank Sum Test (based on the White modification of the Wilcoxon Rank Sum Test) indicated there was no difference in the rate at which equatorial sakis were encountered in igapó vs. terra firme habitats (T=349, m=367.5, S=77.1, Z=0.234<1.96, n.s.).

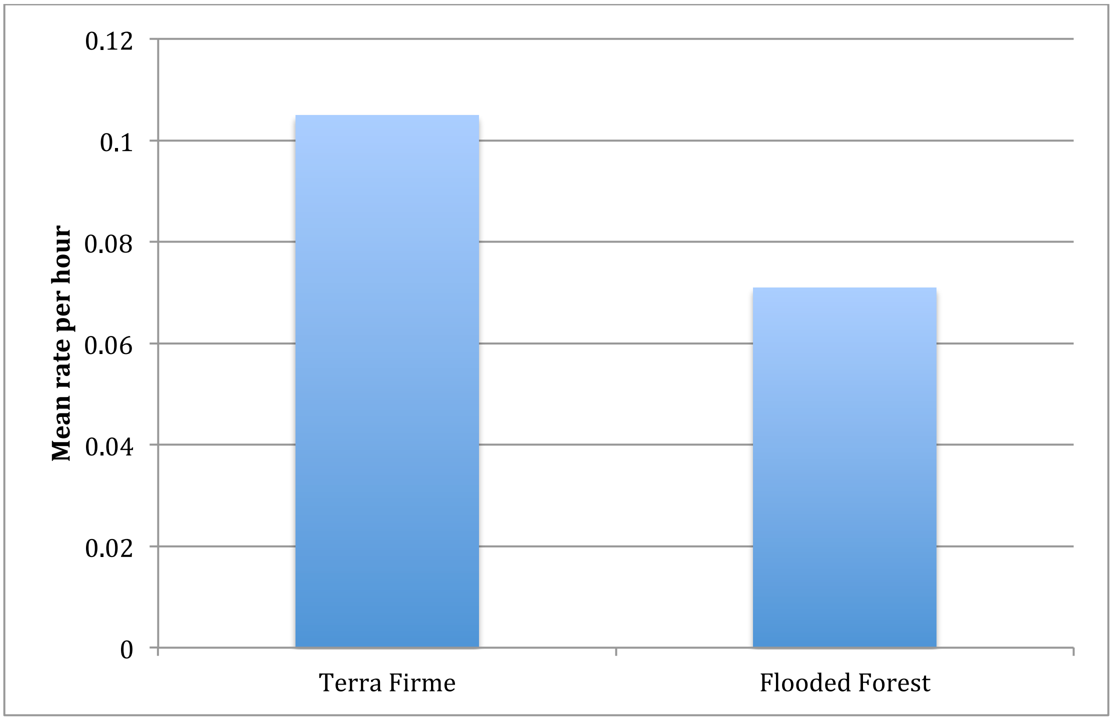

Figure 8. Mean equatorial saki groups encountered per hour in terra firme and flooded forest habitats.

Monk Saki Habitat Distribution

During the 28.45 hours of searching for sakis in terra firme habitat, no monk sakis were encountered. During the 295.28 hours of searching for sakis in igapó habitat, I encountered one group of monk sakis. In addition, a tourist also encountered one group of monk sakis in flooded forest during the study period as confirmed by photos the tourist took of the group. Comparing the photos of the monk saki group I encountered (one adult male and one adult female) to the monk saki group the tourist encountered (one adult male and one adult female), it appeared that these were two distinct groups. There are not sufficient data to test the hypothesis that monk sakis are more likely to be found in terra firme than igapó forest, although the two monk saki groups encountered during our search were found in igapó forest.

Estimates of Minimum Number of Equatorial Saki and Monk Saki Groups Encountered

Both sightings of monk saki groups occurred on the trail grid and comparison of pictures of both groups suggests these are a minimum of two monk saki groups with home ranges that include the trail grid (Table 3).

During the entire study period we encountered nine equatorial saki groups on the trail grid (Table 3). On July 20, I encountered two equatorial saki groups having an intergroup encounter in the northwest quadrant of the grid and, therefore, I am certain of two separate saki groups with home ranges that overlap in this area. On July 26, the interns encountered two different equatorial saki groups in the southeast quadrant of the grid and, therefore I am certain of two separate saki groups with home ranges that overlap in this area. It is unlikely that the groups found in the northwest quadrant are the same groups found in the southeast quadrant. The remaining five equatorial saki groups observed during the study were all observed on different days. One of the groups was observed in the southwest quadrant and the remaining four groups were observed in the northwest quadrant. It is possible that the four groups observed in the northwest quadrant are from the same two groups observed on July 20 and are not counted as distinct groups. It is possible that the group observed in the southwest quadrant is a distinct group. Therefore, I estimate I encountered a minimum of five different equatorial saki groups on the trail grid.

During the entire study period we encountered equatorial saki groups on twelve different days in the Tahuayo River study area (Table 3). Three equatorial saki groups were observed downriver from the research station. One of these groups was observed at the far limits of the area searched and I consider this group to be distinct from the two other groups that were observed a short distance from the research center. For the minimum group estimate, I counted the two equatorial saki groups observed a short distance downriver from the research station as one group, for a total of a minimum of two groups observed downriver from the research station.

Nine equatorial saki group sightings occurred upriver from the research station. Two of the sightings were the same equatorial group in a sleeping tree that I observed on the afternoon of 21 July and the morning of 22 July on the west side of the river a short distance upriver from the research center. A different group was observed on the east side of the river a short distance upriver from the research center. I observed one group of equatorial sakis in the Colpayo area and assumed it to be a group distinct from the other sightings. I observed one adult male equatorial saki jumping across the Tahuayo River (Figure 7) at a location at a sufficient distance from the other sightings to be considered distinct from the other groups observed on the Tahuayo River. As I only observed the adult male jumping across the river, I am not sure if this was a lone individual or if he was part of a group. In order to be conservative in my minimum group estimate, I do not count this male as part of a group. I observed one equatorial saki group approximately 4 km upriver from the research station and the interns observed a second equatorial saki group a similar distance upriver from the research station on a different day. For the minimum estimate, I assumed these last two groups are the same group. Two groups of equatorial sakis were observed on opposite sides of the Tangarana River a short distance upriver from the research station with different group compositions, and are counted as two distinct groups. This brings the minimum number of equatorial saki groups encountered in the Tahuayo River search area to eight (Table 3).

I observed one equatorial saki group in the Tangarana River search area. No saki groups were observed in the TRARC terra firme search area. I observed two distinct equatorial saki groups on the same day in the Diamante terra firme search area (Table 3).

Table 3. Estimates of the minimum number of distinct saki groups encountered in each search area.

	Total Equatorial Saki Groups Encountered	**Minimum Number of Distinct Equatorial Groups**	**Total Monk Saki Groups Encountered**	**Minimum Number of Distinct Monk Saki Groups**
Trail Grid – igapó	9	5	2	2
Tahuayo River – igapó	12	8	0	0
Tangarana River – terra firme	1	1	0	0
TRARC – terra firme	0	0	0	0
Diamante – terra firme	2	2	0	0
Total	24	16	2	2

Frequency of Encountering Equatorial Saki vs. Monk Saki Groups

During 323.73 hours of combined searching for all sakis in terra firme and igapó forest I encountered a minimum of 16 distinct equatorial saki groups and 2 distinct monk saki groups. Using the chi square goodness of fit test I determined that equatorial sakis are much more likely to be encountered in both habitats searched than are monk sakis (x^2=10.889, d.f.=1, p=0.0010).

During the 295.28 hours of searching for all sakis in igapó forest I encountered a minimum of 13 distinct equatorial saki groups and 2 monk saki groups. Using the chi square goodness of fit test I determined that equatorial sakis are much more likely to be found in the igapó habitat searched than are monk sakis (x^2=8.067, d.f.=1, p=0.0045).

During my study, I encountered 3 saki groups that I could not identify as equatorial or monk sakis. None of these encounters were included in any of my data.

Population Density Estimates of Sakis in Igapó Forest on the Trail Grid

The equatorial saki groups I encountered during the study ranged from 2-5 individuals per group. Based on the observations of the minimum of five equatorial saki groups on the grid, I estimate the average group was comprised of four individuals. Each of the two monk saki groups observed on the grid was comprised of two individuals. The grid is 400 hectares or 2 km^2. Based on this, I estimate the minimum population density of all sakis on the grid is 12 individuals/km^2, the minimum population density of equatorial sakis on the grid is 10 individuals/km^2, and the minimum population density of monk sakis on the grid is 2 individuals/km^2.

DISCUSSION

Habitat Preference

It appears that the monk and equatorial saki groups in my study area are not separating themselves simply by forest type. I first predicted that that monk and equatorial sakis separate themselves by forest type in the ACRCTT, with monk sakis more likely to be found in terra firme than igapó forest, but I did not collect sufficient data to test this prediction. I only observed two monk saki groups during the study period, and both were in igapó forest. I do not have sufficient data to make any kind of statement on monk saki habitat preference.

With regards to my second prediction that equatorial sakis are more likely to be found in igapó forest than terra firme forest, my data showed no significant difference in the rate at which equatorial sakis were encountered in igapó vs. terra firme habitats. As my data showed there was no difference in which forest type equatorial sakis were most likely to be encountered in, and I did not collect sufficient data to test my hypothesis that monk sakis were more likely to be found in terra firme forest than igapó forest, I cannot support my hypothesis that monk and equatorial sakis are separating themselves by forest type in the ACRCTT. The fact that equatorial sakis do not appear to have a forest habitat preference indicates that that monk and equatorial sakis are not separating themselves by igapó versus terra firme forest in the ACRCTT during this period of falling water.

While I did not find that monk and equatorial sakis are separating themselves by forest habitat, the competitive exclusion principle suggests that these two species should not be sharing the same ecological niche (Hardin

1960). I propose at least five alternative explanations for my results, all of which would require further testing.

Distance from Major Rivers as the Niche Separation Factor

The first alternative is that their niche separation is not by forest type, but that monk and equatorial sakis are separating themselves based on distance from the rivers. All of my data were collected within 5 km of one of several rivers (Tahuayo River, Tangarana River and Blanco River) in the ACRCTT, and most of it was collected within 2 km of these rivers. The ACRCTT is over 420,000 hectares (Penn 2009), and over three-quarters of the reserve is comprised of terra firme forest (Puertas & Bodmer 1993), with much of it located greater than 5 km away from the rivers (Figure 6). During my observations outside the village of Diamante in terra firme forest, one of the local hunters remarked that he only saw monk sakis at least a two-day hike into terra firme forest away from the Blanco River, and almost never close to the river. This corresponds to information provided to Chism by hunters in the ACRCTT (Chism J personal comm).

My data show equatorial sakis have no preference as to whether the forest they are found in experiences seasonal flooding. It is entirely possible that equatorial sakis have claimed the forest nearest the rivers, regardless of whether such forest floods. Pitheciins have been described as the least terrestrial of all platryrrhines, and sakis have rarely been observed on the ground (Barnett et al. 2012). As sakis spend the majority of their lives in the trees, it is entirely possible they do not differentiate between igapó and terra firme forest in their habitat selection, because seasonal flooding does not impede their movement through trees. While the structure and composition of the two forest systems differ, the igapó forests of Peru are more várzea-like than igapó forests located farther down the Amazon River (Prance 1979), and there did not appear to be a lack of fruit in the igapó forest I surveyed during my study period.

If the equatorial sakis are residing close to the rivers, it is possible that the monk sakis primarily occupy areas deeper into terra firme away from the rivers as previously suggested by local hunters. Both monk saki groups observed during my survey were sighted more than 1km east of the Tahuayo River. These two monk saki groups may have been taking advantage of seasonal fruiting, such as the aguaje palm that was fruiting during the study period. Under this alternative explanation, it is possible that the equatorial sakis have pushed the monk sakis away from the rivers or, conversely, that the monk sakis have pushed the equatorial sakis out of terra firme into the forests along the rivers.

Territories vs. Home Ranges

Very few long-term studies have been conducted focusing on saki home ranges, and most are part of general primate surveys. A review by Norconk and Setz (2013) show a home range variance for *Pithecia* spp. from 10.3 ha > 200ha. One of the few long-term studies on saki habitat use followed five bald-faced saki groups (*P. irrorata*) in Peru for three years and calculated an average home range size of 35.9 ha with four of the groups having between 5% and 33% home range overlap (Palminteri and Peres 2012). In addition to having relatively small home ranges, sakis form small social groups and have been observed exhibiting territorial behaviors (Norconk 2007). A survey of primates in Brownsberg Natuurpark, Surinam, observed repeated intergroup encounters of white-faced sakis exhibiting territorial behavior (Norconk et al. 2003). A study in Ecuador looking at adult male replacement in equatorial saki groups suggested that equatorial sakis are territorial (Di Fiore et al. 2007). Thus home range size, social structure and observations of territorial behavior point to sakis being territorial. On the other hand, an early survey that included monk sakis suggested that monk saki groups are nomadic (Izawa 1976).

A second alternative is that monk and/or equatorial sakis do not have classic territories, and that they move greater distances than previously thought to take advantage of seasonal food sources. During my study period, most of my encounters with saki groups on the trail grid occurred in the northwest quadrant of the grid while I did not encounter any sakis in the northeast quadrant of the grid. Two previous surveys of sakis during the same time of the year in 2008 and 2010 showed the highest encounter rates of sakis in the northeast quadrant of the grid (Frisoli 2009, Kieran 2012). During my study period, I observed two monk saki groups on the trail grid. In 2008 Frisoli observed monk saki groups on the trail grid, but in 2010 Kieran observed no monk saki groups on the trail grid (Frisoli 2009, Kieran 2012). In a classic territorial species, one should be able to reliably locate groups in a particular area. Both the equatorial and monk sakis on the trail grid seem to shift areas of use from year to year and none of the surveys in the trail grid have yielded groups with predictable territories (Chism personal comm.).

It is possible that their resource base is too seasonal and/or unpredictable for sakis to have small, defended territories, and that monk and equatorial saki groups are moving to areas where the fruit and seeds are available or at a concentrated food source when not much else is available. Their home ranges may be larger than previously thought, and these ranges may overlap where food resources are rich. Setz et al. (2103) hypothesize that sakis and uakaris may alter their ranging and foraging behavior on a seasonal basis related to food source availability. Equatorial sakis may try to defend core areas that are a small subset of their home ranges that may overlap with other equatorial saki home ranges. While only one study hypothesized that monk saki groups may be nomadic (Izawa 1976), it is possible that the monk saki groups observed on the grid are making forays from deeper in terra firme into equatorial saki home ranges to take advantage of seasonal fruiting.

Alternate Niches

My original hypothesis was that the factor dividing monk and equatorial saki niches was habitat. This simple explanation assumed monk sakis and equatorial sakis were ecospecies, ecologically equivalent congeners that are most often separated by distinct biogeographical boundaries (Peres & Janson 1999). A third alternative is that monk and equatorial sakis are not separated by habitat type, but separate by an ecological component of their niche that is not readily apparent. Habitat, food and time are the three main axes along which niches usually diverge (Schoener 1974). In a study of callitrichids by Heymann and Buchanan-Smith (2000), they found that niche separation is achieved by vertical segregation that leads to prey differences and allows for mixed-species troops. In another study of three guenon species in the Taï Forest of Côte d'Ivoire, there was divergence in their use of vertical strata and food items consumed (Buzzard 2006). It is possible that monk and equatorial sakis occupy different niches, but further study would be needed to identify how they are partitioning themselves.

Currently Defining Niches

A fourth alternative is that monk and equatorial sakis are currently in the midst of competing for the same niche. One of the key tenets of the competitive exclusion principle is that when two sympatric species compete for the same ecological niche, at some point one will out-compete the other for that niche (Hardin 1960). It is entirely possible what we are witnessing in the ACRCTT is monk and equatorial sakis competing for the same niche, but one species has not yet displaced the other.

A Single, Highly Variable Species

A fifth alternative is that monk and equatorial sakis are actually part of the same highly variable species. As noted previously, Marsh (2014) published a new taxonomy of *Pithecia.* What we have identified as equatorial sakis

(*P. aequatorialis*) within the ACRCTT using the taxonomy of Hershkovitz (1987), Marsh has renamed the monk saki (*P. monachus*). What we have identified as monk sakis (*P. monachus*) within the ACRCTT using the taxonomy of Hershkovitz, Marsh has renamed the burnished saki (*P. inusta*). Marsh admits that more research and data are needed on these two species and with more data it may be determined that *P. monachus* and *P. inusta* are the same species with large variations in pelage coloration or that there are even more species of saki in this region besides these two species (Marsh 2014). Given the current state of uncertainty of the taxonomy of *Pithecia* as a whole and the lack of long-term research, it is not surprising that there is no consensus on what constitutes a species within *Pithecia*. It is possible that Marsh is correct and the two species I have identified as monk and equatorial in my study area, are actually the same species with large variations in pelage coloration. However, while it is possible, I do not think it is likely.

If the equatorial and monk sakis of this study are the same species, what has caused this variability? Stump-tailed macaques (*Macaca arctoides*) of Thailand present significant variation in pelage color as a result of geographical isolation caused by temporary seaways created during Pleistocene pluvial periods (Koyabu et al. 2008). While the river systems in the Amazon basin are good candidates for creating geographic isolation, we would expect to see variation from one area to another, not a rare variant in the midst of a common one.

The most telling difference between the two species is the sexual dimorphism in equatorial sakis versus the minimal sexual morphic differences in monk sakis. Previous studies in the ACRCTT on these two species have observed the same morphic differences between the two species (Frisoli 2009, Chism et al. in review). In addition, group composition is usually consistent between the species. There have been very few reports of equatorial and monk sakis traveling together in the same group. Aquino et al. (2009) reported one group where a female equatorial saki was traveling with a group of three monk sakis. Until such time as it is feasible to make genetic comparisons between the two morphs, I remain convinced there are two species of saki monkey in the ACRCTT – *P. monachus* and *P. aequatorialis* using the taxonomy of Hershkovitz (1987) or *P. monachus* and *P. inusta* using the taxonomy of Marsh (2104).

Hybridization

Given the evidence that monk and equatorial sakis are both sympatric and syntopic (Aquino et al. 2009, Chism et al. in review), the question remains whether hybridization could be occurring between the two species. Modern groups of New World monkeys are believed to have separated into their major existing families during the Miocene (Porter et al. 1997, Kay et al. 2013), making the possibility of hybridization unlikely. However, recent genetic evidence places most speciation in the Plio-Pleistocene or later (Schneider et al. 2001), increasing the likelihood of successful hybridization. Arnold and Meyer (2006) suggest that successful hybridization has occurred within howler monkeys (*Alouatta*), marmosets (*Callithrix*) and tamarins (*Saguinus*).

Chism et al. (in review) report a rare third morph of saki occurring within the ACRCTT. This morph is characterized by long, creamy white fur on the forehead surrounding a dark face, creamy white malar stripes and a black triangular area between the brows. All of the individuals with this morph were identified as adult females within equatorial saki groups (Chism et al, in review). On 20 July, I observed an adult female saki with this rare third morph in an equatorial saki group on the trail grid (Figure 9). This female was in a group with an adult equatorial male and two juveniles. Chism et al. (in review) suggest it is possible that monk and equatorial sakis may be hybridizing in this area with the possibility of reduced viability of male hybrids. Until such time as these individuals can be genetically tested, hybridization is plausible, but uncertain.

Figure 9. Photo of an adult female with the rare white-faced morph that was part of a saki group with an equatorial male and two juveniles taken on the trail grid in the ACRCTT on July 20, 2016.

Dispersal Across Rivers

The riverine barrier hypothesis posits that large rivers serve as barriers to gene flow between populations and have contributed to vertebrate speciation in the Neotropics (Haffer 1997). The roots of this hypothesis, as it relates to primates, can be traced back to Alfred Russell Wallace (1852) who observed ranges of primate species sometimes being delineated by major rivers. However, more recent studies demonstrate a weakening of this hypothesis and suggest that rivers may not be impermeable barriers as was once thought (Haffer 1997, Gascon et al. 2000). Haffer (1997) argues that the riverine barrier hypothesis is flawed based on three arguments, including: the development of the rivers and forests was most likely one interrelated process and not an existing great forest that was bisected by the development of the Amazon river system; the lack of geographical separation in headwater areas; and, the frequent passive transport of animals across rivers when meander loops are cut off or a new river course is carved out. More recent molecular studies have shown mixed results for the support of the riverine barrier hypothesis (Gascon 2000).

During my study, I observed an equatorial male saki make an approximately 3m jump between two trees on opposite sides of the Tahuayo River (see Fig. 7, W 073°.17439’, S 04°.24.566’). The river was approximately 15m wide at the spot of the jump, with the two trees on either bank reaching out over the river creating the 3m gap. While the Tahuayo River is not the same category of barrier as the much larger Amazon River, it is a tributary of the Amazon River and one of the larger rivers in the ACRCTT. The confirmation of a saki crossing this river further bolsters the idea that rivers are not serving as a barrier to these two species of saki monkeys.

Frequency of Monk vs. Equatorial Sakis in the ACRCTT

The second question I set out to answer was: Are monk sakis the more common saki species in the ACRCTT as earlier surveys have suggested? My data show that equatorial sakis were much more likely to be encountered in my study area than were monk sakis, whether looking at all habitats surveyed (terra firme and igapó forests) or just igapó forest. These results contradict earlier reports in the ACRCTT that clearly indicated monk sakis were the more common, if not the only, saki species in the ACRCTT (e.g. Puertas and Bodmer 1993).

There are possibly a few explanations for the discrepancy between my results and earlier surveys. First, my study specifically focused on these two saki species. Most of the earlier efforts were based on brief surveys on primates in general and the researchers may have assumed there was only one species of saki in the ACRCTT. As identifying the difference between monk and equatorial sakis in the field is not easy, given their cryptic nature and coloring, previous researchers may have counted equatorial sakis as monk sakis in error (Aquino and Encarnación 1994).

Second, my study area was a relatively small section of the ACRCTT and close to the rivers. It appears the equatorial sakis prefer habitat close to the rivers. Some of the earlier studies were in other areas of the ACRCTT, and some spent more time in terra firme forests where it is possible that monk saki concentrations are higher. It is also possible that my study area has a higher concentration of equatorial sakis than do other parts of the ACRCTT. However, one very thorough study of sakis that took place in the western part of the reserve clearly identified monk sakis as the only species of saki in their study area (Fleck et al. 1999).

Population Density and Group Size

Population density estimates of sakis range from <1 individuals/km^2 to 36 individuals/km^2. However, these estimates may not be entirely accurate as sakis are cryptic, are not easily habituated to human observers, and tend to leave an area when encountered (Norconk & Setz 2013). A small number of studies of *P. pithecia* have shown they form cohesive social groups (Setz et al. 2013). However, at least one study in Brazil observed buffy saki (*P. albicans*) groups that were fragmented temporarily while foraging (Peres 1993b). A study of equatorial sakis in Peru found the mean group size to be 3.5 individuals with a range of 2-8 individuals (Aquino et al. 2009). A study of white-faced sakis in Guiana found the mean group size to be 4.8 individuals. Norconk (2007) reports that most saki groups fall in a range of 2-5 individuals, although some researchers have observed white-faced saki groups as large as 12 individuals (Setz et al. 2013). It is possible these large groups may represent more than one group engaged in an intergroup encounter.

While the purpose of my study was not to determine the population density of sakis and my methods were not designed to do so, I still was able to make a rough estimate of the population density of sakis on the trail grid in the ACRCTT. I estimate that during the period of my study there was a minimum of 12 sakis/km^2 in the trail grid area. This falls within the range reported in other studies. This is only an estimate and I suspect the actual population density is higher because I found the sakis during this study to be very cryptic and I suspect many groups in our path avoided detection. The number of individuals I observed in the groups I encountered ranged from 2 to 5 individuals per group. This range is in line with earlier studies of saki groups.

Conservation Implications

My data show that equatorial sakis can found in igapó forest habitat within the ACRCTT. Similarly, Aquino at al, (2009) found equatorial sakis alongside the riverbanks of three rivers north of the Amazon River in Peru. The implication is that habitat alongside rivers is ecologically important to equatorial sakis. Anthropogenic habitat loss from human encroachment, logging, and clear-cutting for agricultural use negatively affects primates in Peru (Pitman et al. 2003, Porter et al. 2013). Habitat loss is usually more concentrated alongside the rivers where access is easier than in terra firme (Kvist and Nebel 2001). Primates in terra firme habitat in interfluvial regions are less susceptible to anthropogenic habitat disturbance (Peres 1993). Thus, protecting the igapó habitat used by equatorial sakis in Peru is one of the keys to their future survival.

The good news is that we confirmed the presence of equatorial sakis within the protected reserve of the ACRCTT (Chism et al. in review). But the range of equatorial sakis in Peru extends well beyond the borders of the reserve (Figure 3). And while equatorial sakis are regarded as of least concern on the IUCN Red List (Marsh and Veiga 2008b), like all primates, that could quickly change should these sakis lose their habitat. Recognizing the importance of igapó forest to equatorial sakis, protection of igapó forest should factor into any equatorial saki conservation efforts.

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