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Effects of hunting on primate populations in Pacaya-Samiria National Reserve, Peru

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Abstract

The main forest macro-habitats found in the Amazon basin are non-flooded *terra firme* forests and seasonally inundated *várzea* forests. They harbour different assemblages of flora and fauna, which diverge greatly in species richness, density and biomass. However, hunting can severely affect the faunal assemblages in these forests. Primates are highly valued by hunters across the basin and large-bodied primate genera such as *Ateles*, *Lagothrix* and *Alouatta* are often prime targets, leading to severe declines in abundance or local extinctions. Depletion of these large-bodied species could result in increased abundances of smaller-bodied species. In this thesis, I describe the primate community in Pacaya-Samiria National Reserve and investigate the effects of hunting on primate populations. Line-transect censuses were conducted in sites with high, intermediate and low hunting pressure and density estimates for seven primate species were calculated under each level of hunting pressure. Densities were calculated using distance sampling and non-metric multidimensional scaling used to visualize effects of hunting on assemblage structure. A total of ten primate species was recorded. Overall, squirrel monkey was the most abundant, followed by large-headed capuchin and saddleback tamarin. Isabel's saki monkey and white-fronted capuchin were uncommon. Red howler monkey and woolly monkey densities were relatively low, yet these species comprised most of the aggregated biomass. There was a significant effect of hunting pressure on woolly monkey, red howler monkey, large-headed capuchin, squirrel monkey and Isabel's saki monkey. Saddleback tamarin and white-fronted capuchin did not show any significant difference between different hunting pressures. Woolly monkey, red howler monkey and large-headed capuchin were found at significantly lower densities under high hunting pressure compared to low hunting pressure. Contrastingly, squirrel monkey densities increased significantly with increasing hunting pressure. Isabel's saki monkey had a significantly higher density under high hunting pressure compared to intermediate hunting pressure. Consequently, primate assemblage structure diverged considerably between areas with high and low hunting pressure. The effects of hunting observed in the current study largely mirror those found elsewhere, with the strongest negative effect on larger-bodied primates. The increased abundance of smaller-bodied squirrel monkeys at sites with high hunting pressure may be evidence of competitive release. In terms of conservation, my results underline the importance of large protected areas, where core areas unaffected by hunting can serve as source areas for the local fauna.

Sammendrag

De viktigste makrohabitatene av skog som finnes i Amasonas bassenget er terra firme skoger som ikke blir oversvømt og sesongmessig oversvømte *várzea* skoger. Disse skogene huser ulike ansamlinger av flora og fauna, som avviker sterkt i forhold til artsrikdom, tetthet og biomasse. Jakt kan midlertidig ha en sterk påvirkning på fauna ansamlingene i disse skogene. Primater er høyt verdsatt av jegere gjennom hele bassenget og store primater slik som *Ateles*, *Lagothrix* og *Alouatta* er ofte hovedmål, noe som fører til en sterk nedgang i abundans eller lokale utryddelser av disse artene. Utslettelse av disse store artene kan føre til økt abundans for små primater. I denne oppgaven beskriver jeg primat samfunnet i Pacaya-Samiria Nasjonale Reservat og undersøker effektene jakt har på primatpopulasjonene. Linjetranskter ble utført i områder med høyt, middels og lavt jakttrykk, og populasjonstetthet for syv primatarter ble estimert under hvert jakttrykk. Tetthetene ble estimert ved hjelp av programmet Distance, og ikke-metrisk multidimensjonal skalering ble brukt til å visualisere effekten jakt hadde på primat ansamlingene. Samlet sett, så var ekornapen den mest abundante arten, etterfulgt av stor-hodet kapusinerape og tamarin. Isabel's saki ape og hvitpannet kapusin var uvanlige. Rødbroleape og ullape hadde forholdsvis lave tettheter, men disse to artene utgjorde store deler av den aggregerte biomassen. Jakttrykk hadde en signifikant effekt på ullape, rødbroleape og stor-hodet kapusinerape. Tamarin og hvitpannet kapusinerape viste ingen signifikante forskjeller mellom ulikt jakttrykk. Ekornapene økte i tetthet med økende jakttrykk. Isabel's saki ape hadde en signifikant høyere tetthet under høyt jakttrykk sammenlignet med middels jakttrykk. Følgelig, så var primat ansamlingsstrukturen forskjellig mellom områder med høyt og lavt jakttrykk. De observerte effektene jakt hadde på primatene i denne studien er stort sett de samme som er funnet andre steder, der den sterkeste negative effekten er å se hos store primater. Den økte abundansen av små ekornaper kan komme som en følge av konkurransefrigjørelse. Når det kommer til bevaring, så understreker mine resultater viktigheten av store beskyttede områder, hvor kjerneområder som ikke påvirkes av jakt kan fungere som kildeområder for den lokale faunaen.

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Introduction

The Amazon basin comprises the largest remaining tropical rainforest on earth, and is widely recognized as one of the most biodiverse areas in the world (Gentry 1988; Wilson 1992). At a regional scale, the western part of the basin has the highest levels of local diversity of most plant and vertebrate taxa, including mammals, amphibians, reptiles and trees (Hoorn et al. 2010). However, species richness is not ubiquitously high throughout the western Amazon basin. Local variation can be high as Amazonia is comprised of a wide range of juxtaposed vegetation types that drive the distribution of the regional biota.

The main forest macro-habitats are unflooded forests (hereafter termed *terra firme*) and seasonally flooded forests. Terra firme forests lie beyond the flood level of the large rivers and streams traversing the basin. Contrastingly, seasonally flooded forests lie on river floodplains and may be inundated for as long as 6-7 months of the year, as the annual water level fluctuation of the Amazonian rivers can be extremely high (>14 meters in amplitude). Several types of floodplain forest exist (Prance 1979), but *várzea* forests that grow on floodplains seasonally inundated by white-water rivers are probably most extensive (Junk et al. 2011). White-water rivers carry large amounts of nutrient-rich sediments from the Andes making *várzea* forests highly fertile, whereas unflooded terra firme forests occur on heavily leached and nutrient poor soils (Haugaasen & Peres 2006). These differences consequently mean that these forests harbour different assemblages of flora and fauna, which diverge greatly in species richness, density and biomass (Haugaasen & Peres 2005a; Haugaasen & Peres 2005b; Haugaasen & Peres 2006).

However, human forest encroachments can also severely affect floral and faunal assemblages. For example, hunting is a widespread practice throughout the Amazon basin (Alvard et al. 1997; De Souza-Mazurek et al. 2000; Peres et al. 2016) and forest peoples rely heavily on game animals for their daily subsistence (Jerozolinski & Peres 2003). Hunters deplete many harvest-sensitive populations of large vertebrates (Peres & Palacios 2007), and may consequently precipitate great changes in the large vertebrate assemblages (e.g. Peres 2000). Primates are particularly valued by hunters across the basin and this group is therefore one of the mammalian taxa most hunted in Neotropical forests (Stafford et al. 2017). However, all primates are not equally targeted. Body size is the most important determining factor for the majority of hunters, leading to a skewed selection against large-bodied species (Bodmer 1995; Jerozolinski & Peres 2003). The three Ateline genera, *Ateles* (spider monkeys), *Lagothrix* (woolly monkeys) and

Alouatta (howler monkeys), are often the main target (Peres 1990) – frequently leading to severe declines in abundance or local extinctions and a dramatic decrease in primate biomass (Peres 1990; Peres et al. 2016).

On the contrary, in undisturbed Neotropical forests primates often contribute with the majority of the aggregated mammalian biomass (Endo et al. 2010; Haugaasen & Peres 2005a). They can be categorized into several different foraging guilds (Haugaasen & Peres 2005b), but a common denominator is that fruits are an important component in their diet when available (Dew 2005; Garber 1993; Rosenberger 2011; Stevenson et al. 2000; Stone 2007). Thus, they serve as important seed dispersal agents (Chapman 1995; Garber 1986). Hunting therefore depletes key populations of large-bodied seed dispersers, disrupting the recruitment of many tropical forest trees and lianas. This activity may have knock-on effects on forest structure and composition in the long-term and such changes in tree recruitment have already been observed at heavily hunted sites in the Peruvian Amazon (Terborgh et al. 2008). Hunting of larger-bodied species may also result in density compensation by smaller species. However, evidence for this is ambiguous. For example, Peres and Dolman (2000) found only weak or no evidence for compensatory release of small-bodied species in hunted sites with increasing levels of hunting pressure, whereas Peres (2000) report an increase in smaller-bodied animals with increasing hunting pressure.

Despite the negative effects of hunting, the survival of many vertebrate species will likely rely on safeguarding populations within indigenous territories and other human-occupied parks. As human-occupied parks in Amazonia often are large with a relatively sparse human population, they may play a key role in preventing biodiversity erosion in the future (Peres & Terborgh 1995; Schwartzman et al. 2000). Populations of many game species still persist within the larger reserves, despite the local subsistence hunting pressure. This persistence is largely attributed to source-sink dynamics, in that non-hunted portions of the reserves protect game populations that produce surplus immigrants to be hunted near villages (Novaro et al. 2000; Peres 2001). Provided that the non-hunted source areas are large enough, such ‘reserves within reserves’ could provide a long-term source of game as well as preserve a full complement of vertebrate species.

The Pacaya-Samiria National Reserve is a big protected area located in the Peruvian Amazon. This reserve is surrounded by two large white-water rivers, where a high number of rural and indigenous settlements are located. It also harbours a vast amount of natural resources important for the people living in this area (Takasaki et al. 2001). Hunting is one of the main resource

extraction activities practiced by the communities for subsistence (Takasaki et al. 2001). Yet, little is known about the effects of hunting on the fauna in this area. In this study, I examine the effects of hunting on primate populations in Pacaya-Samiria National Reserve. Firstly, I describe the primate community in PSNR. Secondly, I determine species-specific primate densities in areas with high, intermediate and low hunting pressure. Thirdly, I examine differences in assemblage structure and composition among sites with different hunting pressure. I discuss the results in light of previous information and conclude with some notes on the conservation implications of this work.

Methods and material

Study area

The current study was conducted within the Pacaya-Samiria National Reserve (hereafter PSNR) in the Loreto region of northeastern Peru ($4^{\circ}33'51.6''\text{S}$ $73^{\circ}54'56.6''\text{W}$, Figure 1). PSNR was created in 1972 and covers 20 800 km² of lowland tropical rainforest, making it the biggest National Reserve in Peru (AECID et al. 2009; Servicio Nacional De Áreas Naturales Protegidas Por El Estado 2016).

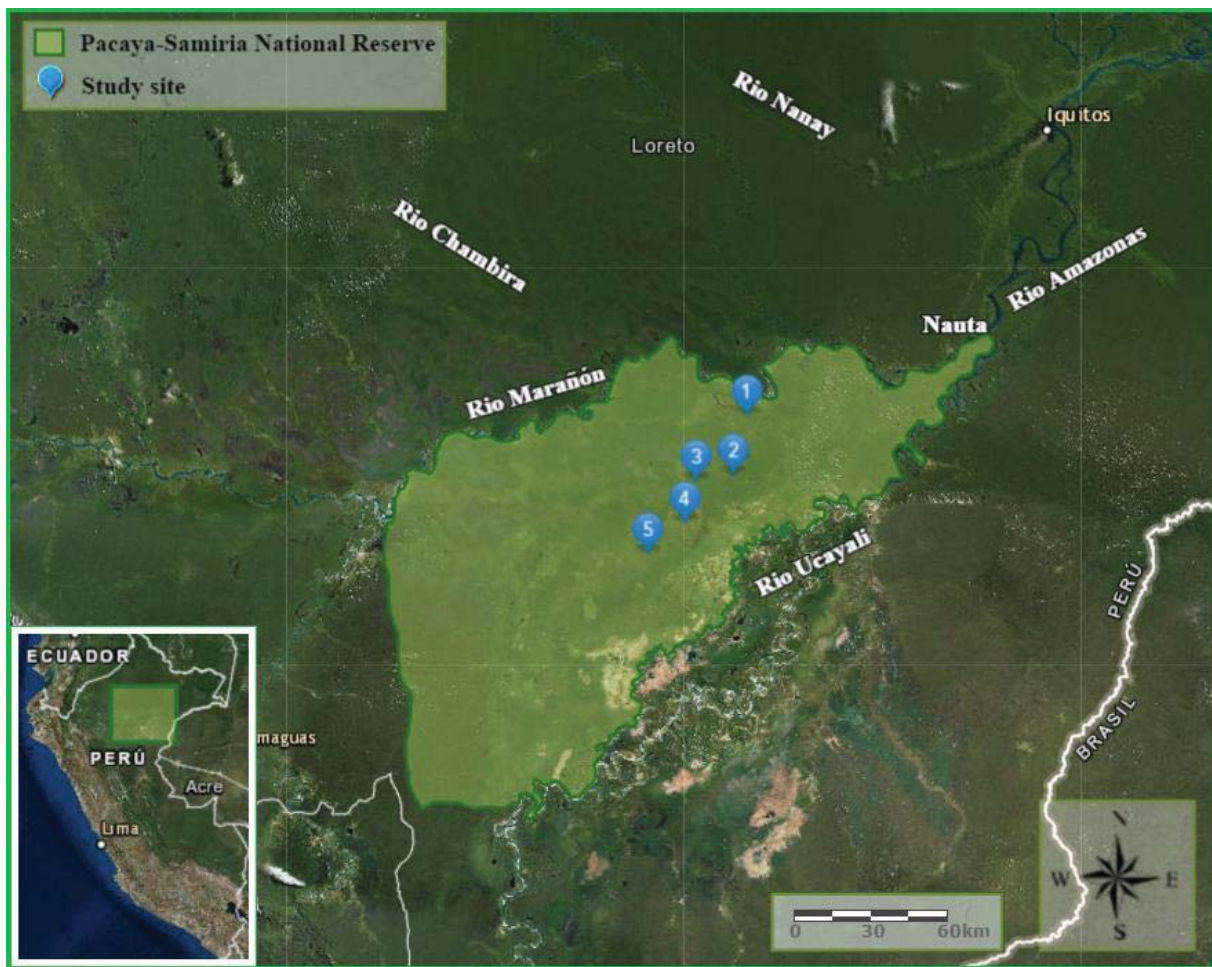


Figure 1: Study areas within the Pacaya-Samiria National Reserve. Map made on esri.com.

The climate is hot and humid with an annual average temperature of 27 °C and annual rainfall between 2-3000mm. However, there is a marked seasonality to the annual rainfall with February-April being the wettest months and June-August being driest (Servicio Nacional de Meteorología e Hidrología del Perú 2008) This, together with rainfall over the Andean mountains, leads to significant seasonal differences in river water levels (Rodríguez-Achung et al. 1996); Figure 2).

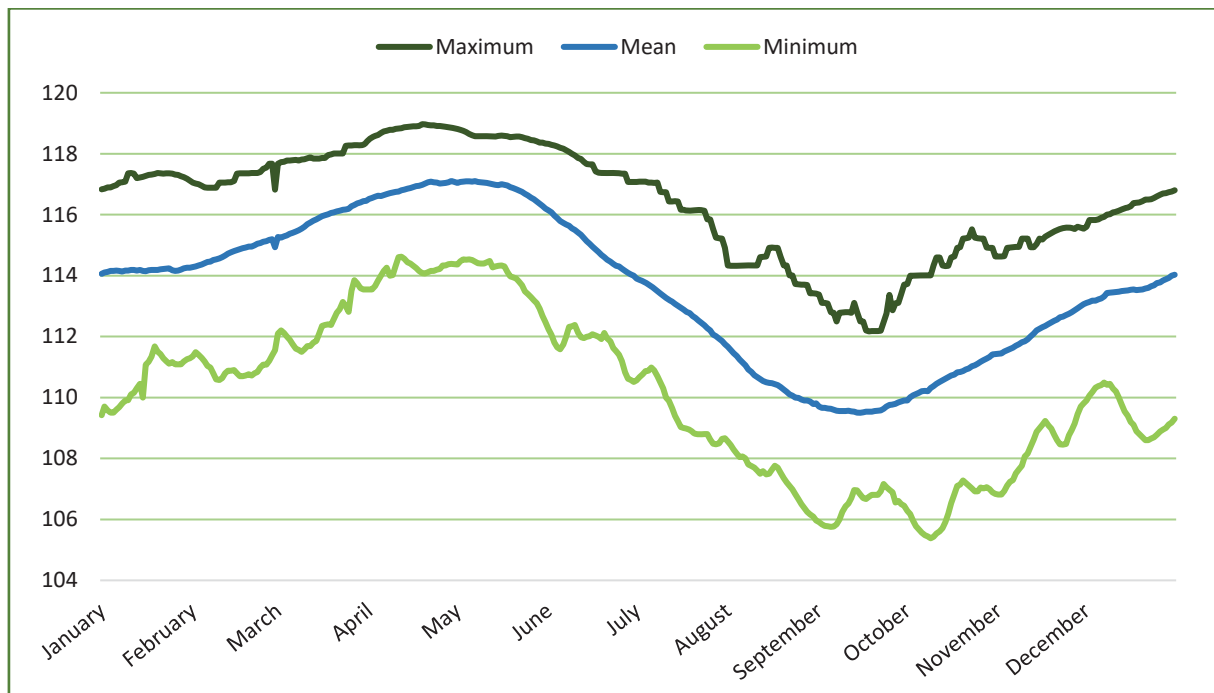


Figure 2: Changes in water level (measured in meters) in Amazon river near Iquitos for the years 1965-2015.

The Marañón and Ucayali rivers border the reserve to the north and south, respectively, and converge near Nauta forming the Amazon river (Figure 1). These are white-water rivers carrying large amounts of nutrient-rich sediments, and inundate the floodplain forest during the seasonal floods (Prance 1979). In fact, approximately 90 percent of the PSNR is seasonally flooded, while the rest consists of non-flooded *terra firme* forest (Kvist & Nebel 2001). The várzea forest in PSNR can be inundated for as long as 7 months depending on the annual changes in water levels (Rodríguez-Achung et al. 1996).

As várzea forest soils are highly fertile (Haugaasen & Peres 2006) and productive (Junk & Piedade 1993), the PSNR provide habitat for a diverse vertebrate community and harbours important natural resources important for the rural settlements in the area (Takasaki et al. 2001). In 2009, there were 68.195 people living in the reserve buffer zone, and 23.930 people living within the reserve. The indigenous population numbered 3.716 inhabitants in the reserve buffer zone and 5.812 inhabitants within the reserve (AECID et al. 2009). Most of the indigenous population belong to the Cocama-Cocamilla ethnic group or people of mixed ancestry known as *riberieños* (APECO and Eco studien (2005) cited in AECID et al. 2009). Although *riberieños* are not strictly indigenous, they have many of the same traditions and similar knowledge of the forest as the Cocama-Cocamilla people (Takasaki et al. 2001).

Sampling sites

The current study took place in the Samiria river basin, a sub-basin of the Marañón river basin. The Samiria river is a blackwater tributary to Marañón, but during the seasonal floods the white-water from Marañón mixes with the black water from Samiria (Kvist & Nebel 2001), resulting in flooding of the surrounding area with white-water. The study was carried out at five different study sites with three different levels of hunting pressure (high, intermediate and low; Figure 3). All study sites, except for Wishto, are situated in areas near park guard stations (PV stations).

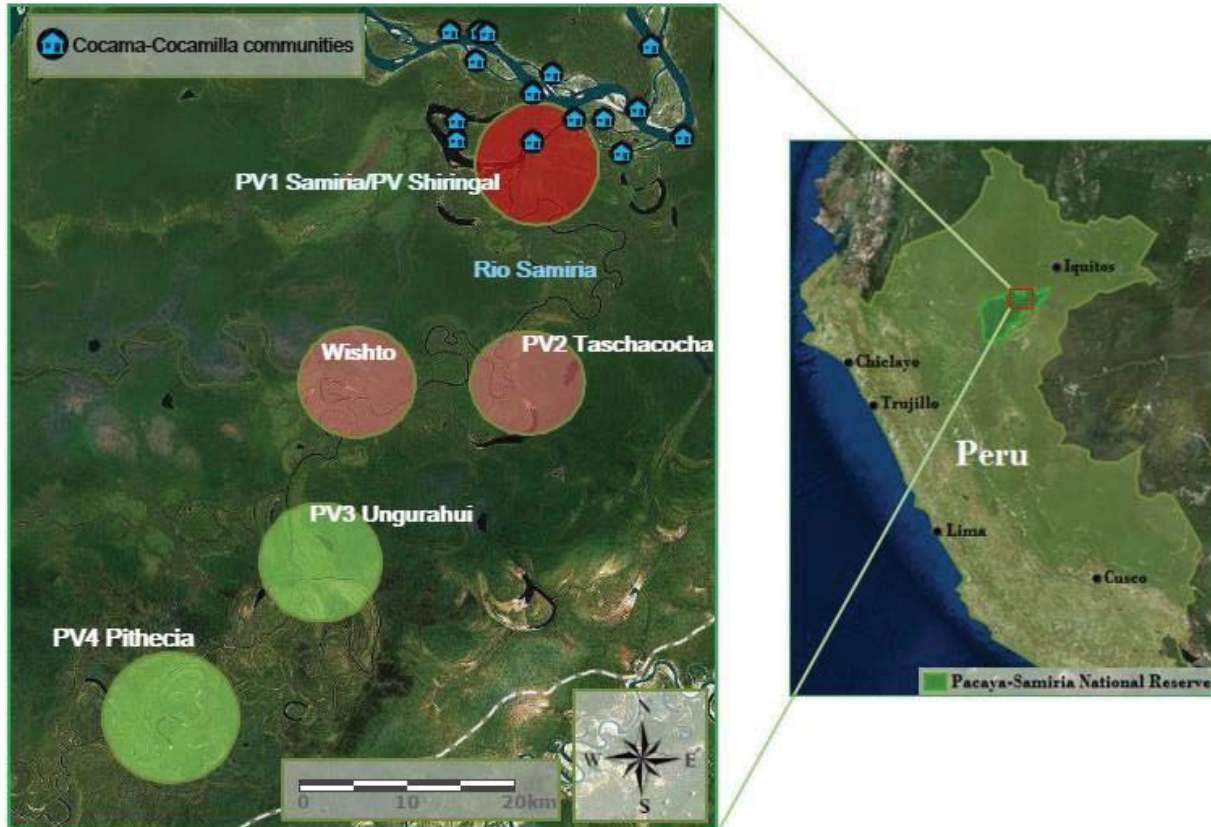


Figure 3: Study sites with high (red circles), intermediate (pink circles) and low (green circles) hunting pressure within the Pacaya-Samiria National Reserve, Peru. Map made on esri.com.

Study site 1 (PV1 Shiringal/PV Samiria) is located near the confluence of Marañón and Samiria rivers ($4^{\circ}42'18.2''\text{S}$ $74^{\circ}20'01.4''\text{W}$). This study site has high hunting pressure, and is located near several Cocama-Cocamilla communities (Figure 3). The other four study sites are situated along Samiria river. Study site 2 (PV2 Taschacocha) is approximately 45 km upriver of the Cocama-Cocamilla communities, which roughly translates to a half day's boat drive. This study site has intermediate hunting pressure, as has study site number 3 (Wishto), which is located approximately 85 km upriver from the communities (Figure 3). Study site 4 (PV3 Ungurahui) and 5 (PV4 Pithecia) are in the interior of the reserve, about 115 km and 140 km upriver of the communities, and have low hunting pressure (Figure 3).

Line-transect survey

Data on primate populations were derived from line-transect surveys conducted during 2006, 2008 and 2010-2016. My fieldwork was conducted between June and August 2016, data from 2006 to 2015 were obtained from Operation Wallacea and Fund Amazonia.

All line-transect surveys were conducted largely following Peres (1999). In brief, transects of 1-5 km were cut prior to starting the survey. The transects were measured with a 50-m rope and marked every 50 m. The number of observers varied between 2-14 people, but trained professionals with good knowledge of the area and study species led the surveys.

Census walks were conducted twice daily at a pace of 1.5-2 km/hour. Two-way morning censuses started between 07:00-08:00h and ended around 12:00h +/- one hour, while the two-way afternoon censuses started at 14:00-14:30h and ended at around 17:00-17:30h. Since observers had a break at the end of each transect (30 minutes), the two-way censuses were treated as independent surveys. The resulting census effort for each study site, number of transects surveyed, number of primate sightings and number of species sighted are presented in Table 1. Censuses were not conducted during rain or high wind. Upon detection of a primate group, several measurements were taken: sighting location along the transect, species, time of day, perpendicular distance to the first sighted animal, group size, activity, detection cue and habitat type. All surveys were carried out during day time. To my knowledge, all surveys were conducted in várzea forest.

Table 1: Total survey effort, number of transects, number of primate sightings and number of species at the five study sites within Pacaya-Samiria National Reserve (all years combined).

Hunting pressure	High	Intermediate		Low		Total
Study site	1 Samiria/Shiringal	2 Taschacocha	3 Wishto	4 Ungurahui	5 Pithecia	
Total survey effort	693.11 km	2854.85 km	642.5 km	563.95 km	192.7 km	4942.31 km
Number of transects	7	10	7	8	4	12
Primate sightings	399	1867	421	438	158	3283
Number of species	10	8	8	7	7	10

Data analysis

Data handling

I excluded all non-terrestrial surveys (i.e. with a canoe). Although transects with canoe can be compared with terrestrial transects (Haugaasen & Peres 2005b), to my knowledge the current aquatic transects were conducted along the main river and did not transverse into the forest.

Density estimates

The software Distance version 7.0 Release 1 (Thomas et al. 2010) was used to derive density estimates. I used the Conventional Distance Sampling Analysis (CDS) to estimate detection function. All detections were included in the analysis, but data were truncated to remove outliers and improve the estimator models. The detection function was chosen based on the model with lowest AIC value. To see if the model was a good fit for the data, I used Q-Q plot and three goodness-of-fit tests (Kolmogorov-Smirnov test, Cramer-von Mises family tests and Chi-square test). Since the Chi-square goodness-of-fit test has low statistical power, the model fit was mainly based on the Kolmogorov-Smirnov and Cramer-von Mises family tests (Buckland et al. 2004). The chosen models for detection functions and adjustments varied by species and study site, and are presented in Appendix 1.

I analyzed species independently, stratified by study site, and fitted one detection function per stratum. Moreover, I fitted a global detection function incorporating all detections across all study sites for species with small sample sizes (i.e., not large enough to fit a detection function by study site). This made it possible to estimate density despite small sample sizes for those species. By doing so, I could derive density estimates per transect for each study site.

Some datasets proved to be problematic because of an excessive number of observations at zero distance from the transect. These problems are likely due to poor field techniques as previous observers have rounded the perpendicular distance to zero, even though the animal sighted was not exactly on the transect. The chosen model was unable to provide a good fit for these excessive zeros. This is, however, not as problematic as it sounds. Since the excessive zero's probably arose from poor field techniques, the density estimate would have been overestimated by using a model that could fit these excessive zeros (Buckland et al. 2004). Instead, my estimates should be conservative.

Biomass

Population biomass was calculated using 80 percent of mean body weight for a given species following Peres (1997b), multiplied with the mean individual density estimate for each species.

Effects of hunting pressure

R (version 3.3.2) with the graphical user interface R Commander (version 2.3-1) were used for further investigation of impacts of hunting pressure (Fox & Bouchet-Valat 2017; R Core Team 2016). An ANOVA type II test was used together with Tukey HSD and Tukey multiple comparison post-hoc test to further explore differences in density and aggregate biomass between hunting pressure.

Community composition

I used PRIMER version 5 to conduct a non-parametric multidimensional scaling (MDS) ordination (Clarke 1993). The MDS was based on Bray-Curtis similarity measure to explore differences between hunting pressures based on the density estimates of each species at the transect level. All species were included as single entities, but the MDS plot visualizes the overall assemblage structure between areas with high, intermediate and low hunting pressure.

Results

Overall species richness and density

Total survey effort for all study sites combined was 4942.31 km, totaling 3283 primate sightings of 10 species (Table 1, Table 2). Seven species were widespread observed in all five study sites, including saddleback tamarin (*Saguinus fuscicollis*), squirrel monkey (*Saimiri boliviensis*), white-fronted capuchin (*Cebus albifrons*), large-headed capuchin (*Sapajus macrocephalus*), Isabel's saki monkey (*Pithecia isabela*), red howler monkey (*Alouatta seniculus*) and woolly monkey (*Lagothrix poeppigii*; Figure 4). Nancy Ma's Night Monkey (*Aotus nancymae*) was recorded in study site 1 (Shiringal/Samiria), 2 (Taschacocha) and 3 (Wishto), while the Pygmy Marmoset (*Cebuella pygmaea*) and Red Titi monkey (*Callicebus discolor*) were only recorded at study site 1. Pygmy marmoset was recorded only once and red titi monkey was recorded twice. These latter three species were excluded from further analysis due to nocturnal behaviour (*A. nancymae*) and small sample size (*C. pygmaea* and *C. discolor*). Additionally, the study area is within the geographic range of the White-bellied spider monkey (*Ateles belzebuth*), but this species was never observed.

Table 2: Species and mean body mass of species sighted in my study area ordered by family and weight.

Family ^a	Subfamily ^a	Species ^b	Common name	Mean body mass ^d
Cebidae	Callitrichinae	<i>Cebuella pygmaea</i>	Pygmy marmoset	0.116 kg
		<i>Saguinus fuscicollis</i>	Saddleback tamarin	0.35 kg
	Cebinae	<i>Saimiri boliviensis</i>	Squirrel monkey	0.81 kg
		<i>Cebus albifrons</i>	White-fronted capuchin	2.73 kg
		<i>Sapajus macrocephalus</i>	Large-headed capuchin	3.1 kg
Pitheciidae	Pitheciinae	<i>Pithecia Isabelae</i> ^c	Isabel's saki monkey	2.36 kg*
	Homunculinae	<i>Callicebus discolor</i>	Red titi monkey	1.07
		<i>Aotus nancymae</i>	Nancy Ma's Night monkey	0.787
Atelidae	Atelinae	<i>Alouatta seniculus</i>	Red howler monkey	6.1 kg
		<i>Lagothrix poeppigii</i>	Woolly monkey	7.15 kg*

a) Taxonomy following Rosenberger (2011)

b) Taxonomy following the IUCN list for threatened species (IUCN 2016)

c) Taxonomy following Marsh (2014)

d) Measurements of mean body mass are derived from Smith and Jungers (1997).

* Mean body mass of *Pithecia monacus* and *Lagothrix* spp.

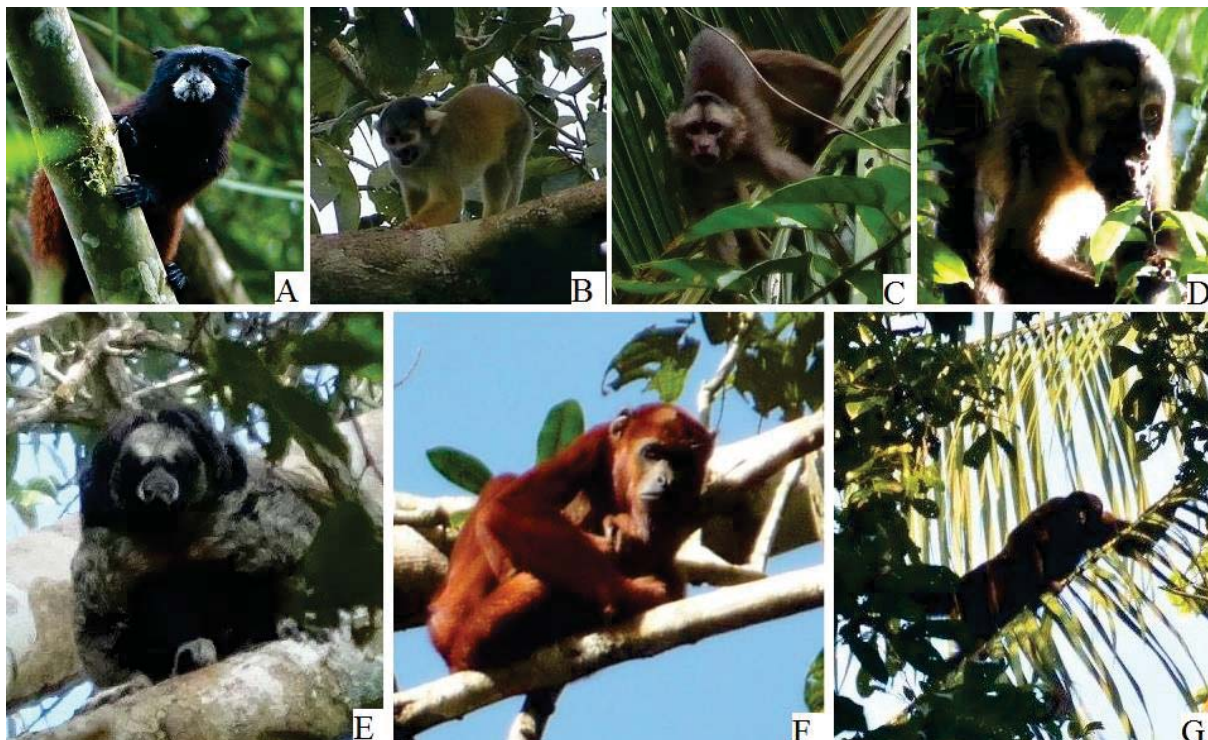


Figure 4: The seven most common species in Pacaya-Samiria National Reserve. A) Saddleback tamarin, photo: Catherine Yates, B) Squirrel monkey, photo: Matthew Owen C) White-fronted capuchin, photo: Marimar Garciego, D) Large-headed capuchin, photo: Catherine Yates, E) Isabel's saki monkey, photo Marimar Garciego, F) Red howler monkey, photo: Rolin Rongifo Mendoza, E) Woolly monkey, photo: Magnus Trollestad.

Overall, squirrel monkey was by far the most abundant species, followed by brown capuchin and saddleback tamarin (Figure 5). Isabel's saki monkey and white-fronted capuchin were

uncommon and had relatively low density estimates (Figure 5). Red howler monkey and woolly monkey densities were also relatively low (Figure 5), yet these species comprised most (54.97 %) of the aggregate primate biomass (201.19 kg/km²) in the study area (Figure 6) due to their large size. However, the small-bodied squirrel monkeys also contributed significantly to the aggregate biomass because of their high numerical abundance (Figure 6).

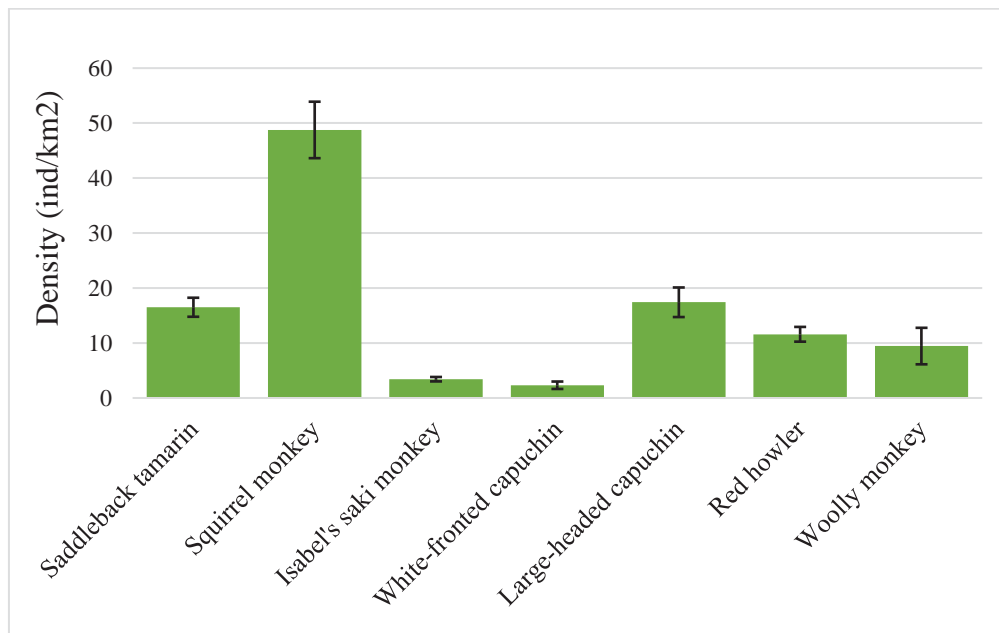


Figure 5: Mean density (\pm SE) of the seven most common primate species in Pacaya-Samiria National reserve.

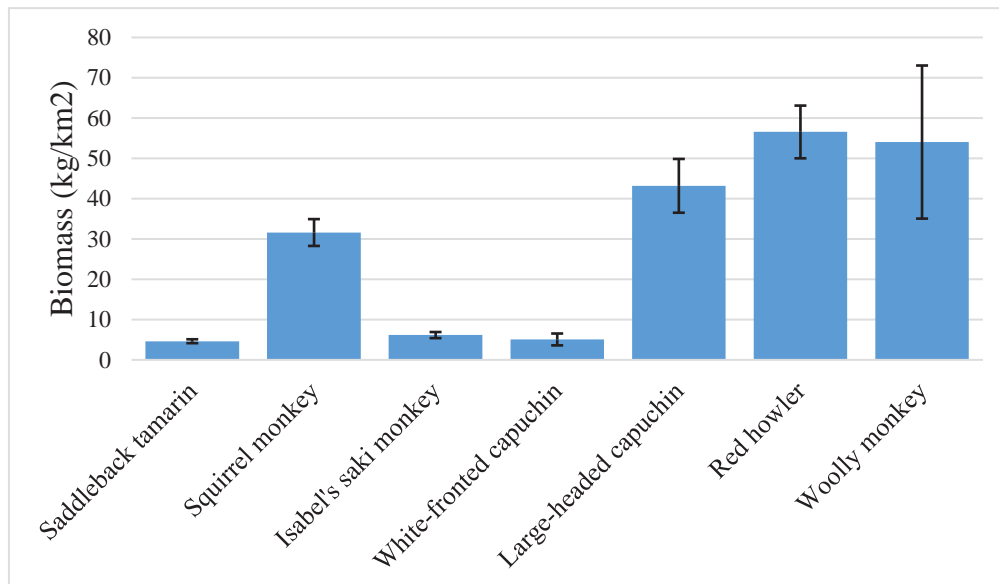


Figure 6: Mean biomass densities (\pm SE) of the seven most common species found in Pacaya-Samiria National Reserve.

Effects of hunting

There was a significant effect of hunting pressure on woolly monkey (ANOVA $F_{2,33}=7.0808$, $p=0.002762$), red howler monkey (ANOVA $F_{2,33}=4.6249$, $p=0.01696$), large-headed capuchin (ANOVA $F_{2,33}=9.1858$, $p=0.0006738$), squirrel monkey (ANOVA $F_{2,33}=6.3961$, $p=0.004492$), and Isabel's saki monkey (ANOVA $F_{2,33}=3.8259$, $p=0.03204$). Saddleback tamarin (ANOVA, $F_{2,33}$, $p=0.79$) and white-fronted capuchin (ANOVA $F_{2,33}=2.1759$, $p=0.1295$) did not show any significant difference between different hunting pressures (Figure 7A-G).

The strongest negative effect was observed for the two largest primate species (woolly monkey and red howler monkey), and the medium-sized brown capuchin (Table 3, Figure 7A-C). For these species, Tukey's post-hoc tests revealed significant differences in density estimates for low and high hunting pressure (woolly monkey: $p<0.001$; red howler: $p=0.012$; large-headed capuchin: $p<0.001$). In fact, woolly monkeys have virtually disappeared from areas with high hunting pressure (Table 3, Figure 7A). Contrastingly, squirrel monkeys had highest density under high and intermediate hunting pressure, following by a marked decline under low hunting pressure (Table 3, Figure 7D), but this decline was only significant between intermediate and low hunting pressure (Tukey multiple comparison $p=0.0121$). Isabel's saki monkey was the only species with highest density at the site with high hunting pressure, and this proved to be significant, but this was only the case between high and intermediate hunting pressure (Tukey multiple comparison, $p=0.023$; Table 3, Figure 7G). White-fronted capuchin were uncommon throughout the study area, but had a slight increase under low hunting pressure, although not significant (Table 3, Figure 7F).

Table 3: Mean primate density and biomass estimates under high, intermediate and low hunting pressures at Pacaya-Samiria National Reserve, Peru. $D_{\text{ind}/\text{km}^2}$ = density of individuals/ km^2 . Superscript letters refer to subsets from Tukey's post-hoc test.

Species	High pressure		Intermediate pressure		Low pressure	
	$D_{\text{ind}/\text{km}^2}$	Biomass(kg)/ km^2	$D_{\text{ind}/\text{km}^2}$	Biomass (kg)/ km^2	$D_{\text{ind}/\text{km}^2}$	Biomass (kg)/ km^2
Red woolly monkey	0.41 ^b	2.35	4.92 ^{ab}	28.14	21.13 ^a	120.86
Red howler monkey	6.80 ^b	33.18	10.06 ^{ab}	49.09	16.55 ^a	80.77
Large-headed capuchin	6.86 ^b	17.02	12.97 ^b	32.17	29.85 ^a	74.03
Squirrel monkey	54.17 ^{ab}	35.10	62.27 ^a	40.35	26.45 ^b	17.14
Saddleback tamarin	17.94 ^a	5.02	15.25 ^a	4.27	17.45 ^a	4.89
White-fronted capuchin	0.72 ^a	1.57	1.67 ^a	3.65	4.18 ^a	9.13
Isabel's saki monkey	5.03 ^a	9.50	2.32 ^b	4.38	3.55 ^{ab}	6.70
Total	91.93	103.74	109.46	162.05	119.16	313.52

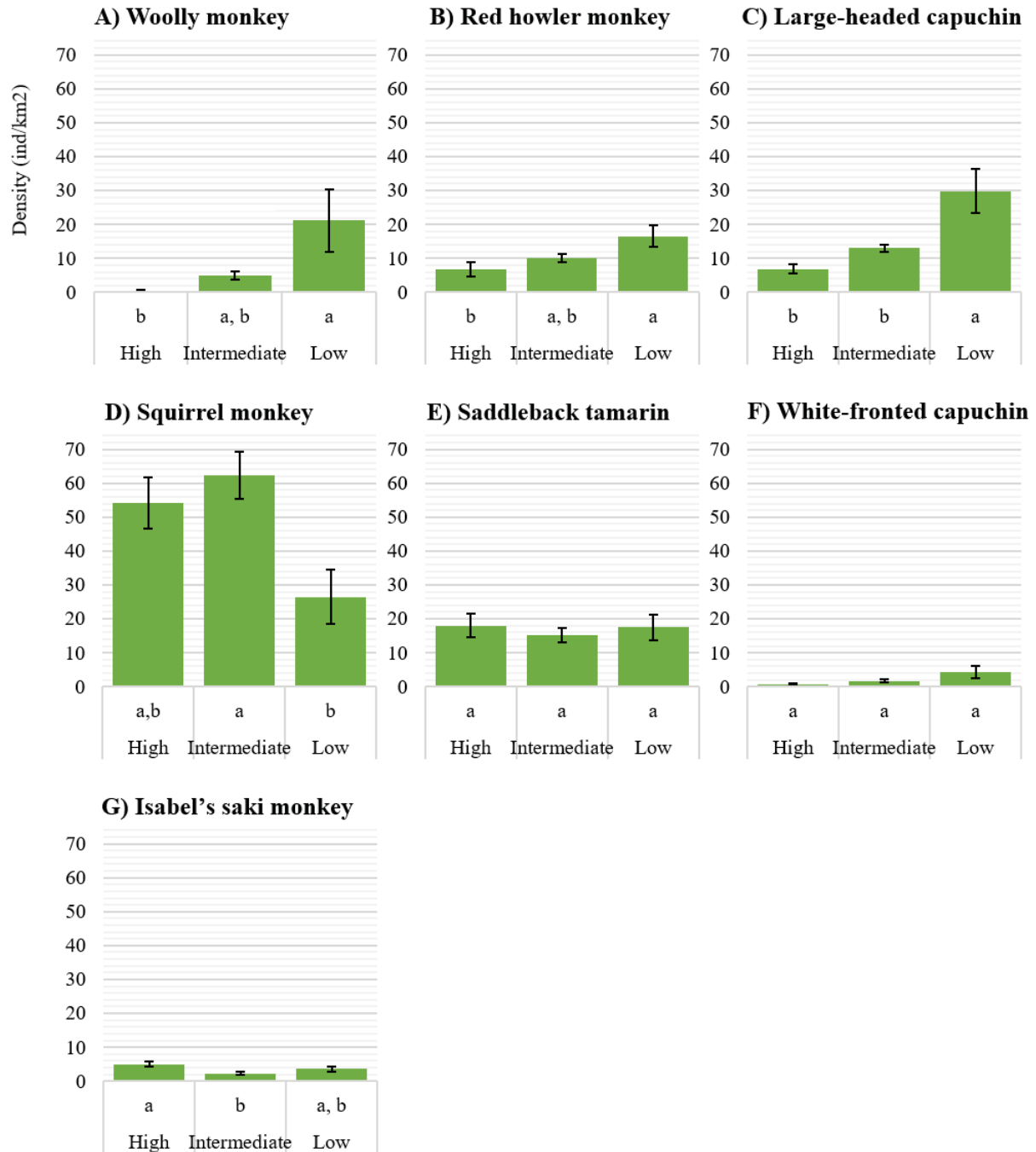


Figure 7A-G: Mean density estimates \pm SE of each of the seven most common species found in Pacaya-Samiria National Reserve under high, intermediate and low hunting pressure. A-G = subsets from Tukey HSD post-hoc test.

Assemblage structure and composition

Hunting pressure had a significant effect on the aggregate biomass for the seven most common primate species (ANOVA $F_{2,33}=3.3231$ $p=0.04883$), where aggregate biomass increased with decreasing hunting pressure (Table 3). In fact, overall primate biomass was almost three times lower under high hunting pressure than under low hunting pressure (Table 3), although this

difference was marginally non-significant (Tukey multiple comparison $p = 0.0572$). The biomass decrease observed is due to a dramatic reduction in biomass of the large-bodied woolly monkey and howler monkey, and medium-sized large-headed capuchin (Table 3).

A strong effect of hunting was supported by the non-metric multi-dimensional scaling (MDS) based on Bray-Curtis similarities of species composition and abundance among transects. The MDS plot showed a relatively distinct clustering by hunting pressure (Figure 8). Most of the transects within the high hunting pressure zone are grouped in the left part of the diagram, while most transects with no hunting pressure are clustered towards the right (Figure 8), indicating that the primate communities are dissimilar. The transects with intermediate hunting pressure are placed between those of high and low hunting pressure (Figure 8). In addition, sites with high hunting pressure were distinctly clustered and therefore had a more homogenous primate community than sites with low hunting pressure that were more loosely clustered.

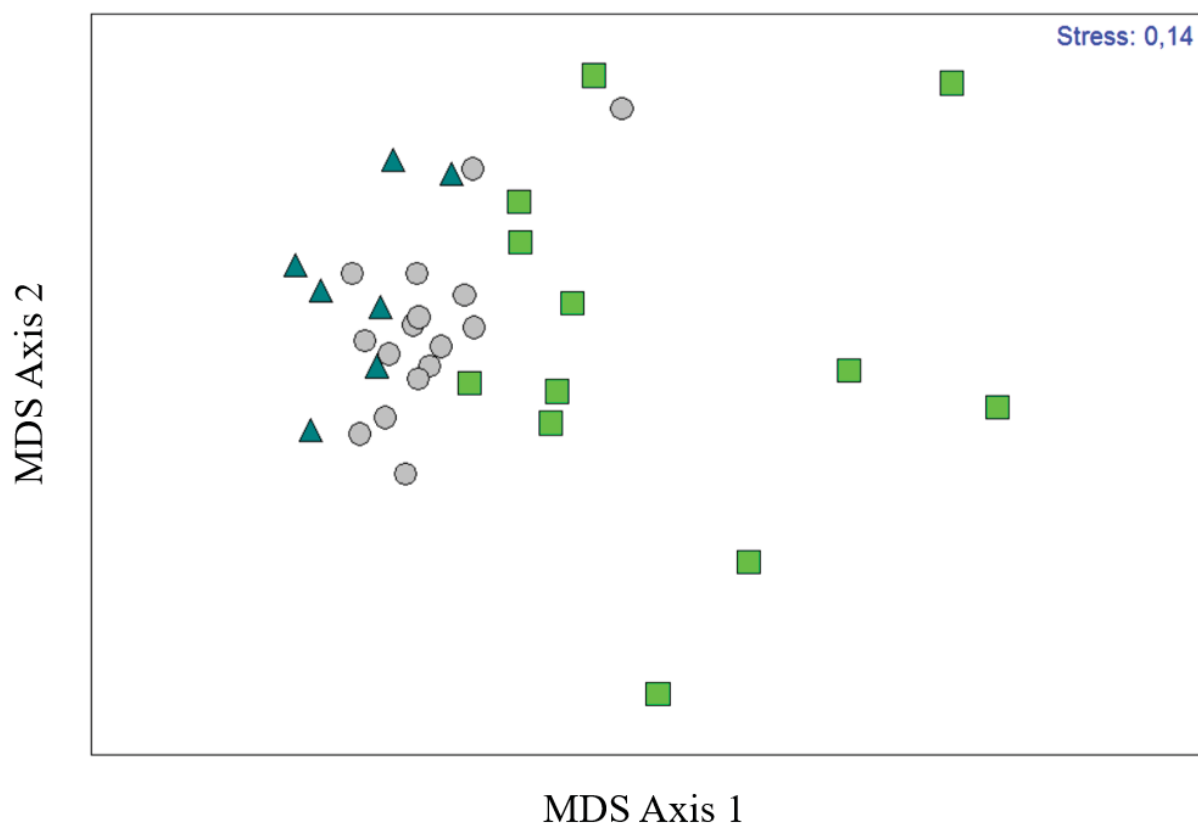


Figure 8: MDS plot of primate assemblages based on Bray-Curtis similarity in study areas with high (triangles), intermediate (circles) and low (squares) hunting pressure.

Discussion

Overall species richness and density

Overall, 10 sympatric primate species were observed during the period of this study. This exceeds the number of primate species observed in várzea forest at other locations in the central-western Amazon. For example, Haugaasen and Peres (2005b) and Peres (1997b) observed a maximum of eight and seven species in várzea forest, respectively.

Overall, the most common species in the current study was the squirrel monkey. Large-headed capuchins, saddleback tamarins, woolly monkeys and red howler monkeys were also abundant. The high abundance of squirrel monkeys is similar to that found in várzea forests elsewhere in Amazonia (Terborgh 1983b). This is a typical floodplain species – in fact this species is the only small primate from similar species assemblages that are found in várzea forests completely isolated from terra firme (Haugaasen & Peres 2005b). A lack of competition from other small-bodied insectivorous primates has been touted as the possible reason for the high abundance of this species in várzea forest (Rylands 1987). They are commonly found in mixed-species groups with Brown capuchins (*Sapajus apella*; (Haugaasen & Peres 2009). The large-headed capuchin (*Sapajus macrocephalus*) from the study area was until recently classed as *S. apella* (Alfaro et al. 2012), but no information about mixed species groups from the PSNR exists. However, the fact that *S. macrocephalus* was commonly encountered throughout the study area is probably due to the same habitat plasticity and generalist diet shown by *S. apella* elsewhere (Brown & Zunino 1990). Howler monkeys are also typical floodplain species. Evidence suggests that this may be due to their folivorous diet. Since várzea floodplains are highly productive (Prance 1979), plants may experience a less limiting nutrient uptake and thus have fewer phytochemical defenses than plants in terra firme forest. Indeed, several other folivorous species appear to be largely restricted to várzea forests throughout the Amazon basin (Haugaasen & Peres 2005a; Peres 1997a)

In contrast, the saddleback tamarin was found at relatively high density in this study compared to other studies done in várzea forests (Haugaasen & Peres 2005b; Peres 1997b). In fact, tamarins appear to be infrequent visitors of várzea forest elsewhere (e.g. Peres 1997b). A similar trend was found for the woolly monkey (*Lagothrix poeppigii*). This species was observed at all study sites in this study and this is in accordance with an earlier study done in the same area (Bodmer et al. 1997). However, compared to other studies undertaken at different locations, this is somewhat unusual. *Lagothrix* spp. are usually not found in várzea forests. In fact, this

species was never observed in várzea forest despite a huge survey effort with both seasonal and yearly replicates in the Purus river basin (Haugaasen & Peres 2005b).

White-fronted capuchin and Isabel's saki monkey were uncommon in the PSNR forest matrix. White-fronted capuchins and other saki monkey species are also uncommonly found in várzea forests at other sites (Haugaasen & Peres 2005b). They seem to prefer terra firme forests and are found at higher densities in this forest type (Haugaasen & Peres 2005b). Yet, both saki monkey and white-fronted capuchins generally have low sighting rates in studies throughout Amazonia. Low group density, relatively large home ranges and heavy reliance on widely dispersed fruit crops, such as figs, may explain the paucity of white-fronted capuchin observations (Terborgh 1983a). Saki monkeys may escape the untrained eye as they move swiftly and quietly through the upper canopy when disturbed (T. Haugaasen pers. comm.), but are probably naturally rare.

The pygmy marmoset and red titi monkey were only observed at study site 1, which had the highest hunting pressure and highest level of human disturbance. The pygmy marmoset prefers habitats with high levels of natural disturbance, and is found both in várzea (Soini 1982) and terra firme forest habitats exposed to natural disturbance (e.g. treefall gaps; (Peres 1993). Moreover, this species is likely patchily distributed, as Haugaasen and Peres (2005b) did not detect the species although their study area was located within its geographic range. The fact that the pygmy marmoset was only sighted on one occasion during this study, gives support to the notion that the species is patchily distributed. Yet, this is one of the smallest primates in the world (Smith & Jungers 1997) and may easily go undetected by inexperienced surveyors. The red titi monkey is also a species associated with habitats with high levels of natural or human disturbance and their preference for secondary or disturbed habitats is well documented (Haugaasen & Peres 2005b; Peres 1993; Rylands 1987). Surprisingly, van Roosmalen et al. (2002) states that titi monkeys (*Callicebus* spp.) do not occur in várzea forests because of dispersal limitations imposed by large white-water rivers. However, in Ecuador red titi monkeys (*C. discolor*) appear to actually prefer this habitat (de la Torre et al. (1995) cited in Veiga 2008), and the fact that it was encountered in várzea forest in this study may suggest that titi monkeys are not as limited by large rivers as has been indicated.

In sum, the overall primate assemblage structure registered within the study area indicates that perhaps these várzea forest are influenced by nearby or adjacent terra firme forests. This could explain the high densities of saddleback tamarins and woolly monkeys compared to studies conducted at other várzea forest sites (Haugaasen & Peres 2005b; Peres 1997b). Indeed,

Haugaasen and Peres (2005b) and Haugaasen and Peres (2007) observed a periodic use of floodplain forests by some terra firme species, seasonally boosting the species richness of these areas. These seasonal movements into várzea forest appeared to be closely related to a higher fruit availability in várzea forests during the high-water period (Haugaasen & Peres 2005b; Haugaasen & Peres 2007).

Effects of hunting

There was a clear effect of hunting on the large-sized Ateline primates. Woolly monkeys and red howler monkeys were found at significantly lower densities under high hunting pressure than under low hunting pressure. This indicates that hunters in the study region show a similar preference for these large primates as is found throughout the geographic range of these genera (*Lagothrix* spp. and *Alouatta* spp.; Jerozolinski & Peres 2003). However, the woolly monkey appears to be more affected by hunting than the red howler monkey as they were found at lower mean densities under high hunting pressure and did not reach high densities before being subjected to low hunting pressure. This is in agreement with other studies - the vast majority of which have reported a severe depletion of woolly monkeys, and cases of local extinctions, in areas where they are exposed to high hunting pressure (Peres 1990; Peres 1991; Peres et al. 2016). The fact that this species reaches sexual maturity at a late age and gives birth to one offspring approximately every other year (Bowler et al. 2014) could contribute to making this species sensitive to hunting. In addition, they are likely an easier target because of their large group size and being noisy when travelling through the forest (pers. obs.) making it easier for hunters to spot them. Moreover, the bigger group size opens the opportunity for hunters to kill more individuals when a group is detected (Peres 1991).

In this study, red howler monkey appeared to cope somewhat better under high hunting pressure than the woolly monkey. However, it may also be an artefact of hunter preference where woolly monkeys are preferred over red howler monkeys, as is the case in other areas (da Silva et al. 2005; Peres & Dolman 2000). Without monitoring hunter offtake, it will be difficult to assess whether this is in fact the case. Another contributing factor could also be that the small group size and docile behaviour (Braza et al. 1981) of howler monkeys could make them harder to detect. Moreover, they are known to be more resistant to human disturbance and can survive in highly fragmented forest landscapes (Benchimol & Venticinque 2014).

The results of this study indicate that also the large-headed capuchin is a preferred species for meat consumption by hunters in the study area. This could be attributed to the fact that woolly

monkeys were uncommon under both high and intermediate hunting pressure, making hunters target this species.

White-fronted capuchins also appeared to be negatively affected by hunting, although the decrease was not significant. However, this could be masked by their general rarity in the forest matrix. Since the species is infrequently encountered, I am inclined to speculate that the decrease from low to high hunting pressure is due to opportunistic hunting of this species.

The smaller sized primates (squirrel monkey and saddleback tamarin) were not negatively affected by hunting. This is consistent with previous studies elsewhere in Amazonia, showing that hunters do normally not target small-bodied primates (Jerozolinski & Peres 2003; Peres & Dolman 2000; Peres & Nascimento 2006). In fact, squirrel monkeys were found at higher densities under high and intermediate hunting pressure than low hunting pressure. Variable densities between transects in the areas with low or no hunting pressure could account for this difference, yielding lower than expected densities when data were pooled. However, small primates have been found to increase with increasing hunting pressure at other sites (Rosin & Swamy 2013). This suggests that the squirrel monkey in the study area is experiencing competitive release (Peres & Dolman 2000). In other words, as the larger primates are depleted in hunted areas, more resources are available to smaller primates and they can consequently persist at higher abundances. However, the small saddleback tamarin did not show any obvious trends across hunting pressures in this study. This difference may be due to differences in life history and behaviour. Squirrel monkeys live in very large groups and use large home areas (Zimble-DeLorenzo & Stone 2011), whereas the saddleback tamarins live in small family groups, are more sedentary and very territorial (Soini 1987). Squirrel monkeys therefore have a better prerequisite for increasing their abundance after the larger primates have been depleted. Although saki monkeys had significantly lower densities with intermediate hunting pressure compared to high hunting pressure, these differences are unlikely to be more than natural variation between sites.

Assemblage structure and composition

Primate biomass in the PSNR was severely affected by hunting. In fact, there was a three-fold decrease in primate biomass from lightly hunted/unhunted sites to heavily hunted sites. This biomass collapse was largely driven by a dramatic reduction in biomass for the larger-bodied primates. This is of course linked to the significant decrease in density of these species due to hunting. The only species to show a substantial increase in biomass with increasing hunting

pressure was the squirrel monkey. This is again mirroring the increase in density, perhaps as a result of competitive release.

The big variation among sites without hunting is probably due to large natural differences among sites. With increasing hunting pressure, the primate assemblages become increasingly homogenous because the larger primates are virtually being eradicated from the assemblage and the assemblage structure is dominated by a few abundant species.

Study limitations

The current study is based on data collected by different volunteers, assisted by a local guide, across several years. Despite the local guide, the data may suffer from significant observer bias due to the large number of different observers. For example, distance sampling is very sensitive to changes in the perpendicular distance at which an animal is observed. Differences among observers in their ability to detect certain species or variability in the measurement of perpendicular distances could therefore significantly influence the results. In addition, large groups of observers were often used and this can affect the detectability of focal animals (e.g. more noise created whilst traversing over the dry leaves on the forest floor). Flushing animals or failing to notice the acoustic signals could consequently lead to an underestimation of densities if the animal fails to be registered or is registered further away from the trail than where it in reality was when the observers arrived (Buckland et al. 2004). This could, for example, be a problem for such species as howler monkeys and saki monkeys as they are extremely quiet and often move around in the upper canopy.

In addition, the perpendicular distance recorded by volunteers was to the first animal sighted in a primate group rather than, and irrespective of, the geometric center of the group. This causes a density overestimation because it is more likely that the animal first observed is closer to the transect. Some authors of other studies have tried to correct this by measuring the spread of the group and incorporate this in the perpendicular distance measurements before analysis (Peres 1990). However, this was not done for this study.

Yet, despite these potential problems and biases, the results presented are comparable to other studies investigating the effects of hunting on primate populations (e.g. Peres 1990). I am therefore inclined to believe that the trends observed are a reasonable reflection of the current status of primate populations in the PSNR.

Conservation implications

There was a clear effect of hunting on woolly monkeys, red howler monkeys and large-headed capuchins, indicating that hunting decreases with increasing distance to the indigenous communities. This is consistent with other studies, as the highest hunting effort is normally found in areas near human settlements (Jerozolinski & Peres 2003). This underlines the importance of large protected areas, where animals can take refuge in core areas with minimal hunting pressure.

However, although the surrounding rural and indigenous populations exert hunting pressure on the primates, they also look after their resources and renders support for the protection of their territories. This is especially important in the Peruvian Amazon and around PSNR, as large areas are being subjected to petro-chemical exploration (Finer et al. 2008).

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Appendix

Appendix 1:

Species	Study site	Detection function	Key function	Series expansion	Adjustment terms
Brown capuchin	Shiringal	Stratum	Half-normal		
Brown capuchin	Taschacocha	Stratum	Uniform	Cosine	1
Brown capuchin	Wishto	Stratum	Uniform	Cosine	1
Brown capuchin	Ungurahui	Stratum	Half-normal		
Brown capuchin	Pithecia	Stratum	Hazard Rate		
Monk saki monkey	Shiringal	Stratum	Uniform	Cosine	1
Monk saki monkey	Taschacocha	Stratum	Uniform	Cosine	1
Monk saki monkey	Wishto	Stratum	Uniform		
Monk saki monkey	Ungurahui	Stratum	Uniform	Cosine	1
Monk saki monkey	Pithecia	Global	Uniform	Cosine	1
Red howler monkey	Shiringal	Stratum	Half-normal		
Red howler monkey	Taschacocha	Stratum	Half-normal		
Red howler monkey	Wishto	Stratum	Half-normal		
Red howler monkey	Ungurahui	Stratum	Half-normal		
Red howler monkey	Pithecia	Stratum	Half-normal		
Woolly monkey	Shiringal	Global	Uniform	Cosine	1
Woolly monkey	Taschacocha	Stratum	Uniform	Cosine	1, 2,
Woolly monkey	Wishto	Stratum	Uniform	Cosine	1
Woolly monkey	Ungurahui	Stratum	Half-normal		
Woolly monkey	Pithecia	Stratum	Uniform	Cosine	1
Squirrel monkey	Shiringal	Stratum	Uniform	Cosine	1
Squirrel monkey	Taschacocha	Stratum	Uniform	Cosine	1, 2, 3, 4
Squirrel monkey	Wishto	Stratum	Hazard Rate		
Squirrel monkey	Ungurahui	Stratum	Hazard Rate		
Squirrel monkey	Pithecia	Stratum	Uniform	Cosine	1
Saddleback tamarin	Shiringal	Stratum	Hazard Rate		
Saddleback tamarin	Taschacocha	Stratum	Half-normal		
Saddleback tamarin	Wishto	Stratum	Half-normal		
Saddleback tamarin	Ungurahui	Stratum	Half-normal		
Saddleback tamarin	Pithecia	Stratum	Uniform	Cosine	1
White-fronted capuchin	Shiringal	Stratum	Uniform		
White-fronted capuchin	Taschacocha	Stratum	Hazard Rate		
White-fronted capuchin	Wishto	Global	Uniform	Cosine	1, 2
White-fronted capuchin	Ungurahui	Stratum	Half-normal		
White-fronted capuchin	Pithecia	Global	Uniform	Cosine	1, 2



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