

Chapter 9

Influence of Time and Flood on Diurnal Mammal Diversity and Story Level Use in Igapó Forest in the Peruvian Amazon



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9.1 Introduction

Rainforests represent less than seven percent of the Earth's surface but support the highest biodiversity in the world (Wilson and Peter 1988) containing approximately 50% of all terrestrial species (Myers 1988; Mittermeier et al. 1998). Rainforests are also among the most severely threatened ecosystems (Myers 1988; Phillips 1997; Laurance 2004) mainly due to forest destruction causing changes in species composition, species interactions, ecosystem processes, and microclimate modifications (Newmark 1991; Terborgh 1992; Bierregaard et al. 1992; Hall et al. 1996; Benitez-Malvido 1998; Laurance 1998). Rainforest deforestation is also predicted to affect local and global climate due to an increase in temperature, reduction of evapotranspiration and precipitation, and increase in runoff (Nobre et al. 1991; Laurance and Williamson 2002). Additionally, forest harvest affects water cycles and increases susceptibility to fire, while predicted droughts due to climate change also will increase fire in rainforests (Nobre et al. 1991; Laurance 1998; Laurance and Williamson 2002). Climate change is expected to have a great impact on rainforest ecosystems due to the narrow range of daily and yearly temperature to which species are adapted, as well as their dependence on rainfall (Malhi et al. 2009). Even subtle temperature changes, and, most importantly, changes in precipitation, such as extreme drought events, will affect species distribution, presence, and abundance and are predicted to drive a great percentage of species to extinction (Thomas et al. 2004; Parry et al. 2007; Malhi et al. 2009). Techniques such as rapid inventories, systematic surveys, and monitoring programs are important to measure

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and document changes in species diversity and species distribution over time, and even some behavioral patterns (Wilson 1985; Haila and Margules 1996). These tools provide important knowledge for conservation and management of rainforest ecosystems (Haila and Margules 1996).

Rainforests, particularly the Peruvian Amazon, have a more heterogeneous landscape than previously reported (Tuomisto et al. 1995). This has important implications since heterogeneity is positively correlated with species diversity (Pianka 1966). Species diversity is also related to forest structure and differs between canopy and story levels when forests are stratified vertically (Basset et al. 2001; Bernard 2001; Schulze et al. 2001; Viveiros Grelle 2003; Fermon et al. 2005). Each story has unique physical characteristics, microclimate, and resource availability and harbors a unique flora and fauna (Frith 1984; Basset et al. 2001; Bernard 2001; Basset et al. 2003). Consideration of all vertical strata is necessary for accurate estimates of forest biodiversity and abundance since some species use multiple story levels (Bernard 2001; Viveiros Grelle 2003; Stork and Grimbacher 2006).

Rainforests are home to the greatest mammalian species richness in the world, and mammals occupy all vertical strata (Estrada and Coates-Estrada 1985; Bernard 2001; Monteiro Vieira and Monteiro-Filho 2003; Viveiros Grelle 2003); however, little is known about most rainforest species. In the neotropics, mammalian diversity is being discovered at an average of one new genus and eight new species annually (Patterson 2000), but the rate of extinction is unknown. Mammals play important roles in rainforests and can provide ecological services such as seed dispersal and pollination (Gessman and MacMahon 1984; Terborgh 1988; Jansen et al. 2012). Mammals also drive the dynamics and complexity of biological communities by serving as predators and providing a prey base (Gessman and MacMahon 1984; Terborgh 1988). Therefore, changes in mammal communities may have implications for the dynamics and function of rainforest ecosystems with unknown consequences.

We conducted surveys in the Peruvian rainforest to determine what the diurnal mammalian diversity was and if this diversity was influenced by flood and varied by story level. To answer these questions, we stratified the forest vertically into four levels and predicted that the upper canopy would have the highest diversity index compared to the midstory, understory, and ground due to the advantages that a dense canopy offers for protection from predators and high food production and that use of lower levels would decrease in a year of flooding and deposition of silt at the ground level. We also predicted that diversity would be higher during a wet year compared to a dry year because of the influence that rainfall has on resource availability.

9.2 Methods

9.2.1 Study Site

Our study site was a 400 ha research grid located in the Peruvian Amazon at the Amazon Research Center (ARC). The ARC is located in Tamshiyacu-Tahuayo Reserve (TTR) in northeastern Peruvian Amazon between the Tamshiyacu-Tahuayo and Yavarí Miri rivers in the state of Loreto, near the Brazilian border (4°39'S, 73°26'W). This 322,500 ha conservation area is a lowland, evergreen, and seasonally flooded forest that was created by local communities due to overexploitation of natural resources by outside commercial interests (Newing and Bodmer 2003). Hunting without regulation, poaching, large-scale commercial fishing, fishing with chemicals, and large-scale logging were the main disturbances that affected the area (Newing and Bodmer 2003). The plant communities found within the study area include palm swamps (low-lying areas of poor drainage, low tree diversity; the most common species is moriche palm or *Mauritia flexuosa*), bajial (floods with a water level of 5–7 m, low tree diversity, small trees, none to sparse vegetation in understory), high restinga (unflooded forest, clay soils, high tree diversity, and large trees are common), and low restinga (floods with a water level of 2.5–5 m, low tree diversity; Prance 1979; Kvist and Nebel 2001; Myster 2009).

In 2009, the study site experienced above average rainfall, and in 2010 a severe drought affected the area. In 2009, the mean low temperature was 23.3 °C (\pm 0.05 SE), and the mean high temperature was 28.2 °C (\pm 0.11 SE). In 2010 the mean low temperature was 23.2 °C (\pm 0.07 SE), and the mean high temperature was 29.4 °C (\pm 0.13 SE). Total rainfall was 3914 mm in the wet year of 2009 compared to 3100 mm in the dry year of 2010, a difference of 21%. The lodge at ARC is built on stilts because of seasonal flooding. On 31 May 2009, the depth of water at the lodge was 1.5 m, and on the same day in 2010, the depth of water was 0 m.

9.2.2 Mammalian Survey

In June and July of 2009 and 2010, we conducted mammal surveys in forested habitat to compare species diversity of a wet versus a dry year. Each day from 0600 h to 1700 h, we walked two 2 km transects, a total of 42 transects and 84 km each year. During surveys, we recorded species of mammals, number of individuals, time of day, and story level where individuals were found, categorized as ground, understory (<5 m, some cover and vegetation), midstory (5–15 m, little vegetation, mainly bare trunks from large trees), and canopy (>15 m, usually very dense foliage). We stratified the forest vertically into these story levels to determine whether mammalian diversity varied by level. In the rainforest, these four story levels are distinct and easily recognizable.

9.2.3 Analysis

We used the Shannon-Wiener diversity index to estimate diurnal mammal diversity for wet (2009) and dry (2010) years as well as by story level. We analyzed differences between wet (2009) and dry (2010) years using the Shannon diversity t-test in program PAST (Hammer et al. 2001). We estimated mammalian alpha, beta, and gamma diversity for the four different story levels as different types of habitat for wet, dry, and both years combined (Whittaker 1972). We created a contingency table in program JMP 10 (SAS Institute, INC., Cary, NC) and used a log-likelihood ratio to determine if the frequency of sightings by species varied by time of day or story level.

9.3 Results

The diurnal mammalian diversity index did not differ between wet and dry years ($t_{807.04} = -1.623$, $P = 0.105$; Table 9.1). Species richness was higher in the wet year, at 19 species, compared to 17 species sighted in the dry year, and evenness was low for both years (Fig. 9.1). We sighted a total of 22 different species over 2 years, and 14 species were detected in both years (Table 10.2). In the wet year, we sighted a total of 438 individuals and 829 individuals in the dry year.

The diversity index by story level differed between years, but the diversity index was highest in the canopy for both years (Table 9.1). In the wet year, the diversity index was high in the understory after the canopy, followed by midstory and ground (Table 9.1). Species richness was highest in the canopy, followed by ground, understory, and finally midstory (Fig. 9.2). Evenness was high for ground and canopy and low for understory and midstory (Fig. 9.2). In the dry year, the diversity index was high in the midstory after the canopy, followed by ground and understory (Table 9.1). Species richness was highest in the canopy followed by midstory, ground, and finally understory (Fig. 9.2). Evenness was high for canopy and understory and low for ground and midstory (Fig. 9.2).

Table 9.1 Shannon-Wiener diversity index comparison between wet and dry year and among different story levels and alpha, gamma, and beta diversity by year and combined. Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010

Year	Diversity index total	Diversity index by story level				Diversity		
		Ground	Understory	Midstory	Canopy	Alpha	Gamma	Beta
Wet (2009)	2.01	0.69	1.34	0.95	1.88	7	19	2.7
Dry (2010)	2.08	1.48	0.8	1.64	2.02	8	17	2.1
Combined	–	–	–	–	–	10	22	2.2

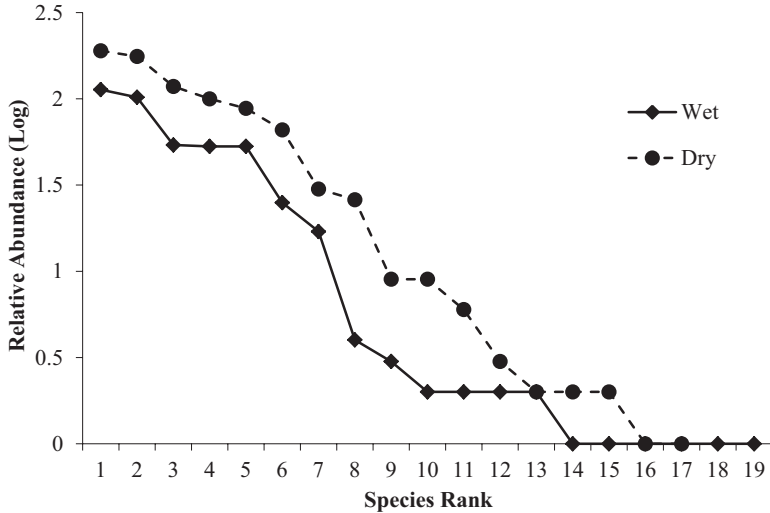


Fig. 9.1 Rank abundance curve: comparison of species richness between wet and dry years, relative species abundance, as well as evenness for both years. On the x -axis, each number represents a species and is ranked by the relative abundance. A steep slope indicates low evenness, and a shallow slope indicates high evenness since relative abundance among species is similar. Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010

Alpha, beta, and gamma diversity were different for both years separately and combined. Alpha diversity was higher in the dry year compared to the wet year, and gamma and beta diversity were higher in the wet year compared to the dry year (Table 9.1).

Species richness for the wet year and dry year combined was 22, representing 6 orders of mammals (Table 9.2). Primates was the most diverse and most abundant with 8 different species and 967 individuals sighted. Rodentia was represented by 6 species with 171 individuals. We sighted 2 species of the order Carnivora with 116 individuals; the South American coati (*Nasua nasua*) was the most common carnivore species in the study area. Artiodactyla was represented by three species with eight individuals sighted. Pilosa was represented by two species with four individuals, and Didelphimorphia was represented by a single species with one individual sighted (Table 9.1).

During the wet and dry year, the frequency of sightings of species was influenced by time of day ($X^2 = 511.063$, $n = 438$, $P = <0.001$; $X^2 = 473.400$, $n = 829$, $P = <0.001$; Fig. 9.3) and varied by story level ($X^2 = 430.811$, $n = 438$, $P = <0.001$; $X^2 = 403.854$, $n = 829$, $P = <0.001$; Fig. 9.4). We sighted more mammal species during the late morning and early afternoon compared to the early morning and late afternoon, and although there was a difference in the amount of flooding between years, our frequency of sightings of species was similar across time periods for both years (Fig. 9.3). Some mammal species were sighted in only one story level, and several species were sighted in different story levels at different frequencies (Fig. 9.4).

Table 9.2 Mammal abundance and story level sighted (percentage of sightings from both years combined) in 2009 and 2010. Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010

Order	Common name	Scientific name	Abundance		Story level			
			Wet (2009)	Dry (2010)	Ground	Understory	Midstory	Canopy
Didelphimorphia	Common opossum	<i>Didelphis marsupialis</i>	1	0	100	–	–	–
	Two-toed sloth	<i>Choloepus</i> sp.	1	0	–	–	–	100
Pilosa	Southern tamandua	<i>Tamandua tetradactyla</i>	1	2	–	–	–	100
	Pygmy marmoset	<i>Cebuella pygmaea</i>	0	9	–	–	78	22
	Saddleback tamarin	<i>Saguinus fuscicollis</i>	53	190	–	14	51	35
	Black-chested mustached tamarin	<i>Saguinus mystax</i>	54	176	–	1	50	49
	White-fronted capuchin	<i>Cebus albifrons</i>	0	30	–	–	–	100
	Tufted capuchin	<i>Cebus apella</i>	1	66	–	–	30	70
	Common squirrel monkey	<i>Saimiri sciureus</i>	102	100	–	15	12	73
Rodentia	Dusky titi monkey	<i>Callicebus moloch</i>	17	26	2	7	47	44
	Monk saki	<i>Pithecia monachus</i>	25	118	–	–	12	88
	Neotropical pygmy squirrel	<i>Sciurillus pusillus</i>	53	88	–	6	15	79
	Northern and southern Amazon red squirrel ^a	<i>Sciurus igniventris</i> , <i>S. spadiceus</i>	2	6	50	13	–	38
	Black agouti	<i>Dasyprocta fuliginosa</i>	4	9	100	–	–	–
	Green acouchi	<i>Myoprocta pratti</i>	0	2	100	–	–	–
	Paca	<i>Cuniculus paca</i>	2	0	100	–	–	–
	Yellow-crowned brush-tailed rat	<i>Isothrix bisriata</i>	3	2	–	80	20	–
	Tayra	<i>Eira barbara</i>	2	1	67	–	–	33
	South American coati	<i>Nasua nasua</i>	113	0	73	–	–	27
Artiodactyla	Collared peccary	<i>Tayassu tajacu</i>	2	0	100	–	–	–
	Red brocket deer	<i>Mazama americana</i>	1	3	100	–	–	–
	Gray brocket deer	<i>Mazama gouazoubira</i>	1	1	100	–	–	–

^aNorthern and southern Amazon red squirrel are too similar to identify in the field due to nearly identical size and color

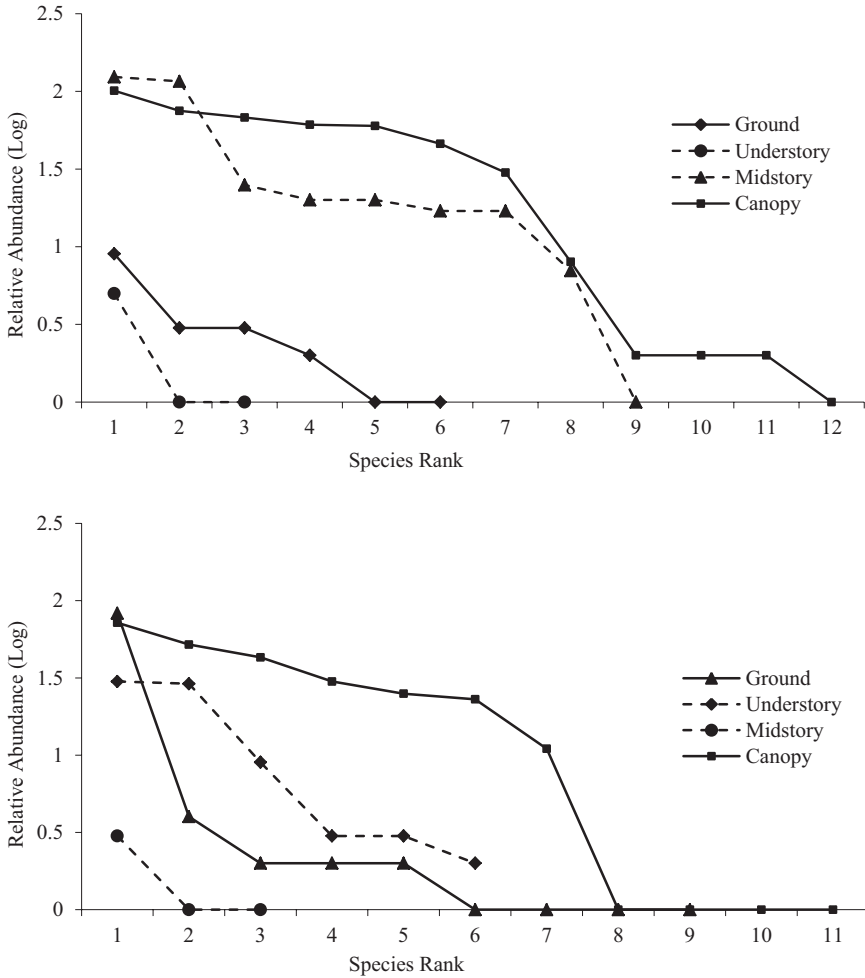


Fig. 9.2 Rank abundance curve: comparison of species richness between the four different story levels in the forest, relative species abundance, and evenness in wet (2009; top) and dry (2010; bottom) year. On the *x*-axis, each number represents a species and is ranked by the relative abundance. A steep slope indicates low evenness, and a shallow slope indicates high evenness since relative abundance among species is similar. Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010

9.4 Discussion

During our sampling in the igapó forest, we observed 48 mammal species, including diurnal, nocturnal, terrestrial, arboreal, and aquatic mammals. Diversity index did not differ between wet and dry year, and this is similar to patterns observed in other areas of Amazonia (Emmons 1984). During mammal surveys in a wet and dry

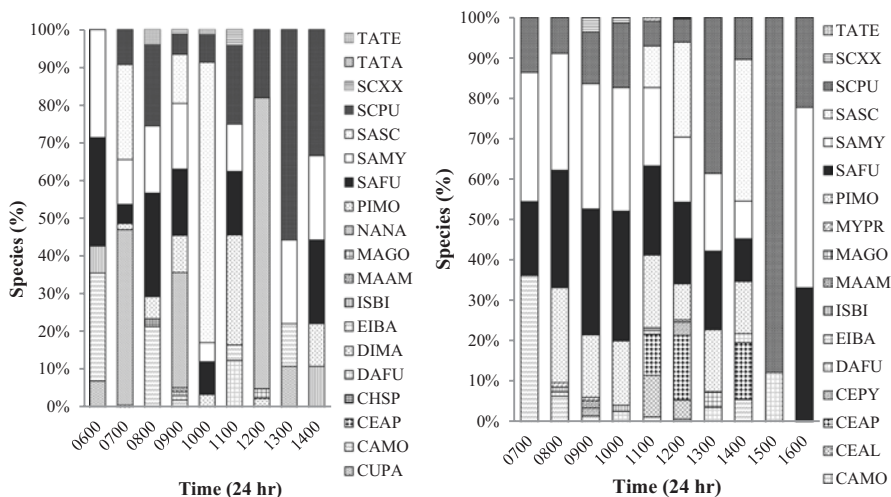


Fig. 9.3 Percentage of mammal species sighted by time in wet year (2009; left) and dry year (2010; right) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010. CUPA *Cuniculus paca*; CAMO *Callicebus moloch*; CEAL *Cebus albifrons*; CEAP *Cebus paella*; CEPY *Cebuella pygmaea*; CHSP *Choloepus* sp.; DAFU *Dasyprocta fuliginosa*; DIMA *Didelphis marsupialis*; EIBA *Eira barbara*; ISBI *Isothrix bistriata*; MAAM *Mazama americana*; MAGO *Mazama gouazoubira*; MYPR *Myoprocta pratti*; NANA *Nasua nasua*; PIMO *Pithecia monachus*; SAFU *Saguinus fuscicollis*; SAMY *Saguinus mystax*; SASC *Saimiri sciureus*; SCPU *Sciurillus pusillus*; SCXX *Sciurus igniventris*, *S. spadiceus*; TATA *Tayassu tajacu*; TATE *Tamandua tetradactyla*

year, we sighted 22 diurnal mammalian species with primates representing the more diverse and abundant order. Although Primates are not usually the most common taxon in Peru (Pacheco et al. 2009), sightings have become more frequent at the TTR since the decrease in hunting after creation of the reserve (Pitman et al. 2003). Most of the primates forage in groups, and some groups include different species, making primates more visible compared to solitary species (Chapman 1990; Klein and Klein 2005). We sighted 2 more species of primates and had a total of 463 more primate sightings during the dry year compared to the wet year, which could be explained by the low food availability observed in the dry year, forcing primates to move more while searching for food (Dawson 1979; Vedder 1984; Boinski 1987; Garber 2005; Di Bitetti 2006).

Although most of the mammal species sighted during our surveys were diurnal (Emmons and Feer 1997; Eisenberg and Redford 1999), species sightings varied by time of day and by story level. This is similar to other areas of the tropics, where species were associated with certain story levels when the forest was stratified vertically (Basset et al. 2001; Bernard 2001; Schulze et al. 2001; Viveiros Grelle 2003; Fermon et al. 2005). Each story level offers unique resources and includes different physical and environmental characteristics (Frith 1984; Basset et al. 2001; Bernard

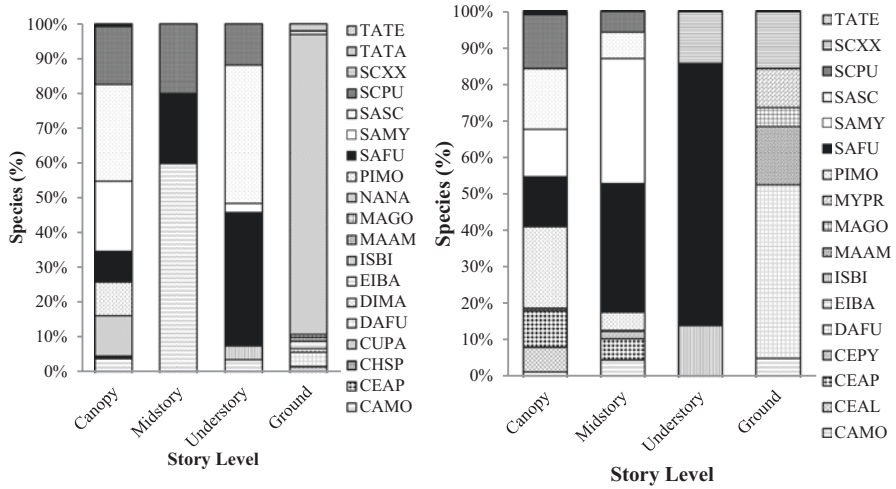


Fig. 9.4 Percentage of mammal species sighted by story level in wet year (2009; left) and dry year (2010; right) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010. CUPA *Cuniculus paca*; CAMO *Callicebus moloch*; CEAL *Cebus albifrons*; CEAP *Cebus paella*; CEPY *Cebuella pygmaea*; CHSP *Choloepus sp.*; DAFU *Dasyprocta fuliginosa*; DIMA *Didelphis marsupialis*; EIBA *Eira barbara*; ISBI *Isothrix bistriata*; MAAM *Mazama americana*; MAGO *Mazama gouazoubira*; MYPR *Myoprocta pratti*; NANA *Nasua nasua*; PIMO *Pithecia monachus*; SAFU *Saguinus fuscicollis*; SAMY *Saguinus mystax*; SASC *Saimiri sciureus*; SCPU *Sciurillus pusillus*; SCXX *Sciurus igniventris*, *S. spadicus*; TATA *Tayassu tajacu*; TATE *Tamandua tetradactyla*

2001; Basset et al. 2003), which allows for a complex community with a great diversity of species to occupy the forest (Basset et al. 2001; Bernard 2001; Schulze et al. 2001; Viveiros Grelle 2003; Fermon et al. 2005).

As we predicted, the upper forest canopy had the highest diversity index and species richness for both years among all forest levels, which suggests the importance of protection and management of forests with large trees and closed canopy due to their contribution to biological diversity (Estrada and Coates-Estrada 1985; Dean et al. 1999; Andersson and Östlund 2004; Ishii et al. 2004; Sorensen 2004). Dense, large canopies are important not just for species that move through them (Emmons 1995; Laurance and Laurance 1999; Wilson et al. 2007) but also for species that spend most of their time on the ground, understory, and midstory. Large, mature trees with large and continuous canopies provide protection, offer greater seed and fruit production to species using different story levels, and create different microclimates that support a high biodiversity (Goodrum et al. 1971; Estrada and Coates-Estrada 1985; Burns and Hokala 1990; Bierregaard et al. 1992). Mammal movements are restricted with reduced canopy connectivity, and mammals and bird species will permanently move away from areas where canopy is destroyed due to fire and where food sources are depleted (Kinnaird and O’Brien 1998; Wilson et al. 2007). Gaps in the canopy or lack of canopy connectivity can bring important ecological changes such as altering the plant community in the understory and subsequently altering the

animal community (Frumhoff 1995; Kinnaird and O'Brien 1998). Observed and predicted impacts of rainforest alteration on mammal communities are more alarming when considering effects of climate change in rainforests (Laurance 1998).

Species diversity on the ground was approximately twice as high in the dry year than in the wet year. This could be explained by two factors, which are influenced by the above average rainfall observed in 2009. First, water level during the wet year was higher than during the dry year, and most of the study site stayed underwater until mid-June, preventing ground-dwelling mammals to occupy the area. In 2010, due to the extreme drought, the study site stayed almost completely dry. With increases in water level as experienced in wet years, most of the ground-dwelling species move to higher ground, or terra firme, seeking larger areas of dry land (Bodmer 1990b; Alho 2008). Only a few individuals stay in high restinga or small patches of forest surrounded by water that are high enough in elevation to avoid inundation most of the years (Bodmer 1990b; Alho 2008). When the water recedes, terrestrial wildlife move through the forest to areas of lower elevation (Bodmer 1990b; Alho 2008). Alternatively, moriche palm is one of the main sources of food for many terrestrial mammals (Bodmer 1990a, 1991; Tobler 2008; Bowler and Bodmer 2011). Ripe fruit drops to the ground and many mammal species forage around these palm trees. In the wet year, we observed fruit production, but, because of the above average rainfall, the fruit fell in the water and rotted. In the dry year, however, fruit production was very low, and perhaps individuals were actively looking for food, making our ground sightings more common (Vedder 1984; Bonaventura et al. 1992; Dussault et al. 2005). In the wet year, we sighted 113 South American coatis. The reason for the great number of coati sightings in the wet year compared to the dry year is unknown, and food availability alone could not explain this pattern. Coatis are omnivorous, and their diet changes according to availability of insects or plants and fruits between wet and dry seasons (Alves-Costa et al. 2004), and they are known to increase the time spent and use of trees to forage and travel during the dry season (Beisiegel and Mantovani 2006).

Mammals play a crucial role in ecosystem function (Gessman and MacMahon 1984; Terborgh 1988; Jansen et al. 2012). Conservation of mammals as well as their diversity is important for maintaining the complexity of biological communities (Gessman and MacMahon 1984; Terborgh 1988), and this is especially true in the tropics, host to some of the most complex biotic communities on Earth (Covich 1988; Tuomisto et al. 1995; Giller 1996; Scarano 2002). Protection of continuous, mature forests with large canopies has important conservation implications as these areas most likely protect the greatest diversity of mammals while also providing shelter and food for other taxa (Bierregaard et al. 1992; Dean et al. 1999; Andersson and Östlund 2004; Ishii et al. 2004; Sorensen 2004). These continuous forests also facilitate movements of ground and canopy dwellers between lowland and higher elevation areas during wet and dry season as well as years with above average rainfall (Frumhoff 1995; Kinnaird and O'Brien 1998; Wilson et al. 2007). Forest characteristics such as large trees with large canopies and flood regimes need to be taken into consideration when designing management and conservation plans that aim to conserve and protect rainforest biodiversity.

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