RESEARCH ARTICLE

Primate Assemblage Structure in Amazonian Flooded and Unflooded Forests

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There is considerable variation in primate species richness across neotropical forest sites, and the richest assemblages are found in western Amazonia. Forest type is an important determinant of the patterns of platyrrhine primate diversity, abundance, and biomass. Here we present data on the assemblage structure of primates in adjacent unflooded (terra firme) and seasonally inundated (várzea and igapó) forests in the lower Purús region of central-western Brazilian Amazonia. A line-transect census of 2,026 km in terra firme, 2,309 km in várzea, and 277 km in igapó was conducted. Twelve primate species were recorded from 2,059 primate group sightings. Although terra firme was found to be consistently more species-rich than várzea, the aggregate primate density in terra firme forest was considerably lower than that in the species-poor várzea. Consequently, the total biomass estimate was much higher in várzea compared to either terra firme or igapó forest. Brown capuchin monkeys (Cebus apella) were the most abundant species in terra firme, but were outnumbered by squirrel monkeys (Saimiri cf. ustus) in the várzea. The results suggest that floodplain forest is a crucial complement to terra firme in terms of primate conservation in Amazonian forests. Am. J. Primatol. 67:243–258, 2005. © 2005 Wiley-Liss, Inc.

Key words: Amazonia; Brazil; New World primates; platyrrhines; primate community

INTRODUCTION

Primates are often the most conspicuous arboreal consumers in paleotropical [Emmons et al., 1983; Leighton & Leighton, 1983] and neotropical forests [Peres, 1999a]. In many areas they comprise a large proportion of the resident vertebrate biomass [Oates et al., 1990; Terborgh, 1983a]. Primate community richness is also


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highly variable. The most species-rich forest sites in South America are located in the western Amazon, with as many as 14 sympatric species occurring along the Rio Jurúa [Peres, 1988], and 13 sympatric species inhabiting Ponta da Castanha [Johns, 1985] and the Urucu [Peres, 1993a].

Amazonia is characterized by a wide range of vegetation types that affect the ecological distribution of the regional biota. While some species exploit a variety of habitats, others are primarily or entirely restricted to particular vegetation types. However, the main determinants of the considerable variation in primate species richness between sites are currently under debate [Eeley & Lawes, 1999; Peres & Janson, 1999]. Peres [1997a] found that on a local scale, habitat heterogeneity within and between different sites (α-diversity and β-diversity, respectively) is the best determinant of primate species richness, and this has also been shown for several other taxa on a regional scale [Gascon et al., 2000]. Therefore, the size and variety of habitats can affect both the number of species and their abundance in a particular area.

The two most widespread forest environments in Amazonia are unflooded forests (hereafter termed “terra firme”) and seasonally flooded forests, which represent the main difference in terrestrial macrohabitats across the region. Terra firme forests account for 83% of the central Amazon basin and are situated on land that never floods [Hess et al., 2003]. Consequently, these unflooded forests are situated on well drained terrain that tends to be heavily leached and nutrient-poor because it has long been deprived of alluvial sediments.

The remaining 17% of the central Amazon basin consists of wetlands, 70% of which is seasonally flooded forest [Hess et al., 2003]. Different types of flooded forest can also be distinguished on the basis of hydrochemical [Sioli, 1968] and floristic [Prance, 1979] differences. Flooded forests along white-water rivers are known as várzea forests. These rivers originate in the Andes or pre-Andean regions, which are geologically young and easily erodable landscapes [Räsänen et al., 1987]. They therefore carry large amounts of nutrient-rich suspended sediments, and the seasonal influx of nutrients makes the várzea forests eutrophic.

Igapó forests are inundated on a seasonal basis by black or clear water that originates in the Amazonian tertiary lowlands or Guiana Shield, and often drain sandy soils of low-nutrient content. igapó forests are therefore oligotrophic, carry less suspended inorganic elements than várzea forests, and contain elevated concentrations of dissolved organic material, such as humic and fulvic acids.

Few studies have presented data on the primate richness and abundance of adjacent flooded and unflooded Amazonian forests, and no study to date has investigated the structure and dynamics of primate assemblages in adjacent terra firme, várzea, and igapó forests. In this study we investigate primate assemblage structure and composition in such a forest macro-mosaic in the lower Rio Purús region of central-western Brazilian Amazonia, and try to pinpoint possible habitat-related determinants of assemblage biomass and diversity. Primate group sizes, population densities, and biomass estimates are reported for individual species in the three forest types, and discussed in relation to other studies. We also include brief notes on each species and their habitat associations and use.

MATERIALS AND METHODS

Study Area

The study took place at Lago Uauacú in the lower Rio Purús region of central-western Brazilian Amazonia (04° 20’S, 62° 28’W; Fig. 1). This area
remains largely undisturbed and incorporates a large landscape mosaic of terra firme and floodplain forests that are inundated by either white water (várzea) or black water (igapó [sensu Prance, 1979]) on a seasonal basis for as long as 6 months of the year. Lago Uauacú itself is a 32-km-long, crescent-shaped, black-water lake. A human population of 30 caboclo families live near the lake and depend on the harvesting of Brazil nuts from natural castanhais (stands of Brazil nut trees (*Bertholletia excelsa*–Lecythidaceae)), in addition to some small-scale commercial fishing, logging, and hunting, for their annual income. However, the forest in the study region remains almost entirely intact, and subsistence hunting was recently restricted to very light offtakes of large-bodied game species such as large rodents and ungulates. Subsistence hunters at Lago Uauacú do not take primates, and hunting had not taken place in the census areas. We therefore assume that the primate assemblages at different sites are largely representative of their respective habitats, and reflect intrinsic differences in forest structure and composition, flooding regimes, and soil fertility rather than varying degrees of anthropogenic disturbance. A more detailed description of the study site is provided elsewhere [Haugaasen, 2004].

**Census Techniques and Data Analyses**

Data on different primate assemblages at Lago Uauacú were obtained during surveys conducted in terra firme, várzea, and igapó forests in 2002 and 2003. All sites were surveyed using a standardized line-transect census protocol, as described in Peres [1999b]. In brief, census walks were conducted from 0700–
1100 hr and 1300–1700 hr. Census walks were terminated during rain. When a group was detected, the time, species identity, group size, perpendicular distance to the approximate geometric center of the group (or subgroup/foraging parties), sighting location along the transect, and detection cue were recorded. Because nocturnal surveys were not carried out, the data presented here focus on diurnal primates, and thus account for all but one species (the southern red-necked night monkey (*Aotus cf. nigriceps*)) that occur at Lago Uauacu.

This study is based on data from a two-way census of 2,026 km in terra firme, 2,309 km in várzea, and 277 km in igapó. Given the smaller sampling conducted at igapó, the data presented for this forest type should be considered preliminary. The censuses were carried out along 13 transects that were marked with flagging tape every 50 m and ranged from 4,000 to 5,000 m in length. This amounts to a total census effort of 4,612 km walked along 62.5 km of transects. Replicate census walks within each sampling block were systematically alternated between terra firme and floodplain forests to minimize any confounding effects of seasonality. In the high-water season, censuses along the várzea and igapó forest transects were conducted with the use of unmotorized dugout canoes, and used the same paths as censuses on foot during the low-water season. Flags along high-water transects had to be frequently renewed because of changes in the water level.

The census data were analyzed with the use of DISTANCE 4.0 software [Thomas et al., 2002]. All visual and acoustic detection events were included in the analyses. In some cases, however, the perpendicular distance data were truncated to remove any outliers from the analysis, which provided a better fit to the various model estimators used to derive detectability functions. Group density estimates were derived from half-normal models with either a cosine or a polynomial adjustment. Population density estimates were then calculated using mean group sizes obtained from reliable group counts during visual detection events. Crude biomass estimates were calculated using body mass data compiled by Peres and Dolman [2000] and Peres [2001] (Table 1).

Detection data for the two sympatric tamarin species—the black-capped moustached tamarin (*Saguinus mystax* ssp.) and the Avila Pires saddleback tamarin (*Saguinus fuscicollis avilapiresi*)—were pooled because the exact composition of mixed-species groups of tamarins was lacking for a number of observations. In such cases, the individual density and biomass estimates were extrapolated from the total sample of observations in which reliable group counts were available for each species. We also note that although moustached tamarins at Lago Uauacu occur within the geographic range of the red-capped moustached tamarin (*S. m. pileatus*), they are more similar to the epiphenotype of black-capped tamarin (*S. m. mystax*), which previously were not known to occur east of the Jurúa River [Peres, 1993b].

Nonmetric multidimensional scaling (MDS) ordination based on the Bray-Curtis similarity measure was used to further explore within- and between-habitat differences in community structure at the transect level. With the use of the computer software PRIMER v. 5 [Clarke, 1993], all species were entered in the ordination as single entities. However, detection data for the two sympatric tamarin species were again pooled together and the night monkey was excluded from the analysis. Red titi monkeys were also excluded from the analysis because they were abundant only in secondary forest throughout the study area. Forest sites were thus positioned in the ordination space according to their primate species composition and abundance. The abundance measure used in the ordination was the number of groups observed per 10 km walked. An index of
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Species are ordered according to body mass within families.

Mean body mass, trophic classifications and stratification use were derived from Peres and Dolman [2000] and Peres [2001].

Diet; ex, exudate feeder; fr, frugivore; in, insectivore; sp, seed predator; vp, vertebrate predator; fo, folivore. Listed in order of preference.

Forest levels; c, canopy; sc, sub-canopy; u, understorey. Listed in order of preference.
multivariate dispersion [Warwick & Clarke, 1993] was calculated to investigate the variability among replicate terra firme, várzea, and igapó forest samples.

RESULTS

Species Richness

A total of 2,059 primate sightings of 12 primate species were recorded at Lago Uauacú (Table I). These included the Avila Pires saddleback tamarin (*Saguinus fuscicollis avilapiresi*), black-capped moustached tamarin (*Saguinus mystax* ssp.), golden-backed squirrel monkey (*Saimiri cf. ustus*), night monkey (*Aotus cf. nigriceps*), red titi monkey (*Callicebus cupreus*), collared titi monkey (*Callicebus torquatus purinus*),uffy saki monkey (*Pithecia albicans*), white-fronted capuchin (*Cebus albifrons versicolor*), brown capuchin (*Cebus apella*), red howler monkey (*Alouatta seniculus seniculus*), gray woolly monkey (*Lagothrix lagotricha cana*), and black spider monkey (*Ateles chamek*). Additionally, the study area is within the geographic range of the pygmy marmoset (*Cebuella pygmaea*), and several local reports confirmed that this species occurred in fringe forest habitat characterized by high levels of disturbance. However, if indeed it is present, this species must be very patchily distributed, because we have no records of pygmy marmosets being found in the main forest matrix during more than 3 years of field work at Lago Uauacú.

Spatial Organization of the Primate Assemblage

All 12 primate species encountered during the censuses occurred in terra firme forest, whereas the maximum number of sympatric species observed in the várzea and igapó forest sites was 8 and 11 species, respectively. However, a maximum of only three primate species—*C. apella*, *A. seniculus*, and *Saimiri cf. ustus*—occurred in várzea sites F, G, I, and J, which were isolated from neighboring terra firme by a ~50-m-wide river (paraná) channel, whereas as many as five additional species (*S. fuscicollis*, *S. mystax*, *P. albicans*, *C. albifrons*, and *A. chamek*) were found at várzea site K, which was physically connected to the terra firme forest matrix. An effective fluvial barrier within várzea forest therefore exacerbated the difference in species richness between the forest types. This also indicates that the five species that occur in várzea site K but not in unconnected várzea sites cannot be entirely restricted to várzea, and depend on terra firme forest habitat for at least part of their year-round metabolic needs.

On the other hand, a total of four primate species that occur in terra firme were never observed in várzea, whereas only one terra firme forest primate—the red titi monkey—was consistently absent from igapó forest. In contrast, all primate species encountered in várzea forest were also found in adjacent terra firme forest. The most marked contrast in species composition was therefore found between the primate assemblages of terra firme and várzea forest, whereas igapó forest exhibited a very similar set of primate species compared to terra firme. This is not surprising given the spatial configuration and extent of the igapó forest, which formed narrow corridors of seasonally flooded forest that interdigitate the terra firme forest matrix along perennial streams in the shady area.

These observations are supported by the MDS ordination (Fig. 2). On the basis of the primate species composition and group encounter rates observed at different sites, terra firme and várzea forests form two clearly distinct clusters on the left and right sides of the MDS ordination plot, respectively, and diverge primarily along the first axis (Fig. 2). As expected, the igapó forest sites (L and M)
and várzea site K were intermediate between terra firme and várzea (Fig. 2) due to their interdigitation with terra firme forest terraces. Terra firme site H is portrayed as an outlier in the ordination, primarily because of the high encounter rates of brown capuchins and squirrel monkeys at this site compared to the other terra firme forest sites.

The index of multivariate dispersion shows that igapó forests are more dispersed (1.259) than terra firme and várzea forests (1.032 and 0.926, respectively), which show more cohesion despite the outlier found within each group of sites. The high dispersion value observed between the igapó plots is probably best explained by the small sampling effort made at these sites, which affected the number of species observed and their encounter rates between the two sites.

Patterns of Abundance and Biomass

The aggregate population density of all primate species in terra firme and igapó forest was considerably lower than that in várzea forest, despite the lower species-richness of the latter (Table II). The overall density of primate groups in várzea forest was more than twice that of terra firme, resulting in a similar difference in densities of individuals. Consequently, the aggregate primate biomass in várzea (364.1 kg/km²) was considerably higher than that of terra firme (277.6 kg/km²) and igapó forest (283.4 kg/km²). However, this difference was not as great as could be expected from the difference in numerical abundance because the small-bodied squirrel monkeys were the most common primates in both types of flooded forest (especially in várzea forest). In summary, the várzea forests were
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1Species are ordered according to body size within families.
2Mean group size obtained from all visual detection events.
3Number of individual detection events.
4All densities derived with DISTANCE [Thomas et al., 2002] using the half normal model except * where King’s method was used. In this case, the density estimate was calculated on the basis of the effective strip width in other forest types.
5Biomass estimates calculated using data presented in Peres and Dolman [2000] and Peres [2001].
6Although moustached tamarins at Lago Uauáçu occur within the geographic range of the reddish-capped Saguinus mystax pileatus, these are more similar to the epiphenotype of the black-capped Saguinus mystax mystax.
7p=present in this forest type but population density estimate is unavailable
characterized by low primate species richness and high assemblage biomass compared to the adjacent terra firme and igapó forests.

**Habitat Differences at the Species Level**

Despite the similarities between terra firme and igapó in species richness, abundance, and biomass, there were marked differences in population densities at the species level. Golden-backed squirrel monkeys were the most abundant primate species in várzea and igapó, whereas brown capuchins, closely followed by moustached tamarins, were the most abundant species in terra firme. Howler monkeys were also far more common in várzea and igapó than in terra firme forest, whereas both of the tamarin species and woolly monkeys were common in terra firme. Collared titis, buffy sakis, and white-fronted capuchins were primarily found in terra firme and igapó, and the two former species were observed in surprisingly high densities in igapó forest. The only true habitat generalist with high population densities in all forest types was the brown capuchin. In fact, this ubiquitous, midsized species had the highest biomass density of all primate species in all three forest types, closely followed by woolly monkeys in terra firme, squirrel monkeys in várzea, and howler monkeys in igapó forest (Table II). In summary, várzea and igapó converged in terms of primate densities at the species level, while terra firme and igapó converged in richness, abundance, and biomass. However, more extensive surveys in igapó are needed to better elucidate the perceived differences between forest types.

**DISCUSSION**

**Species Richness and Spatial Characteristics of the Primate Assemblage**

In terms of species number and composition, the primate assemblage at Lago Uauáçu is similar to those documented at other central and western Amazonian forest sites, where as many as 13 [Peres, 1993a, 1997a] or 14 [Johns, 1985] sympatric primate species can be found. Our findings closely match those reported for primate assemblages along the Juruá River, where várzea forest is consistently species-poor compared to the adjacent terra firme forest [Peres, 1997a]. Peres [1997a] also estimated the biomass of the primate assemblage in the várzea along the Juruá to be more than twice that of terra firme, which is similar to the results reported here. However, our aggregate primate biomass estimates for várzea forest are significantly lower than those obtained along the Rio Juruá, primarily because of the lower howler monkey densities at Lago Uauáçu. Likewise, the primate biomass noted at a similar terra firme site in central-western Brazilian Amazonia (Urucu [Peres, 1993a]) was higher than our estimates, mainly because of the lower densities of woolly monkeys at Lago Uauáçu.

The spatial characteristics of the primate assemblages appear to be largely a function of physical connectivity and proximity to adjacent terra firme forests. There was a considerable reduction in species richness across the river channel from the várzea transect K, which abutted terra firme terraces, to unconnected várzea transects (F, G, I, and J). This suggests that the ∼50-m-wide paraná channel provides an effective fluvial barrier to dispersal and movements by primates, which is consistent with evidence presented elsewhere [Ayres & Clutton-Brock, 1992; Heymann et al., 2002]. The close resemblance in species composition between igapó and terra firme forest is similarly due to the year-
round physical connection between these forest types, which ensures that lateral movements by several species are not hindered.

However, despite the high species richness exhibited by the igapó forest and várzea transect K, it is clear from data presented elsewhere [Haugaasen, 2004] that apart from the three primate species (C. apella, A. seniculus, and Saimiri cf. ustus) that consistently occur in unconnected várzea sites, all of the other species appear to use várzea and igapó only sporadically. Thus the species richness of these areas was only temporarily boosted at certain times of the year. In fact, the sporadic use of floodplain forests by some terra firme species (e.g., P. albicans, C. albifrons, A. chamek, and L. lagotricha) appear to be intimately related to ephemeral pulses in fruit availability in these environments [Haugaasen, 2004].

Few specific attempts have been made to document the use of várzea or igapó forest by primates; however, extensive use of seasonally flooded forest appears to be a consistent trait throughout the Amazon basin [e.g., Boubli, 1999; Branch, 1983; Defler, 1996; Peres, 1993a; Trolle, 2003] (M.G.M van Roosmalen, personal communication). The general consensus is that the use of these environments is largely driven by spatial and temporal variability in food availability [Clutton-Brock, 1977; Janson & Emmons, 1990; Terborgh, 1983a]. The ability to select and move across habitats, or include within the home range different habitats that exhibit distinct temporal peaks in food resources, may have positive effects on population densities by reducing the impact of local food shortages in any one habitat [Janson et al., 1981]. For example, spider monkeys (Ateles belzebuth) that use home ranges consisting of 50% flooded forest can live at higher densities than conspecifics in other home ranges that contain either greater or smaller proportions of flooded forest [Ahumada et al., 1998]. It is therefore likely that, all other things being equal, a mosaic of floodplain and terra firme forests has a positive impact in buffering local resource scarcity, and can also boost the abundance of the primary consumer fauna. Evidently, more work is needed to further map the extent to which flooded forest complements terra firme in terms of resources, given the community-wide patterns of plant phenology found in each forest type.

In any case, floodplain forests should not be seen as just marginal habitats that occasionally subsidize terra firme forest specialists. Interestingly, mounting evidence suggests that species that are frequently regarded as inhabitants of flooded forest may perform movements in the opposite direction, i.e., into unflooded terra firme forest. In particular, this has been observed in large group-living pitheciine primates such as black uakaries (Cacajao melanocephalus) [Barnett & Brandon-Jones, 1997; Barnett & de Castilho, 2000; Boubli, 1999; Defler, 1989, 2001] (C.A. Peres, unpublished data), white uakaries (Cacajao calvus) [Peres, 1997b], and squirrel monkeys (Saimiri spp.) appear to follow a similar pattern [Peres, 1993a; Terborgh, 1983a] (T. Haugaasen, personal observation).

Environmental Factors That Shape the Primate Assemblage

Apart from habitat connectivity, differences in floristic composition, habitat structure, and soil fertility may provide the most plausible explanations for the dramatic differences in primate assemblage structure found between terra firme, várzea, and igapó forests. For example, the lower species richness of várzea and igapó may be due to their lower floristic diversity compared to terra firme [Ayres, 1993; Balslev et al., 1987; Campbell et al., 1986; Haugaasen & Peres, 2004]. As a
result of flooding, várzea environments also have a considerably simplified forest structure, because the understory and ground layers are completely submerged for much of the year. This may prohibit a suite of species from surviving in these environments on a year-round basis. Indeed, small-bodied understory insectivores, such as the pygmy marmoset (*Cebuella pygmaea*), tamarin (*Saguinus* spp.), and Goeldi’s monkey (*Callimico goeldii*), do not occur in large expanses of annually flooded várzea forests along the Rio Jurua, presumably because of the seasonal submersion or lack of understory foraging substrates [Peres, 1997a].

The apparent success of the three “true” várzea and igapó species may therefore be best explained by their better adaptation to the seasonal disruption of certain food supplies by flooding. Brown capuchins and squirrel monkeys use all forest strata from the ground layer to the canopy, and feed on a mixture of fruit and arthropods [e.g., Lima & Ferrari, 2003; Zhang, 1995]. Brown capuchins also consume a variety of flowers and other nonreproductive plant materials, such as the basal leaf of bromeliad rosettes (C. Peres, personal observation), understory palm pith [Terborgh, 1983a, b], young bamboo shoots, and new leaf shoots of the Jauari palm (*Astrocaryum jauari*) in várzea forest (T. Haugaasen, personal observation).

The success of howler monkeys in várzea forest is probably due to their ability to consume and digest foliage. Chemical analyses of the soil macronutrients that are crucial to plants (N, P, K, Na, Ca, and Mg) consistently showed that the alluvial soils of várzea forest at Lago Uauacú were far more fertile than those of terra firme and igapó forests [Haugaasen & Peres, in review], which is in agreement with other findings from Amazonian forests [Irion, 1978]. The levels of phytochemical defenses may therefore decrease in várzea forest because of less limiting nutrient uptake. Foliage quality may thus be more favorable to arboreal folivores, since the plant metabolic costs of replacing leaf tissue lost to herbivores are relatively low [Janzen, 1974]. This is consistent with the overwhelmingly greater biomass density of many folivore species in várzea forest, such as howler monkeys, two genera of sloths (*Bradypus* and *Choloepus*), hoatzins (*Opisthocomus hoazin*), horned screamers (*Anhima cornuta*), and iguanas (*Iguana iguana*) [Haugaasen & Peres, 2005; Peres, 1997b, 1999a; Queiroz, 1995]. Haugaasen and Peres [in press] also showed that várzea and igapó forests are more deciduous than terra firme forest. This results in lower leaf longevity and a higher abundance of young foliage, which has a more favorable nutrient level and contains reduced levels of chemical defenses compared to mature foliage [Klinge et al., 1983]. However, it is less apparent why howlers are so abundant in igapó forest despite the geochemical similarities between this forest type and terra firme forests. High levels of tree deciduousness and close proximity to terra firme forest may be possible explanations.

Furthermore, the high fertility of the young alluvial soils renewed in várzea forest every year may increase overall fruit production in this forest type. Indeed, comparable data sets from terra firme, várzea, and igapó sites at Lago Uauacú show that várzea on average have a higher number of trees bearing fruit during any given month of the year [Haugaasen & Peres, in press]. Similarly, the flood disturbance may generate a more heterogeneous environment with a greater diversity of successional habitats, which tend to fruit at different times of the year. This may allow higher densities of primates to persist in várzea forest, whereas habitat diversity in the terra firme and igapó forest matrix tends to be lower, and the lack of alternative fruit resources during periods of scarcity may severely limit the carrying capacity of these forest types. These are probably the primary explanations as to why terra firme and igapó converge in terms of
primate group densities, abundance, and biomass. If nutrient input is an important determinant of primary productivity, the lack of seasonal influx of nutrient-rich sediments should limit the availability of macronutrients to plants on terra firme and igapó soils, and in turn affect the overall primary productivity available to primary consumers in these environments [Peres, 1997a].

**Patterns of Habitat Use**

The habitat plasticity shown by brown capuchins may be attributed to their generalist diet, highly destructive manipulative foraging (especially during the dry season), and heavy reliance on palm resources [Peres, 1994; Spironello, 1991; Terborgh, 1983a, b]. This plasticity, combined with their apparently small home ranges and the nonexistent hunting pressure at Lago Uauacú, could explain their relatively high densities in all forest types. The contribution of brown capuchins to the assemblage-wide biomass estimate lies within the range of other studies. However, the estimates for Lago Uauacú are among the highest found at similar forest types elsewhere in Amazonia [Peres, 1997a].

In contrast to forest sites along the Rio Juruá that were sampled during the low-water season [Peres, 1997a], white-fronted capuchins were more abundant in terra firme than várzea forest on a year-round basis. This is in accordance with Rylands [1987], who stated that this species generally avoids flooded forest. Observations of white-fronted capuchins in várzea forest directly adjacent to terra firme coincided with the height of the fruiting season [Haugaasen, 2004], which suggests that some groups may travel long distances to take advantage of abundant fruit resources. Defler [1979] made similar observations of *C. albibrans* in Colombia, which heavily utilized seasonally flooded forest at the peak of the *Goupia glabra* (Celastraceae) fruiting season. The generally low rate of sightings of this large group-living primate may be explained by their low group density, relatively large home ranges, and heavy reliance on widely dispersed fruit crops, such as figs [Terborgh, 1983b].

The poorly studied buffy saki [cf., Peres, 1993c] was observed in all three forest types, which is consistent with observations of this species entering inundated forest on a seasonal basis elsewhere in central-western Amazonia [Rylands, 1987] (C. Peres, unpublished data). However, buffy sakis were entirely restricted to várzea sites that extensively interfaced with abutting terra firme forest, and these sightings coincided with the height of the várzea fruiting season. This suggests that this species could not subsist on a year-round basis in home ranges consisting of várzea forest only, but could take advantage of abundant fruit resources in flooded forest.

The two tamarin species occurred at higher densities in terra firme forest sites at Lago Uauacú than at the nearest site where tamarins have been studied (Urucu [Peres, 1993a]). At Lago Uauacú, moustached tamarins were the second most abundant species (following brown capuchins) in the terra firme forest matrix. Although mixed-species groups of tamarins occurred primarily in terra firme, those occupying home ranges along the várzea–terra firme interface made frequent incursions into várzea forest. However, they used only fringe várzea habitats that were not far from terra firme forest, which is consistent with observations made by Peres [1997a].

Howler monkeys (*Alouatta* spp.) are arguably the best studied of all platyrrhine primates. Distance from white-water rivers, soil fertility, forest structure, and rainfall seasonality have all been shown to be good predictors of howler monkey densities in neotropical forests [Peres, 1997b]. Their consistent
rarity in terra firme forest at Lago Uauacu is typical of other central-western Amazonian forests, and the density we report for várzea forest is considerably lower that found at most other sites [Peres, 1997b], and is on a par with moderately hunted várzea sites along the Rio Juruá [Peres, 1997a]. However, the densities of howler monkeys are highly variable throughout Amazonia [Peres, 1997b], albeit less so within broad classes of forest types.

Woolly monkeys were never observed in várzea forest at Lago Uauacu, despite the proximity of this habitat to the home-range boundaries of several groups. This is consistent with the findings of Peres [1997a], who classified *Lagothrix lagotricha* as a hallmark terra firme species, but contrasts with Rylands’ [1987] report of this species entering inundated forest at times of high fruit abundance. However, Rylands [1987] did not specify what type of inundated forest was referred to in that study. Local reports at Lago Uauacu suggest that this species uses extensive portions of igapó forest at the height of the fruiting season, although woolly monkeys were seen using this habitat only once. Further investigations into the ranging movements of the woolly monkey, and additional censuses in igapó forest are clearly needed.

The squirrel monkey was by far the most abundant primate species found at Lago Uauacu, considering all forest types. Their terra firme forest densities were remarkably similar to those of congeners in the same habitat along the Rio Juruá [Peres, 1997a]. On the other hand, their densities in várzea have been observed to be even higher than those reported here [Peres, 1997a]. It has been suggested that the high abundance of this species in várzea may result from a lack of competition from other small-bodied insectivorous primates [Rylands, 1987]. Although both tamarins (*Saguinus spp.*) and marmosets (*Callithrix spp.*) can occur in sympatry with squirrel monkeys, these callitrichids never occur in large tracts of várzea forest that are far removed from terra firme and subjected to an annual flood pulse. Squirrel monkeys in terra firme were never sighted far away from várzea or igapó forest, which suggests that they require proximity to seasonally inundated forest. All but two observations coincided with the onset of the fruiting season in terra firme forest (T. Haugaasen, unpublished data), and thus this species appears to exhibit reverse lateral movement compared to the movements of other primates (i.e., occasionally squirrel monkeys tracks terra firme forest resources within large home ranges that predominantly consist of várzea forest).

The limited, patchy distribution of spider monkeys at Lago Uauacu may result from small-scale habitat variation within terra firme forest [Klein & Klein, 1976] and competition with woolly monkeys [Rylands, 1987]. In our study area, spider monkeys were most commonly encountered along the broad interface between várzea and terra firme forest. This underlines the possibility that foraging incursions into várzea may play a vital role in the ecology of black spider monkeys at Lago Uauacu. Furthermore, congeners in central Suriname perform similar seasonal foraging forays into different forest types at times of fruit scarcity [van Roosmalen, 1985]. Indeed, both our observations and local reports suggest that this species enters várzea on a seasonal basis at the height of the fruiting season.

Observations of collared titi monkeys (*Callicebus torquatus*) were rare, but these monkeys appeared to express a consistent habitat preference for terra firme and igapó forest, confirming earlier reports [Defler, 1994]. The myth that this species is an edaphic specialist restricted to Amazonian forests on white-sand soils [Kinzey & Gentry, 1979] has been solidly refuted [Defler, 1994; Peres, 1997a], and is also contradicted by observations of the species in this study.

The rarity of red titi monkeys (*Callicebus cupreus*) in the overall primary forest matrix at Lago Uauacu is explained by the strong preference of this species
for secondary growth close to human habitation. Their preference for secondary or disturbance-dependent habitats is well documented [Peres, 1993a; Rylands, 1987].

Conservation Implications

The consistently lower species richness observed in várzea forest should not imply that this major Amazonian forest type should be neglected in future conservation planning [cf., Goulding et al., 2003; Peres & Terborgh, 1995]. We have demonstrated that várzea forests differ profoundly from terra firme forests in terms of primate species composition, abundance, and biomass, even in areas where the two forest types are juxtaposed. The data provided here and elsewhere also show that several unflooded forest primate species may use flooded forests on a seasonal basis, which suggests that landscape-scale habitat heterogeneity is crucial to the long-term population viability of some species. Failure to protect the greatest expression of seasonally flooded forests on Earth may also alter or disrupt the seed dispersal services provided by primates. These results suggest that várzea and igapó forests are important complements to terra firme forest in terms of regional-scale primate conservation, and that conservation planning in Amazonian forests must be considered on a landscape scale.

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REFERENCES


