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Primate communities in Amazonian forests: their habitats and food resources

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Key words. Primate habitats; primate foods; Amazonia; seasonality; body size.

Introduction

Neotropical primates are forest dwellers and a large number of them occur in, or are restricted to the forests of the Amazon river basin and the Guianas (hereafter referred to as Amazonia). The most recent taxonomic revisions identify 43 primate species in this region (out of 65 for the whole neotropics), belonging to 14 of the 16 extant New World primate genera [51–53,97]. These species are not uniformly distributed throughout Amazonia and most of them have restricted distributions, most frequently delimited by rivers, notably the Rio Solimões-Amazonas, Rio Negro, Rio Japurá-Caquetá, Rio Juruá, Rio Madeira and the Rio Tapajós[10,51,135]. Only three genera include sympatric congeneric species (*Saguinus, Cebus and Callicebus*), otherwise primate communities within Amazonia are composed of single representatives of each genus. The number of genera included in a community can be as many as 12, for example in the middle and upper Amazon Basin in northwest Brazil and Peru[96,140] and according to known and supposed distributions, forests south of the Rio Solimões between the Rios Javarí and Juruá may include as many as 15 sympatric primate species. The study of the ecology and behavior of Amazonian primates has received little attention, although the situation has improved considerably since the early 1970s[106,149]. With information from recent field studies and studies of the same or closely related species outside Amazonia, this review examines the ecological and behavioral differences between Amazonian primates in order to see how a community of 15 species, for example, share or divide up the food resources and habitats available in what is broadly termed the Amazonian tropical rainforest.

Habitats

Distribution maps of Amazonian primates give an erroneous impression of the homogeneity of the presence of a particular species within its range. There are a great variety of habitats from the primate's point of view even within a few square kilometers. Klein and Klein[76] illustrate this, describing eight types of forest communities in and near floodplain forest at La Macarena, Colombia, using the criteria of the abundance or presence of several easily identifiable tree species within their study site of 780 ha. Revilla[125] describes six plant communities within a flooded forest of the Rio Negro, Brazil, which he distinguishes by soil types, flooding patterns, physiognomy and floristic composition. Even with edaphic features held constant, patches of different floristic communities result from tree falls of different sizes which give rise to secondary pioneer vegetation at varying stages of succession[49,157]. These small communities form mosaics within broader categories of forest types. Mittermeier[94] describes 18 forest types occupied by primates in Surinam. Similarly Eisenberg and Redford[31] describe the Guiana shield in Venezuela as a mosaic of open savannas, lowland tropical forest, premontane and montane forest. Amazonian forest types and their general characteristics are listed in table 1. They are divided into terra-firme (or upland or dryland) forests and inundation forests and are broadly distinguished by topography, physiognomy, climate, soils, drainage, and floristic communities, including plant species endemicity and diversity.

Some primate species are abundant in a wide variety of forest types while others are restricted to only very few, which results in patchy distributions. Most explanations of a primate species' preference for a particular forest type involve observed or assumed specializations for particular features of the habitat, usually food resources, whereas in the reverse case (absence from a forest type) it is difficult to explain why a species has not adapted to rather different conditions in, say, physiognomically similar forests to those which it occupies. Patchy distributions and forest type preference or avoidance remain largely unexplained with our present limited knowledge of the primate's needs and what the forest types have or have not to offer. The answers probably lie in the species' dependance on the presence of certain types of food resources at a time of food shortage or 'lean period'[15,149]. Tree species have patchy distributions, and fine-grained differences in floristic communities, resulting from local or widespread changes in soil conditions, climate or topography, for example, are critical to a primate group's survival in a particular forest.

Habitats – vertical stratification

The forest provides a three-dimensional environment which, as described above, is not uniform horizontally, and neither is it uniform vertically. In the vertical plane its structure (orientation, size and density of supports for locomotion), foliage density[111], microclimates[19] and the types, density and distribution of food items (both animal[5,33,34] and plant[6,127,128]) change from the emergent trees and canopy down to the undergrowth. Different forest types and floristic communities differ in these aspects. 'Igapó' forest, for example, tends to have a more closed canopy and greater numbers of epiphytes when compared to 'várzea' forest[2]. Sympatric primate species show a vertical stratification in their use of the forest[99] which is associated with different modes of locomotion related to the predominant structure of the forest at different levels[35,70] as well as to their feeding habits.

Primate foods

Primate foods may be broadly grouped into animal prey, non-reproductive and reproductive plant parts.

1. *Animal prey*. This includes arthropods (mainly insects), snails, frogs, lizards and bird's eggs and nestlings, which are difficult to obtain but widely distributed and easy to digest sources of protein and fats. It is useful to distinguish two foraging methods. The first is a foliage-gleaning searching amongst leaves and along branches for frequently cryptically camouflaged but easily accessible

Table 1. Forest types in Amazonia (References 2, 7, 16, 29, 32, 82, 94, 100, 113, 114, 117, 118, 121, 125, 160)

Terra-firme forest	
High forest	Large biomass, tall trees, closed canopy, sparse ground cover, large lianes of limited density, high plant species diversity.
Liane forest	Intermediate biomass, dense in lianes.
Low forest	Low biomass, thick ground cover, low trees due to limiting factors (slopes, altitude, rainfall).
Campinarana and Caatinga	Intermediate biomass, high forest on white sand soil, high light penetration, rich in epiphytes.
Dry transition forest	Transition of Amazon forest to cerrado of central Brazil and savannas, intermediate biomass, high light penetration, abundant in small lianes, semi-deciduous.
Young secondary forest	Low dense forest of highly clumped, quick-growing, light-loving pioneer spp. reverting to high forest.
Old secondary forest	Similar to high forest except in terms of numbers of large trees, basal area of trees, tree density and plant species composition.
Bamboo forest	Bamboo dominated forest, very dense.
Forest in Amazonian savanna	Small patches of forest surrounded by transition forest and savanna, semi-deciduous.
Mountain savanna forest	High forest to scrub on permeable, poor soils at high altitudes in Surinam.
Montane forest	Dense low forest, high plant species endemicity. Of Guiana shield and Andean cloud forest above 1400 m.
Inundated forest	
Seasonal várzea	Flooded annually by white-water rivers, less plant spp. diversity than high terra-firme forest. Broken canopy, higher tree density and fewer epiphytes than igapó. Characteristic tree species different to those of igapó.
Seasonal igapó	Flooded annually by black or clear-water rivers, usually on sandy soil, less plant spp. diversity than várzea with different characteristic tree spp. More even and closed canopy and lower tree density than várzea.
Swamp forest	Permanently inundated igapó or várzea, tall forest, low plant spp. diversity.
Floodplain forest	Flooded by irregular rainfall, similar to seasonal várzea but contains many terra-firme forest plant spp.
Mixed-water inundation forest	Forest flooded by mixed black and white-water.
Tidal várzea	High forest, flooded twice-daily by white-water in the lower Amazon. Similar to seasonal várzea.
Mangrove swamps	Estuarine regions and mudflats along the coast, flooded by brackish water.

insects. The second is a manipulative or destructive foraging in specific sites such as humus masses, holes, under bark, in rotten wood, between the leaf axils of epiphytic tank bromeliads, in stems and leaf petioles and leaf litter accumulations for relatively inaccessible animal prey. The separation is simplistic but useful to distinguish predominant foraging methods which also depend on the primate's body size, maneuverability, speed, substrate preference, mode of locomotion and the preferred localities and forest levels used. A third type of insect foraging involves the destruction of nests of social Hymenoptera by *Cebus* species, particularly *C. albifrons*[149] and possibly *C. nigrivittatus*. Marmosets, *Callithrix*, also make use of army ant, *Eciton*, swarm raids to catch insects[133].

2. *Non-reproductive plant parts*. This includes new and old leaves, buds, stems, petioles, bark and exudates such as gums, sap and latex. Leaves are important protein sources but, although widely available, they require the ingestion of large quantities because they are poor in energy content and are difficult to digest owing to fiber and also to digestion inhibitors such as tannins, thus an intestinal flora and for many primate species a distinctive gut morphology is required to deal with them[22]. The production of secondary compounds, either toxins or digestion inhibitors, to protect leaves results in selective feeding. Howler monkeys, *Alouatta* for example, select leaves with the highest ratio of proteins to secondary compounds[47]. New leaves, buds and stems are higher in protein content than mature leaves and, although they also tend to be high in tannin concentrations, they have relatively little fiber and are generally preferred[47, 90, 155, 156]. New leaves and buds are seasonal in their abundance[6, 80, 125].

Exudates are generally unavailable to primates except when plants produce them as a result of damage or insect attack or in certain cases such as *Parkia pendula* (Leguminosae) which produces large quantities of gum from its hanging seed pods[55, 136]. The two marmoset genera, *Cebuella* and *Callithrix*, however, gouge tree trunks, branches and vines (particularly of the families Leguminosae, Anacardiaceae and Vochysiaceae) to obtain saps or to stimulate flow of gums or latex[25, 26, 136, 138]. Feeding on latex (particularly from the family Apocynaceae) is uncommon, but nutritionally both gums and latex are believed to be important carbohydrate sources[14, 129]. Bark eating is also uncommon but may provide an important fiber source for very frugivorous diets.

3. *Reproductive plant parts*. These include fruits and seeds (both ripe and unripe), flowers and nectar. Fruits are important carbohydrate or lipid sources rather than protein sources. Seeds are generally high in proteins and lipids. Fruits are easily obtained and ingested but are more widely dipersed than leaves and available in limited quantities at certain times of the year. Unripe fruit is generally difficult to digest due to high concentrations of tannins, and similarly seeds, although low in tannin concentrations, tend to have hard seed coats which are tannin rich and fibrous[155, 156]. Flowers are also possibly difficult to digest due to toxic secondary compounds[155]. Nectar is rich in carbohydrates but difficult to obtain in sufficient quantities for large primates although some trees produce copious quantities from rather robust inflorescences able to withstand the rough treatment of monkeys which, licking nectar, may act as pollinators[65, 119, 152].

Habitats and primate foods

Arthropod abundance is unlikely to be similar in different forest types, but very little information is available and no studies have been made comparing forest types with the emphasis on primate diets. Using four collecting methods (soil extraction, ground and tree-trunk photoeclectors and canopy-fogging), Adis and Schubart[5] found that the relative abundance of arthropods was highest in the igapó, intermediate in primary dryland forest and lowest in the várzea. Comparisons of canopy arthropod faunas in terra-firme forest, várzea, igapó and mixed-water inundation forest by Erwin[33, 34] indicate that his várzea forest site was richest in numbers of individuals and that mixed-water inundation forest was richest in species. The igapó was poorest in terms of individuals. However, the results should be treated with caution because Erwin's study, for example, analyzed only part of the sample, did not include soft-bodied arthropods, and was carried out in small areas in single sites for each forest type at only one time of year. Adis et al.[4] also studied canopy arthropods by fogging in three forest types in Central Amazonia and found that numbers and biomass were highest in terra-firme forest, intermediate in igapó forest and lowest in várzea. Adis et. al.[4] discuss the discrepancy between these results. Edaphic conditions and floristic communities can vary considerably, even over short distances. Ribeiro and Adis[126] demonstrate that high terra-firme forests only 4 km apart can have markedly different rainfall regimes, which undoubtedly has a significant impact on their arthropod faunas. Problems involved in comparing arthropod densities and biomasses in different Amazonian forest types are discussed by Adis and Schubart[5] and Adis et al.[4].

Klinge et al.[78] compared foliage nutrient levels in igapó and várzea forests in Central Amazonia. Várzea trees tend to be more deciduous with larger leaves which are richer in concentrations of elements compared to igapó trees which have smaller, heavier, evergreen, sclerophyllous leaves with a low element concentration. In second growth forests, leaves tend to have fewer chemical defenses associated with shorter leaf lifespans and higher net productivity[107], which makes them attractive to herbivorous insects. This, Opler[107] suggests, results in greater insect biomasses in secondary growth forest than in mature forest which has a lower net productivity and leaves with longer lifespans and more chemical defenses. However, on the basis of the findings of Klinge et al.[78] a similar argument would predict higher densities of insects in várzea forest compared to igapó, but canopy fogging studies[4] and studies of trunk arthropods[5] indicate that the reverse is true. Nutrient-poor soils such as sand result in high levels of secondary compounds in the leaves[7, 84], suggesting that caatinga forest, igapó and savanna forest patches on sandy soils are more inhospitable to insects and folivorous primates, although, as noted above, Adis and Schubart[5] and Adis et al.[4] found that igapó contained relatively high arthropod densities, including predators. Waterman[156] indicates that mature foliage of lowland forests may be characteristically higher in fiber when compared to high altitude and deciduous forests. Although this has not been tested for Amazonia, the fact that the large majority of Amazonian forests are lowland may be related to the lack of specialist folivores similar to the colobines of the Old World.

Tree species diversity tends to be reduced in sandy soil forests, várzea, and second growth forests compared to terra-firme forests, although in compensation tree species tend to be more numerous and less widely dispersed. Worbes[160] found that tree species diversity is lower in várzea than in igapó but that the basal area of trees of > 5 cm DBH was very much higher in the várzea (60 m^2/ha) than in the igapó (37 m^2/ha), indicating a denser forest with tree species being more abundant in the várzea. These differences undoubtedly affect population densities and the types of primates able to use these forests, just as differences in the leaves described by Klinge et al.[78] possibly affect folivorous monkey populations, but no studies have been made regarding this.

Animal-dispersed fruits (fleshy arils and mesocarps) in second growth forest tend to be produced in large crops over long and sometimes biannual fruiting seasons (for example, *Cecropia* (Moraceae)). Tree species are also highly clumped and their fruits are most frequently small and many-seeded (for example, many members of the family Melastomataceae)[84,108]. Fruits of mature forest, on the other hand, tend to be larger and, although crops of particularly canopy species tend to be very large, tree species are widely dispersed and fruit for shorter periods and more irregularly[107,108].

Seasonality and lean periods

Amazon forests are seasonal in terms of rainfall and, to a lesser extent, temperature. Total annual rainfall varies throughout the basin as does the duration and extremity of the dry season[43,142]. In Central Amazonia, the total annual rainfall is 1780–2800 mm with a rainy season from December to May, when daytime temperatures are lower, and a dry season from June to November, when daytime temperatures are higher and differences between day and night temperatures are more pronounced. The south of the basin has rather longer and more pronounced dry seasons (from April to November or December) with a total annual rainfall of 1640–2090 mm, whereas in northern Peru, Colombia and the northwest of the basin annual rainfall is higher (2040–3500 mm) with practically no dry season. In the northeast of the basin (east of 60° W) rainfall is as high but with short and very pronounced dry seasons from August to November. As noted previously, however, it should be remembered that closely adjacent localities can differ markedly in terms of the intensity, frequency and time of rainfall as well as annual precipitation totals[126].

Although there have been very few plant phenology studies in Amazonia, it is evident that rainfall is an important factor. In terra-firme forests new leaf growth peaks at the end of the wet season, followed by flowering and fruit setting during the dry season (especially the beginning and end), when there is a ground water deficit, and fruiting peaks during the first half of the wet season[6,8,9,29,141,149]. In flooded forests, it is the inundation patterns which affect tree phenology. Many igapó trees, for example, flower when flood levels are subsiding or at their lowest in the late dry season and early wet season, with the result that fruiting peaks at the end of the wet season and during inundation[2,3,125]. Terra-firme forest adjacent to igapó shows a peak in flowering when flood levels are increasing or at their highest at the beginning and middle of the dry season[125].

Seasonality in rainfall also effects arthropod populations[4,5,112], although how pronounced fluctuations may be in comparison to those in the more seasonal forests of Central America, for example, is not known[5,145,146,158]. In Central American forests night-flying insects are more abundant in the early rainy season[146] and certain homopterans are also more abundant during the rainy season[159]. In general terms, dry seasons act in a similar fashion to winters in temperate regions and the duration and dryness of a dry season affects insect populations in the following wet season[158]. In Central Amazonia there are indications of a greater abundance of arthropods on trunks in igapó, várzea and second growth terra-firme forest in the wet season but not in terra-firme primary forest[5], although Penny and Arias[112] found peaks in abundance in terra-firme primary forest at the beginning and end of the wet season. Terborgh[149] recorded reduced capture rates for insect foraging *Cebus, Saimiri* and *Saguinus* in Peru in the late wet and early dry season and higher capture rates in the late dry and early wet season and believes that this finding reflects changes in insect abundance. Igapó forests have pronounced seasonal migrations of arthropods (from forest floor to trunks and canopy as well as out of the igapó to neighboring terra-firme forest) at the onset of flooding[5] which undoubtedly affect their availability to primates. The methodological problems in studying arthropod population fluctuations and the extreme diversity and complexity of their lifestyles[4,5], coupled with a lack of any studies examining primate insect foraging behavior in detail alongside studies monitoring the abundance of their preferred insect prey, make it very difficult to generalize about whether primates experience or are affected by seasonal changes in arthropod abundance in Amazonian forests. In the case of fruits, seeds and new leaves, however, it does seem likely that there are seasonal shortages which can be critical for primates at least in the short term[11,27,28,65,90,93,111,134]. The ability of primate species to find alternative foods during lean periods is critical to their survival in a particular habitat and revealing with regard to dietary differences between sympatric species.

Some effects of body size

Amazonian primates range in size from the diminutive pygmy marmoset, *Cebuella*, of approximately 115 g to the large Atelinae and the howler monkey, *Alouatta*, of 6–8 kg (table 2). All are frugivorous to some extent; the smaller species obtain their protein requirements largely from animal prey and the larger species from leaves[54,68]. Insects, which are a rich but small, widely-distributed but difficult-to-obtain food supply, cannot be caught in sufficient numbers to meet the requirements of large body size[24,87,88]. Similarly only small primates can specialize on plant food resources available in small quantities such as nectar, gums, saps and trees with small numbers of small

Table 2. Mean weights of some Amazonian primate species, N = sample size

	Male wt (g)	N	Female wt (g)	N	Ref.
Cebuella pygmaea	110	36	122	35	146
Callithrix humeralifer	425	3	425	3	134
Saguinus midas	450	3	533	1	35
Saguinus labiatus	491	17	495	12	163
Saguinus fuscicollis	405	4	415	3	163
*Callimico goeldii**	Mean weight-581.5 g N = 6				20
Saimiri sciureus	740	8	635	5	35
Callicebus moloch	1200	2	1266	3	104
Aotus spp.	922	2	1014	2	102
Cebus apella	3890	9	3000	2	35
Pithecia pithecia	1866	5	1875	2	35
Chiropotes albinasus	3175	5	2518	5	11
*Cacajao calvus**	4100	1	3550	1	38
Ateles paniscus	7860	5	7690	7	35
Lagothrix lagotricha	7200	6	5871	7	39
Alouatta seniculus	8530	2	6020	3	35

* Captive animals.

fruits available over extended periods[149]. Larger species with absolutely larger food requirements need larger food concentrations. Leaves are a less rich energy source than fruits but relatively high in proteins, particularly young leaves, but a large body size is necessary to deal with the necessary large quantities of a widely-available but difficult-to-digest food source, which requires long passage times to achieve sufficient digestion and assimilation to meet energy and protein requirements[68, 86, 91, 110].

Frugivorous and insectivorous primates tend to have larger home ranges and longer day range lengths for a given body size than folivores because their foods are more widely dispersed[23, 92, 122], and similarly the larger frugivorous primates, able to travel further, have larger home ranges, enabling them to make use of food resources too widely dispersed to be exploited by smaller species[24].

For a given body size, folivores are generally more numerous then frugivores which are more numerous than insectivores and, within diet types, population densities are inversely correlated with body size[130].

Body size also affects maneuverability, so that small species can occupy the lower strata of tall forests as well as low scrubby forests where thin branches and dense undergrowth predominate, whereas large species tend to be confined to the upper levels of the forest[21, 23]. This factor, and the predominance of small, many-seeded fruits of abundant trees having long fruiting seasons as well as possibly higher herbivorous insect densities[107, 108] indicate that second growth forest is hospitable towards small but not to large primates. Hard-shelled nuts and fruits can be cracked more easily by larger species, although some Amazonian primates have specific dental[71, 96, 120] and behavioral[61, 142] adaptations for this.

Small insectivorous monkeys

Marmosets. The genera of marmosets, *Cebuella* and *Callithrix,* have dental and behavioral adaptations for obtaining gums, saps and latex. Using rodent-like incisor teeth[131], they gouge tree trunks, branches and vines of a wide array of species to stimulate exudate flow[26, 124, 136]. The pygmy marmoset, *Cebuella pygmaea,* feeds mainly on plant exudates, supplementing its diet with arthropods, which they obtain by foliage-gleaning methods in thickets and understoreys of the forest; they only occasionally eat fruits[75, 124, 146]. They are restricted to periodically inundated forest, floodplain forest and second growth and edge forest of the upper Amazon Basin[145]. They live in groups of 2–9 independently locomoting individuals in very small, non-overlapping home ranges of 0.2–0.5 ha, centered round one or two principal exudate sources[146].

The larger Amazonian *Callithrix,* on the other hand, are firstly frugivores and insectivores and only sporadically eat exudates, except at the end of the wet season when fruits are scarce[134]. During the dry season, when fruit is more scarce, they concentrate on the fruits of a few abundant species which have long fruiting periods; these are typically found in secondary forest[134]. They forage for insects mainly by gleaning in dense foliage and thickets in the understoreys (between 0 and 15 m in height). They also follow army ant swarms to catch the insects which the ants disturb[133, 134]. Associated with their larger size and greater degree of frugivory, they have larger home ranges (10–30 ha)[134].

In contrast to *Cebuella,* they avoid floodplain, inundated and river edge forests and are most abundant in terra-firme forests where tall forests are mixed with second growth patches resulting from tree falls or human activities[133]. They also inhabit forest patches in Amazonian savanna and white sand forest[133, 138]. *Cebuella* is sympatric with a number of *Saguinus* species (table 3) but there is no evidence, even amongst south and southeast Brazilian *Callithrix,* of sympatry between marmoset species. It is becoming evident that in more seasonal and drier habitats where they occur (savanna forest, cerrado, gallery forest and forest patches in the dry northeast of Brazil) they increase their dependence on plant exudates[37, 79, 134, 147], and the lack of sympatry may be due to their shared exudate-feeding specialization.

Tamarins. Saguinus, like *Callithrix,* are frugivores and insectivores but only eat exudates when they are readily available[26, 44, 134]. They are similar to *Callithrix* in their habitat preferences and the genera are allopatric except to the south of the lower Rio Amazonas where the distributions of *S. midas* and *C. argentata* overlap, although whether they occupy the same forests is not known. In the upper Amazon Basin the moustached tamarins, *S. mystax, S. labiatus* and *S. imperator*, and the black-mantle tamarin, *S. nigricollis,* are allopatric (possibly excepting the region between the Rios Purús and Madeira[51]) but all are sympatric with the saddleback tamarin, *S. fuscicollis* (table 3). The larger moustached tamarins form mixed species groups with the smaller *S. fuscicollis,* but ecologically they are separated by the levels, sites and modes by which they forage for insects.

The moustached tamarins generally search for smaller insects, using a foliage-gleaning method in the levels above 10 m, employing a more quadrupedal running and jumping locomotion than *S. fuscicollis* which has a more manipulative, specific site (holes, leaf litter piles) foraging method in levels below 10 m, where it tends to catch larger insects; this species moves more by vertical clinging and leaping[116, 149, 163]. There is little information regarding sympatry between *S. nigricollis* and *S. fuscicollis.*

They are reported to feed in the same trees[51] and Izawa[57] indicates that *S. nigricollis* is similar to the moustached tamarins in its insect foraging methods. *Saguinus* which are allopatric (table 3) are expected to be intermediate in their foraging behavior, making use of the best of both methods. *Saguinus* are unable to rely on plant exudates at times of fruit shortage because they lack the specialized dentition and gouging behavior of the marmosets[131], although they are known to raid *Cebuella* exudate trees where they are sympatric[145]. *Saguinus,* like *Callithrix,* also specialize on plants which are abundant and fruit in a piecemeal fashion for extended periods during the dry season when fruits are generally scarcer[149]. It is possible that *Saguinus* are more insectivorous than *Callithrix* or, as shown by Janson et al.[65], that nectar is the important stop-gap at the end of the wet season when fruit is scarce. Dawson[27] reports that *S. oedipus* in seasonal, semi-deciduous forests of Panama, suffers periodic insect and fruit shortages, at which time the groups increase their range sizes and become non-territorial. Shortages as severe as those evidently experienced by these *S. oedipus* have not been recorded for Amazonian callitrichids.

Callitrichids as colonizers. Their small size, use of small, soft fruits of abundant trees with extended piecemeal fruiting patterns, insectivorous diets, preference for dense foliage for foraging, for sleeping sites and possibly for protection against predators,[134] and their more or less accentuated predisposition for vertical clinging and leaping, are evidently factors which favor their use of dense vegetation in second growth forest. Their preference for second growth and edge forest has been widely reported[27, 101, 133, 147, 149]. In callitrichids, twinning, relatively large neonates which mature quickly, a post-partum estrus which enables twice yearly breeding and the short estrus cycles contribute to a capacity for a very rapid rate of reproduction for a single female in comparison to cebids and other anthropoid families[30]. Second growth forest patches and, in the case of *Cebuella,* suitable exudate trees are transient and unpredictable in their appearance and the rapid rate of reproduction characteristic of callitrichids is undoubtedly an adaptation for their colonization.

Table 3. Sympatry in Amazonian callitrichids. X = known or supposed distribution overlap

	Cebuella pygmaea	*Callithrix argentata*	*Callithrix humeralifer*	*Saguinus nigricollis*	*Saguinus fuscicollis*	*Saguinus mystax*	*Saguinus labiatus*	*Saguinus imperator*	*Saguinus midas*	*Saguinus inustus*	*Saguinus bicolor*	*Callimico goeldii*
Cebuella pygmaea	–											
Callithrix argentata	–	–										
Callithrix humeralifer	–	–	–									
Saguinus nigricollis	X	–	–	–								
Saguinus fuscicollis	X	–	–	X	–							
Saguinus mystax	X	–	–	–	X	–						
Saguinus labiatus	X	–	–	–	X	–	–					
Saguinus imperator	X	–	–	–	X	–	–	–				
Saguinus midas	–	?	–	–	–	–	–	–	–			
Saguinus inustus	–	–	–	–	–	–	–	–	–	–		
Saguinus bicolor	–	–	–	–	–	–	–	–	?	–	–	
Callimico goeldii	?	–	–	X	X	X	X	X	–	–	–	–

Goeldi's tamarin. Callimico goeldii is a small, rare frugivore-insectivore of the upper Amazon. It is a habitat specialist, occupying bamboo forest with well-developed, dense, scrubby undergrowth which Izawa[60] argues was widespread in the past but today occurs only in patches in the area between the Rio Caquetá in the north, the Rio Madeira in the south and east and the Andes in the west. The patchiness of the habitat results in a patchy distribution; single groups are often separated by some kilometers[115] and they are apparently absent from large areas within their distribution[60]. They live in small groups of similar size to the callitrichids, but, inlike them, have only single young and can have more than one breeding female in a group[83]. Although they do occur in secondary forest[101], they are evidently not successful colonizers as are *Callithrix* and *Saguinus.* Their geographic distribution broadly overlaps that of *Cebuella* but they are separated by their habitat preference[60]. They do form mixed species groups with *Saguinus*[116] but use the lowest forest levels, confining their activities almost entirely to below 5 m and most frequently to heights of 2–3 m. There they hunt for insects with a predominantly vertical clinging and leaping locomotion and can also make use of fruits such as those of ground-living epiphytes[115]. Although they do eat buds and young leaves, whether they eat bamboo shoots is not known. During the dry season they feed on gums exuded from the hanging seed pods of *Parkia* but do not feed on the *Cecropia* fruits extensively used at that time by *Saguinus*[115].

The squirrel monkey. Saimiri is the smallest and most insectivorous of the cebids, supplementing its diet with fruits. They are widely distributed throughout Amazonia, occurring in a wide variety of habitats including várzea, igapó, mangrove swamps, liane forest and second growth forest and river edge[96, 100, 101]. Although they do inhabit high terra-firme forest it is evident that they require the proximity of flooded forest[96, 137, 151]. They live in large groups of 20–40 or as many as 100 individuals in large home ranges of up to 130 ha[13] or more than 250 ha[149]. They forage for insects using a foliage-gleaning method mainly in the understoreys of the forest[36, 150].

They frequently form mixed species groups with *Cebus apella,* which is a larger, more robust monkey; also insectivorous but less so than *Saimiri*[150]. *C. apella* employs a manipulative, destructive foraging technique, mostly in the lower, middle and upper canopy of the forest. The lower levels used by *Saimiri* are associated with a more saltatory locomotion and its smaller size enables it to use smaller supports than *C. apella* which moves more by quadrupedal running and walking[36]. The fruit part of the diet also differs; *Saimiri* eats smaller soft fruits, specializing particularly in figs (*Ficus* spp. Moraceae)[149] whereas *C. apella* also has access to palm fruits, hard-shelled, tough-skinned fruits and nuts not eaten by *Saimiri*[56, 149]. The advantage of the association between groups of these species is not clear but possibly lies in the increased availability of insects to *Saimiri* from the flushing and destructive foraging of *Cebus*[36, 149]. Studies of polyspecific associations of *Cercopithecus* species in Gabon[46] have shown that they can result in increased efficiency of exploitation of fruit sources but that predator detection was the main factor involved, with species habitually using the upper levels warning of aerial predators and those in the lower levels warning of terrestrial predators. Terborgh[149] believes that *Saimiri* is the initiator and benefactor of the association through improved predator detection and more efficient discovery of food resources.

It would appear that *Saimiri* overlaps largely with *Saguinus* and *Callithrix* in its insect foraging methods and fruit preferences. However, studies of sympatric *S. imperator* and *Saimiri* indicate some important differences[149]. The modal class for substrates used by *Saimiri* during foraging was trees while for *S. imperator* it was vines. While both *Saimiri* and *S. imperator* concentrate on exposed prey (*S. fuscicollis* concentrates on hidden prey), *Saimiri* caught more immobile prey (lepidopteran larvae for example) while the quicker tamarins concentrated more on mobile and larger prey such as orthopterans. Similar differences are probable between *Callithrix* and *Saimiri*. An additional factor is the disturbance caused by the larger groups of *Saimiri* which reduces their ability to catch more mobile prey including lizards and frogs whereas the quieter and quicker marmosets and tamarins hunt by stealth. With regard to fruits, Terborgh[149] emphasizes *Saimiri*'s specialization on widely dispersed fig species which, although they produce large, short-lived fruit crops, do so irregularly, and he believes this to be the reason for *Saimiri*'s very large range sizes. Group sizes are too large to depend on the small, piecemeal fruit crops used by the callitrichids. There is also a general separation of these insectivores by their habitat preference. *Saguinus* and *Callithrix* avoid flooded forest, possibly because of *Saimiri*. Insects are possibly relatively abundant in such habitats as igapó compared to high terra-firme forest although *Saimiri* are likely to experience fluctuations in their availability[2, 5, 149]. They have pronounced breeding seasons (in the wet season)[13] possibly as a result of this. They depend more on fruits when insects are scarce[13], and when fruits are scarce they are also known to lick nectar[65] or become entirely insectivorous[149]. It is possible that *Saimiri*, with its larger body size and large polygamous groups have evolved to exploit large expanses of insect-rich forests such as flooded forests and possibly liane forests, specializing on large, short-lived crops which are widely dispersed, whereas the smaller monogamous callitrichids exploit small transient second growth patches (rich in insects and small fruits available in small quantities over long periods) which are too small to accommodate the large *Saimiri* groups. Recent human activities, creating large expanses of second growth, have disrupted this pattern. Further studies are needed, however.

Small frugivorous monkeys

The titi monkeys. The two Amazonian *Callicebus, moloch* and *torquatus*, are sympatric in parts of their distributions. However Kinzey and co-workers[69–74] have demonstrated clear habitat and dietary differences between them. Both are mainly frugivorous but *C. moloch* supplements its diet with leaves and *C. torquatus* does so with arthropods. They have distinctive dental morphologies associated with these diets[71]. *C. moloch* has a broad distribution in Amazonia but is restricted to clay soil forests when sympatric with *C. torquatus* which occurs in white sand forest (campinarana) the distribution of which (north and west of the basin) is coincident with the distribution of *C. torquatus*[73]. Kinzey and Gentry[73] argue that leaves are generally more scleromorphic and contain more toxic secondary compounds and, although lacking evidence, that arthropod abundance is higher in campinarana forest than in clay soil forest. Associated with their dietary differences, *C. moloch* has small home ranges of 0.5–5 ha whereas *C. torquatus* occupies home ranges of 4–30 ha[69, 72]. *C. moloch* are most abundant in dense understoreys and thickets, especially in older second patches and are rare or absent from tall forest with sparse understoreys[63, 101, 133, 149]. They also inhabit inundated forest[72, 76, 101]. *C. torquatus*, on the other hand, occupies vegetation with relatively sparse understoreys, spending most of its time in the middle layers of the canopy and emergents[70, 74]. With regard to dietary overlap with other primates, it is not known to what extent other species inhabit white sand forest. Possibly *Saguinus* does, but *C. torquatus*, unlike both *Saguinus* and *C. moloch*, eat rather large, hard-shelled fruits and seeds and there are differences in their insect foraging behavior; *Callicebus* being rather a sedentary insect stalker on relatively large horizontal branches[70], compared to the more vigorous rapid searching amongst foliage characteristic of *Saguinus*[149]. The small monogamous family groups defending small home ranges indicate that *C. moloch* is a highly selective feeder[40, 72] and can feed on small patches of young leaves and buds in the lower levels of the forest in dense thickets which are not frequented by larger primates. With regard to fruits, both *Callicebus* species feed on large canopy fruit crops when available but their small range size and body size indicate that they can visit the crops more frequently and continue making use of the crop even when there is too little fruit to attract large wide ranging frugivores such as *Ateles*[72]. *C. moloch* feed on the same fruits as those eaten by *Callithrix* but also include small, sour-tasting fruits, seeds, leaves and leafbuds and palm fruits such as those of *Astryocaryum* which *Callithrix* do not eat[133, 134, 137, 149].

The night monkeys. Aotus is the only nocturnal monkey. Seven allopatric species occupy most of the basin, excepting the Guianas and to the east of the Rio Trombetas in the northeast[52]. They are frugivores, supplementing their diet mainly with leaves but also insects and nectar[65, 161]. They depend on young seeds, nectar and insects when their preferred small ripe fruits are in short supply[65]. They live in small family groups in small home ranges[161] in a wide variety of forest types, including terra-firme forests, flooded forests and small islands in lakes[161], although whether they inhabit white sand forest is not known. They apparently overlap considerably with *Callicebus* in terms of their size, diet, habitats and behavior. However, *Aotus* uses more the upper, more open, levels of the forest which Wright[162] argues is due to the lack of aerial predators at night. Also *Aotus* is able to make use of large canopy fruit crops such as *Brosimum* and *Ficus* (Moraceae) which are attractive to most primates, without being chased from the tree by larger species. Wright[162] argues that both these factors are reasons why *C. moloch* feeds more on smaller fruit crops in the understoreys. *Aotus* also spend many hours feeding and resting in a single fruiting tree[162] which is not typical for other primates and is probably because of the lack of aerial predators and other primate species during the night. *Aotus* has a rather larger home range size than *C. moloch*[72,161] despite their similar sizes and diets, possibly because of their greater use of large canopy fruit crops which are widely dispersed. *Callicebus* is also more folivorous, eating leaves the whole year round whereas *Aotus* does so only when fruits are scarce[161].

Omnivorous capuchin monkeys

The tufted capuchin monkey, *Cebus apella,* occurs throughout Amazonia and is the one species most consistently classified as an omnivore. It is frugivorous and insectivorous but also eats buds, new shoots, pith, stems, seeds, flowers, nectar, arthropods, lizards, frogs, bird's eggs and snakes[42,56,58,59,61,65,149]. It occupies most forest types. Mittermeier and van Roosmalen[100] recorded its presence in 17 of the 18 forest types they identified in Surinam. They are robust and forage in a manipulative and frequently highly destructive fashion. They are very inventive in their methods of obtaining food: tree frog-catching from hollow bamboo internodes[58], use of palm fruits at many stages of their development, including smashing them against branches to open them[61,148,149], splitting open *Cecropia* leaf petioles to obtain ant larvae[137], pulling out young palm and bromeliad leaves to chew on the tender bases[137], peeling back the rachis of palm leaves (*Jessenia bataua*) and chewing it to obtain the sap[137,149] and breaking off whole clusters of spiny *Bactris* palm fruits to carry them away and eat the fruits one by one while holding the clusters with their feet[137].

The other Amazonian capuchin species, *C. albifrons* and *C. nigrivittatus,* are allopatric but sympatric with *C. apella.* They are less robust and longer limbed than *C. apella*[66], they have patchy distributions, and *C. nigrivittatus* and probably *C. albifrons* are very limited in their habitat preference. They generally avoid flooded forests and Mittermeier and van Roosmalen[100] recorded *C. nigrivittatus,* in only three of the 18 Surinam forest types, those being high terra-firme forest, upland savanna forest and liane forest. They have similar diets and foraging habits to *C. apella*[41,56,137] but are less destructive and possibly depend rather more on foliage gleaning foraging[28,64,149]. They are also more frugivorous, concentrating especially on Sapotaceae and on such widely dispersed fruit sources as figs[149] as well as palm fruits (van Roosmalen, pers. comm.) such as those of *Attalea* spp. and *Astrocaryum* spp.[28,137,149]. They also smash palm nuts (although not as efficiently and quickly as *C. apella*[149]) as well as other hard fruits such as *Bertholetia excelsa* (Lecythidaceae)[137], *Phenakospermum* (Musaceae)[28] and *Duroia aquatica* (Rubiaceae) (van Roosmalen, pers. comm.). However, they do not specialize on palm fruits to the extent that *C. apella* does, especially in the dry season[149]. Defler[28] records that *C. albifrons* is more insectivorous at times of fruit shortage, which may also be true of *C. apella*[149].

The tree species use all levels of the forest, although most frequently the middle and lower levels of the canopy[41,99]. In forests including two *Cebus* species, *C. apella* is usually the most abundant[42,99,134]. This is not so, however, in upland forest on sandy soils and hill forest in Surinam and French Guiana (van Roosmalen, pers. comm.). They live in similar sized groups of 6–30 individuals[41] but *C. apella* in Manu National Park, at least, has smaller home ranges (ca 80 ha) than *C. albifrons* (more than 150 ha)[149] and probably *C. nigrivittatus.* During studies of marmosets in the Mato Grosso[134], *C. apella* were observed regularly, almost daily, in the study area of approximately 40 ha whereas *C. albifrons* would appear for some days, attracted to locally abundant *Astrocaryum* or *Pseudolmedia* (Moraceae), for example, and then disappear for up to a month. The smaller range sizes of *C. apella* probably result from a more diverse diet, and their more extensive use of abundant palm species, an important food source in the dry season[149]. *C. albifrons,* and probably *C. nigrivittatus,* on the other hand, like *Saimiri,* depend on widely dispersed fruit crops such as figs[149]. The smaller home ranges of *C. apella* explain their greater abundance. A less diverse diet, depending on locally abundant, widely dispersed fruit crops may also explain the restricted number of forest types occupied by *C. albifrons* and *C. nigrivittatus,* and likewise, the very imaginitive diverse diet of *C. apella* explains its ability to occupy a very wide range of forest types.

Seed predators

The genus Pithecia. Five Amazon species are recognized which are allopatric[52]. Very little is known of these animals. They are frugivores (preferring soft fruits) and seed predators (generally young seeds) in common with other pitheciines, but also eat flowers and leaves[18,48,56,105]. They live in a wide variety of forest types but prefer high terra-firme forest, including savanna forest and liane forest, but are also able to survive in second growth forest[18,48,99,105]. They have also been observed in inundated forest[18,139]. *P. pithecia* occupies mainly the understoreys and lower to middle canopy[18,99] although *P. monachus* is reported to feed mostly in the upper and middle canopy (15–24 m) and travel in rather lower levels 10–19 m)[48]. Their use of lower levels for locomotion is associated with their characteristic leaping and quadrupedal walking on rather small supports[35,48]. They live in small family units, although unlike other monogamous primates, the family units often feed and travel separately[18,48]. Home range size has not been clearly established although it is believed to be small; of the order of 6–10 ha[18,48,105]. Buchanan et al.[18] report that leaf-eating was rare for *P. pithecia* whereas leaves were the second most important dietary item of *P. monachus* studied by Happel[48] in Peru. Of interest is that *Pithecia* is always rare despite its apparently small home ranges. Population estimates for *P. pithecia* range from 0.8 to 12.9 individuals per km^2 and for *P. monachus* and *P. irrorata* from 0.6 to 30 individuals per km^2 [18,134]. *Pithecia* is, however, very elusive and these are possibly underestimates.The lack of territoriality amongst family units[48,105] indicates that they might use widely dispersed food resources that are not worthwhile defending[48]. Seed predation of unripe fruits sets pitheciines apart from other frugivorous primates. *P. pithecia,* however, is sympatric with *Chiropotes satanas* which live in large groups in the upper levels of the forest. Happel[48] argues that the presence of *Chiropotes* is the reason why

P. pithecia use lower levels of the forest than *P. monachus* which, in her study area, is not sympatric with other pitheciines. However, *P. irrorata* sympatric with *C. albinasus* in other regions also uses the upper levels of the forest[11]. Dietary differences between *Pithecia* and *Chiropotes* may lie in *Pithecia*'s use of small crops of fruits, leaves and seeds at times of fruit shortage whereas the larger *Chiropotes* consistently depend on large fruit crops which occur in widely dispersed clumps (see below). In this case *Pithecia* family units may be envisioned as being mainly selective feeders on small food patches in small home ranges, but joining neighboring family units in using larger canopy fruit crops over a wider area when they are available. A small core area, with a large feeding range, any part of which is infrequently used, would explain the low densities and lack of territoriality. Apart from their seed predation, it is not known to what extent they differ from the small frugivores.

The bearded sakis. There are two species of bearded sakis, *Chiropotes satanas* and *C. albinasus*. They are allopatric and restricted to terra-firme forests, only infrequently entering inundated forest[11, 154]. In Surinam, *C. satanas* is restricted to high forest and mountain savanna forest[94, 100]. They occupy the upper and middle canopy almost exclusively; travelling by quadrupedal walking and running on large supports as well as leaping, but less so than *Pithecia* which uses rather lower levels of the forest[35, 99.] They are frugivores and seed predators, eating young seeds and insects throughout the year and when ripe fruit is in short supply at the end of the wet season and during the dry season[11, 12, 154]. They have a specialized dentition which enables them to open tough, thick-husked fruits of the Lecythidaceae and Chrysobalanaceae, for example,[11, 120, 154]. They live in groups of 8–30 individuals which travel widely (2–5 km per day) over large home ranges of more than 250–300 ha, using widely dispersed clumps of large crops of young fruit[11, 154]. The restricted number of forest types occupied by *Chiropotes* is undoubtedly related to their dependence on these. They are rampageous feeders, usually occupying several fruiting trees at any one time, decimating the immediately available crops[11, 137]. *Ateles* and *Lagothrix* also use widely dispersed fruit crops but *Chiropotes* specialize more on young seeds and the atelines depend more on leaves at times of fruit shortage.

The uakaris. Cacajao melanocephalus and *C. calvus* are flooded forest primates and have not been recorded in terra-firme forests[96, 140]. They are largely allopatric with *Chiropotes* although the distributions of *C. satanas* and *C. melanocephalus* overlap in the north part of their ranges in southern Venezuela. They are frugivores and folivores but also eat flowers and seeds[38]. With their large group sizes of 10–30 individuals, they probably occupy large home ranges and, like *Chiropotes*, probably depend on seeds, flowers and insects during times of fruit shortage in the dry season. However, nothing further is known of the ecology of these animals in the wild.

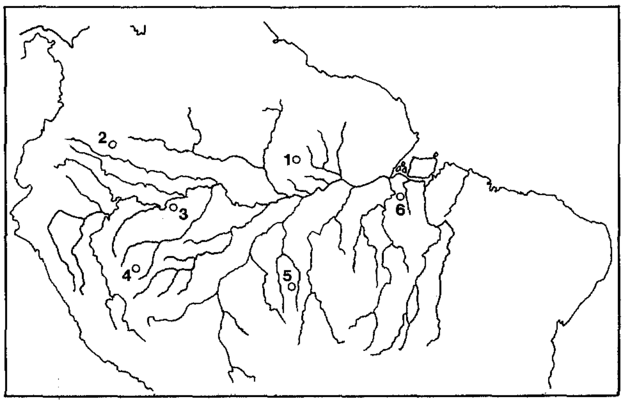
Large frugivores

The Atelinae. The two spider monkey species, *Ateles paniscus* and *A. belzebuth*, and the woolly monkeys, *Lagothrix lagotricha* and *L. flavicauda*, are large, canopy-dwelling, prehensile-tailed frugivores, eating mainly ripe fruit and supplementing their diets with flowers, leaves young seeds, caterpillars, termites and bark[153]. They occur mainly in high terra-firme forest[99, 100, 153] but do enter inundated forests at times of fruit abundance. *L. flavicauda* is restricted to montane rainforest in a small region of the eastern slopes of the Andes in Peru[98]. *Ateles* live in loosely structured communities with matriarchal subgroups of 2–3 individuals as well as single males which spend long periods travelling and feeding separately[77, 137, 153]. They feed mainly on widely dispersed ripe crops of large-seeded fruits and during food scarcity, in the early part of the dry season, they supplement their diet with flowers and new leaves[91, 153]. Terborgh[149] observed that *Ateles* often feed on bitter lauraceous fruits not eaten by other primates, except *Callicebus*, and the palm fruits that they specialize in (*Euterpe* and *Iriartea*) are not extensively exploited by *Cebus*. Unlike *Chiropotes*, they rarely eat young seeds. They feed and travel in the upper canopy, mainly by brachiation, arm-swinging and climbing and rather less by quadrupedal walking and running[35, 95]. They do travel and feed together in larger subgroups when large fruit crops are available, but when food is scarce the groups split and travel separately to permit more selective feeding on widely scattered, small crops of single trees [77, 153]. They eat more young leaves, flowers, young seeds and bark when fruits are scarce. Izawa et al.[62] observed that *A. paniscus* groups unite when feeding at clay licks and believe that it is a means of predator detection while individuals go to the ground in turn.

Very little is known about the woolly monkeys. *L. lagotricha* live in groups of 10–20 individuals[67] and, in areas where there is little hunting, groups may be as large as 40[103]. Like *Ateles* the groups also split into sub-groups, although they tend to be larger[123], probably for the same reasons. It is possible that they depend slightly less on ripe fruit crops and are more folivorous and insectivorous than *Ateles*. *L. flavicauda* is reported to live in groups of 4–10 and feed mainly on fruits, leaves, flowers, buds and petioles of *Cecropia* leaves[81]. The similarity of the ecology and behavior of *Ateles* and *Lagothrix* leads Terborgh[149] to argue that locally patchy distributions of *Lagothrix* result from competition with *Ateles* or a combination of *Ateles* and *Alouatta*. The present knowledge of these genera is sufficient to indicate that there is considerable overlap in their diets and habitat preference, but differences between them await further studies, particularly of *Lagothrix*.

Large folivores

The howler monkey. Alouatta is the best studied of the neotropical primates, and although no studies have been made in lowland Amazonia it is possible to assume that the feeding behavior of the two allopatric Amazonian species, *A. belzebul* and *A. seniculus*, is similar. They are the most folivorous of the South American primates, eating mature leaves but preferring young leaves, although a large part of the diet consists of fruits, especially those of *Ficus* species[17, 45, 47, 92]. Leaves are selected which have the maximum calorific and protein content and minimize the amount of fiber, tannins and toxic second-



The six localities in Amazonia with primate communities listed in table 4. 1) East of the Rio Negro. 2) Between the upper Rio Negro and Rio Japurá-Caquetá. 3) Between the lower Rios Javari and Juruá. 4) Upper Rio Juruá. 5) Between the Rio Roosevelt and Rio Aripuanã. 6) Between the Rio Xingu and the Rio Tocantins.

ary compounds[47,89,155]. Milton[91] demonstrates that their extensive hindgut area and slow passage rates enable them to eat foliage, including mature leaves, when fruits are scarce, but owing to this they require foliage even when fruits are abundant, to provide sufficient protein which is relatively lacking in fruits. She contrasts this with *Ateles* which have fast food passage rates and are therefore able to process larger volumes of fruit more quickly which comes closer to fulfilling their protein requirements, although, not being real insect eaters[77], they too depend on leaves and leaf buds to some extent. Due to their highly folivorous diet, the groups of 5–15 individuals occupy small home ranges relative to their body size[23,92], and occupy a wide variety of forest types, being common in both terra-firme and flooded forests and, unlike the large frugivores, occupy small patches of forest in savannas and the llanos of Venezuela[100,132,153]. They travel and feed mostly in the middle canopy and levels slightly lower than those typical for *Ateles*[99,153]. Their mode of locomotion also contrasts with that of *Ateles*, being predominantly a slow quadrupedal walk on large supports, and while feeding they do a lot of climbing with the aid of their prehensile tails[35].

Primate communities in Amazonia: a summary

The primate species known or assumed to occur in six representative localities in Amazonia are shown in table 4. According to current knowledge of primate distributions, the highest species densities are in the upper Amazon[96,140]. Locality four, for example, between the upper Rios Purùs and Acre has 13 species and locality three between the lower Rios Juruá and Javarí has 15 species, two more because of the inclusion of sympatric *Callicebus* and also *Cacajao calvus*. The localities north and south of the lower Rio Amazonas (one and six) have only nine and eight species respectively.

Small insectivores. The numbers of sympatric small insectivores range from two to five (table 4). Insect foraging methods, the size, dispersion and duration of favored fruit crops and forest type preference separate *Saimiri* from the callitrichids except for *Cebuella*, which is a small specialist exudate-feeder occupying very small home ranges. Vertical stratification and the methods, localities and types of prey caught, separate *S. fuscicollis* from the moustached tamarins and *S. nigricollis* and *Callimico*. *Callithrix* species are geographically separated from *Saguinus* (except for one area to the south of the lower Rio Amazonas) and no *Callithrix* species are sympatric, possibly because of their dependence on plant exudates. *Callithrix* are not sympatric with *Cebuella*.

Table 4. Primate species occurring in six localities in Amazonia according to their known or supposed distributions. Localities are shown in figure 1 (References 50–53, 134, 135 and Hershkovitz P., Am. J. Primat. 7 (1984) 155–210)

	1	2	3	4	5	6
Small insectivores						
Cebuella			*pygmaea*	*pygmaea*		
Callithrix					*humeralifer*	*argentata*
Saguinus	*midas*	*inustus*	*fuscicollis*	*fuscicollis*		*midas*
Saguinus			*mystax*	*imperator*		
Callimico			*goeldii* (?)	*goeldii*		
Saimiri	*sciureus*	*sciureus*	*sciureus*	*boliviensis*	*ustus*	*sciureus*
Small frugivores						
Callicebus		*torquatus*	*torquatus*			
Callicebus			*moloch*	*moloch*	*moloch*	*moloch*
Aotus	*trivirgatus*	*vociferans*	*nancymai*	*nigriceps*	*nigriceps*	*infulatus*
Omnivores						
Cebus	*apella*	*apella*	*apella*	*apella*	*apella*	*apella*
Cebus	*nigrivittatus*	*albifrons*	*albifrons*	*albifrons*	*albifrons*	
Seed predators						
Pithecia	*pithecia*		*monachus*	*irrorata*	*irrorata*	
Chiropotes	*satanas*				*albinasus*	*satanas*
Cacajao		*melanocephalus*	*calvus*			
Large frugivores						
Ateles	*paniscus*	*belzebuth*	*paniscus*	*paniscus*	*paniscus*	*belzebuth*
Lagothrix		*lagotricha*	*lagotricha*	*lagotricha*	*lagotricha*	
Folivore						
Alouatta	*seniculus*	*seniculus*	*seniculus*	*seniculus*	*belzebul*	*belzebul*

Small frugivores. *Callicebus moloch* and the night monkeys, *Aotus*, both occupy the same habitats and overlap considerably in their diets, the latter are nocturnal and for this reason can use higher levels of the forest and feed on large crops of fruits for extended periods without interference from other primates or diurnal predators. *C. moloch* is a selective feeder in the dense understoreys of the forest, using small food patches, including unripe fruit and bitter fruits not eaten by callitrichids, in very small home ranges. *C. torquatus* when sympatric with *C. moloch* is separated by habitat. It is more insectivorous than *C. moloch* and possibly largely isolated from callitrichids. They eat larger, tougher fruits than callitrichids.

Omnivorous capuchins. The *Cebus* species are destructive and inventive foragers and hard fruit smashers, although the more robust *C. apella* is more so than the more gracile *C. albifrons* and *C. nigrivittatus*. This distinguishes them from other primates. The more abundant *C. apella* exploit smaller home ranges more thoroughly (involving a more diverse diet), making more use of abundant palm fruit crops in the dry season than the less abundant *C. albifrons* and *C. nigrivittatus*, which use larger home ranges to include more large fruit crops (of a reduced number of species compared to *C. apella*) which are widely scattered, such as figs, during the year. The palm fruits eaten by *C. apella* are different from those exploited by *Ateles*.

Seed predators. In the Venezuelan Amazon. *Chiropotes satanas, Cacajao melanocephalus* and *P. pithecia* are possible sympatric although *C. melanocephalus* and *C. satanas* are clearly separated by habitat preference. *Chiropotes* is a terra-firme forest primate whereas *Cacajao* is restricted to inundation forest. Whereas the large groups of *Chiropotes* and *Cacajao* use the upper levels of the forest and feed on large, widely dispersed fruit crops, the small family units of *Pithecia* use understoreys more where they feed on smaller food patches and make use of larger fruit crops only when these are available in wider non-defended areas. Their specialization on young seeds from tough fruits sets these species apart from the other primates.

Large frugivores. There are never more than two large sympatric ripe fruit specialists in Amazonian primate communities. *Ateles*, the most frugivorous of the New World primates, supplements its diet with flowers, new leaves, leaf buds, and young seeds. *Lagothrix* is similar but probably more insectivorous and folivorous than *Ateles*. Both have large home ranges as a result of their body size and dependence on large, widely scattered fruit crops. The few studies of *Lagothrix* have not revealed any major habitat or dietary differences between these species.

Large folivores. The howler monkey's folivory and its ability to eat even mature leaves in large quantities at times of fruit shortage in relatively small home ranges sets it apart from other primate species.

Diets and habitat preference

The preceding summary emphasizes behavioral and ecological differences between Amazonian primate species. However, it should be remembered that all are frugivorous and the majority show considerable overlap in terms of fruiting species eaten when these are large fruit crops of large canopy trees. *Cecropia* infructescences, for example, are eaten by *Cebuella, Saguinus, Callithrix, Saimiri, Callicebus, Cebus apella, Ateles, Lagothrix* and *Alouatta*. Infructescences of *Brosimum* spp. (Moraceae) are eaten by all primate species in Amazonia which have been studied in the wild. *Pourouma* and *Ficus* (both Moraceae) are also eaten by the majority of species. When large fruit crops of sweet, easily digested fruits are available, most species can be observed feeding on them. The extent to which species depend on large, widely scattered and irregularly available seasonal fruit crops varies, however, and influences group size, ranging behavior, population densities and the diversity of habitats they can occupy. The larger primates, *Ateles, Lagothrix, Cebus albifrons*, and *C. nigrivittatus*, live in rather large groups with large home ranges in order to include a sufficient area of forest to guarantee a supply of this food source for at least most of the year. *Chiropotes* and *Cacajao* are similar although they exploit tougher fruits and can preempt other large frugivorous primates by eating young seeds[11, 154]. All these species are notably limited in their ability to exploit a wide range of forest types, and have large home ranges and low population densities.

Except for *Cebuella* and possibly *Callimico*, the small insectivorous monkeys are probably limited in their habitat use by the abundance of arthropods and the year-round availability of fruits. *Saguinus* and *Callithrix* use disturbed forest, edge and second growth forest, where they can specialize in feeding from abundant trees which have small fruits available over extended periods, and possibly arthropod abundance is higher. They have small home ranges and patchy distributions, being absent from extensive tracts of primary forest. Populations are accordingly high locally but very low in areas lacking their preferred forest types. Due to its large group sizes, *Saimiri* depends on the widely scattered fruit crops of the larger primates but also possibly on forests with high arthropod abundances. It is possible that only second growth forest, inundation forest and liana forest have arboricolous arthropod densities and large fruit crops sufficient to meet their needs, but only recently have second growth forests become extensive enough (through human activities) to maintain the large groups. In the past, small second growth patches and edge habitats in terra-firme forest resulting from small scale agriculture and tree falls were the domain of the small monogamous callitrichids (*Saguinus* and *Callithrix*), the habitats being too small to accommodate the larger primates or *Saimiri*, which can only make use of them occasionally when they form mosaics within extensive primary forest. Regarding inundation forest, the evidence for arthropod densities and biomass from canopy fogging[4, 5, 33, 34] do not indicate that igapó supports more insects than terra-firme forest although várzea evidently has lower densities and biomasses than igapó. It is not known if this difference is reflected in *Saimiri* densities in the two types of inundation forest. *Saimiri's* preference for inundation forest may result from a combination of forest structure, possibly having denser understoreys compared to terra-firme forest, a greater availability of large fruit crops such as figs away from interference from terra-firme forest primates or a seasonal abundance of insects at times when fruits are scarce.

Cebuella occupies floodplain and inundated forest possibly because only there are there sufficient numbers of exudate sources and insects within a small area coupled with dense undergrowth. Population densities can be very high in these preferred habitats but very much lower away from river edges[145]. In terra-firme forest it would be in competition with *Saguinus,* although it too is known to occupy second growth using such pioneer species as *Inga* (Leguminosae) as exudate sources. *Callimico* is a habitat specialist and rare, but exactly why is not known.

The smaller frugivorous primates *Callicebus* and *Aotus,* with smaller group sizes are able to exploit small understorey fruit crops and a wide range of forest types. *Pithecia* is similar but more restricted due to its greater dependence on large canopy fruit crops.

The tufted capuchin, *Cebus apella,* is the most ubiquitous monkey because of its thorough and inventive methods of obtaining foods in relatively small home ranges irrespective of forest type. Similarly *Alouatta*'s folivory permits it to survive in small forest patches in a very wide variety of habitats. It would be of interest to see whether the differences between várzea and igapó leaves studied by Klinge et al.[78] affects *Alouatta* population densities; they might possibly be higher in várzea.

In summary, dependance on large, widely scattered fruit crops limits the range of habitats occupiable by *Lagothrix, Ateles, Cebus nigrivittatus, C. albifrons, Chiropotes albinasus, C. satanas, Cacajao, Saimiri* and possibly *Pithecia,* whereas *Cebus apella, Callicebus, Aotus, Saguinus* and *Callithrix* and *Alouatta* can make use of mosaics of floristic communities and small patches of suitable habitat within a wide array of forest types. *Cebuella* and *Callimico* have specialized diets and are limited to specific floristic communities.

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The biology of streams as part of Amazonian forest ecology

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Summary. Data on long-term research on the ecology of Central Amazonian forest streams are presented and they reveal the following basic features: Firstly, the essential input of nutrients into these waters consists of forest litter and of the fungi that decompose this litter; consequently, the bulk of the fauna is concentrated in accumulations of submerged litter. Secondly, the nutrients released by the decomposition of this litter do not appear in solution in the stream water, but are tied up throughout in the food web of the aquatic fauna. Thirdly, this food web is relatively robust. This is due to the absence of food specialists in the major channels of energy transfer. One of the staple foods for invertebrate predators consists of chironomid larvae. Fourthly, the degree of acidity and/or the content of dissolved humic substances (more or less black water) has a marked effect on the density and to a lesser extent on the species diversity of the invertebrate fauna, black waters being richer in both. Fifthly, the annual inundations of the forest in the middle and lower courses of the smaller rivers lead to drastic periodic changes of animal densities, and in some cases to annual periodicity of breeding, as exemplified by a three-year study of shrimp populations in the river 'Tarumazinho'.

Key words. Stream ecology; benthos; Amazonas.