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The Ecology and Conservation of the Red Uakari Monkey on the Yavarí River, Peru

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Doctor of Philosophy
In Biodiversity Management
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Summary

The behaviour, ecology and conservation of the red uakari monkey *Cacajao calvus ucayalii* was studied on the Yavarí River in northeastern Peru. The Lago Preto study site has four major habitats comprising *terra firme*, seasonally-flooded *várzea*, floodplain *aguajal* palm-swamp and upland *aguajal* palm-swamp forests that are very different in tree species composition. Productivity studies demonstrated that *várzea* and *aguajal* habitats were very seasonal in their fruit production, while *terra firme* showed less seasonal variation. Uakaris ate mainly unripe seeds for two thirds of the year, but ate large quantities of ripe pulp when *Mauritia flexuosa* palm fruits were available. *Mauritia flexuosa* was the most important species for red uakaris, making up 20% of the diet. *Mauritia flexuosa* was also important because it was available at times when other items were scarce. The abundance of uakaris at different sites on the Yavarí River was not correlated with the abundance of other primates, but was negatively correlated with seed-eating rodents. Uakaris ranged over at least 1200ha at Lago Preto, foraging in *terra firme*, *várzea* and *aguajal* forests depending on the availability of resources in these habitats. Uakari group sizes varied depending on habitat type, and fluctuating group sizes appear to be related to the distribution of food resources. Adult male uakaris were most commonly next to other adult males, and often performed aggressive displays with other males. Uakari calls varied with the context of behaviour. The adaptive significance of the uakari's red face can be explained by both ecological and behavioural adaptations. Uakaris in the Yavarí-Ucayali interfluvium are under threat from logging, hunting and non-timber plant-resource extraction. The effects of logging on the Yavarí will depend largely on the tree species extracted. Currently most valuable species are extracted, the impact is expected to be low, but this could change if less valuable timber is felled. The extraction of *Mauritia flexuosa* palm fruits for market sale is rare on the Yavarí, but on more populous rivers may affect uakari populations. Hunting is the biggest threat to uakari populations on the Yavarí and logging operations are likely to lead to an increase in the hunting of primates. Managing hunting is the priority for red uakari conservation throughout their range. The red uakari monkey is being used as a flagship species in a number of new and proposed reserves. The distribution and density of uakari monkeys within these areas is barely known. The ecological behavioural and distributional information obtained in this thesis will help these reserves determine the conservation requirements for the uakari monkeys.

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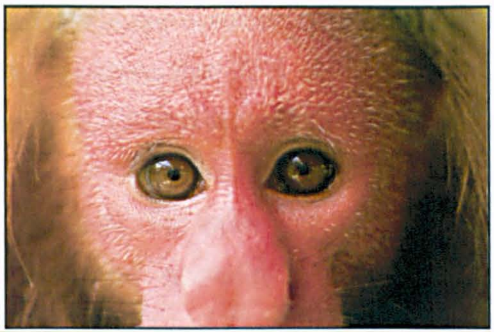

Chapter 1

Introduction

1.1 Endangered primates

The number of primates listed as Endangered or Critically Endangered by the IUCN-World Conservation Union has been steadily growing during the past decade. In 1996, 15% (93 out of 620 taxa) of primates were listed. In 2000, this figure had grown to almost 20%, and in 2005, 26% of the world's primates were Endangered or Critically Endangered according to the IUCN (Mittermeier *et al.* 2005). A further 70 species are recognised as Vulnerable, which means that 37% of the world's primates are threatened with extinction. Entwistle *et al.* (2000) lament that 25% of mammal species face some risk of extinction, and use this figure to suggest that the class might require special attention for conservation. For primates the figure is clearly higher with a total of 230 globally-threatened species. Conservationists must consider the reasons why such a large proportion of the order is threatened, to formulate appropriate strategies to conserve endangered primates and prioritise areas or species for conservation.

As a group, primates present particular conservation challenges. They are largely restricted to tropical areas in developing countries, where economic issues and poverty complicate conservation efforts. They often have restricted ranges, making them vulnerable to habitat disturbance, and have slow rates of reproduction that limit the recovery of reduced populations (Cowlishaw and Dunbar 2000). The threats to primates are similar to those facing many of the world's threatened species. Deforestation for agricultural land removes huge areas of primate habitat across the world each year (Mittermeier *et al.* 2005), and logging, even in areas where it does not lead to complete deforestation, can degrade habitats and open up areas for hunting (Johns 1992). For many primate populations, commercial and subsistence hunting poses an even greater threat than habitat disturbance (Oates 1996). Primates show particularly poor resistance to hunting (e.g. Bodmer *et al.* 1997), because they are easily detected and are likely to be targeted more frequently than other taxa (Kuchikura 1988; Oates 1996). These multiple threats, combined with the sheer number of endangered primates distributed across numerous countries often with their own different economic and political problems, require a variety of solutions that must be carefully considered for each threatened population. Advances in the field of primate conservation biology will need to be combined with species specific research into the ecology and, in some cases, behaviour of threatened species to develop appropriate conservation strategies.

1.2 Prioritising conservation for primates

Entwistle *et al.* (2000) examine the premise that mammals, as a relatively small class of around 4500 species, receive a disproportionate amount of attention within conservation. Recent shifts towards a more holistic approach to conservation, as described by Heywood (1995), have brought traditional single-species approaches into question (Entwistle *et al.* 2000). If mammals receive a disproportionate amount of attention, then surely primates receive even more? There appear to be many organisations and charities dedicated to their conservation, or prepared to fund primate-orientated projects. This is surely, at least in part, because people like them. They are charismatic and share a large part of their evolutionary history with humans (Mittermeier 1988). Cowlishaw and Dunbar (2000) contend that endangered primates merit such favouritism in terms of conservation effort, by virtue of a diverse range of values. Firstly, Cowlishaw and Dunbar (2000) summarise the important ecological roles that primates have been shown to play in many tropical forests, as pollinators or seed dispersers. Losing the primates might threaten the viability of forest communities. Cowlishaw and Dunbar (2000) also point to more direct economic values for primates in some countries, where they are often commercially hunted or have value to the tourist industry. Additionally, primates can often be used as flagship species. They are relatively large and charismatic, and are powerful in attracting attention to conservation projects, whose wider goals might be the conservation of habitats or ecosystems (Dietz *et al.* 1994).

Conservation International base their conservation strategies on spatial patterns of diversity and endemism, alongside measures of threats from human activity. They identify areas where the maximum number of species can be conserved for any given conservation effort. Areas that have high levels of diversity and endemism are considered 'hotspots' (Mittermeier *et al.* 1998); 34 hotspots have been identified covering 2.3% of the Earth's land surface. These contain more than half of the world's terrestrial biodiversity, and about 46% of the world's primate species occur in just 23 hotspots (Mittermeier *et al.* 2005). Many endangered primates occur in hotspots in Madagascar and Asia, where habitat destruction has been most severe. 58% of Malagasy primates and 42% of Asian primates are threatened. The greatest numbers of critically-endangered primate species are endemic to the Atlantic Forest, a hotspot on the coast of Brazil, which has suffered intensive destruction (Mittermeier *et al.* 2005). In the short term, most primate species will probably be saved through efforts focused in these areas, but a large number of primates live outside hotspot areas. The Amazon Basin does not qualify as a hotspot, since it covers too great an area, and has too much of its original vegetation remaining (Mittermeier *et al.* 1998). Amazonia contains some of the most diverse forests on Earth (Gentry 1988), and certain blocks of forest in this vast wilderness have exceptionally high diversities of primate species (Janson and Emmons 1990). Puertas and Bodmer (1993) contend that it is important to conserve these assemblages. While the loss of a primate species from one of these areas is unlikely to lead to the complete extinction of the primate, the integrity of the high-diversity primate community would be lost. Where particularly vulnerable species occur in these diverse primate assemblages, special measures may be required to ensure that these species persist and the diversity of the primate assemblage is maintained.

1.3 The conservation of primates in the Peruvian Amazon

While other tropical forests that are smaller in area appear to demand more urgent conservation, the Amazon region has a high diversity of primates and its own unique conservation problems. Amazonia represents the largest wilderness area in the world (Mittermeier *et al.* 1998), a system where people live throughout, and where impacts range from deforestation for agriculture and selective logging to game hunting and international trade. The forests of the Peruvian Amazon are some of the most diverse on Earth (Gentry 1988), and most of this area is inhabited by people. Some of these people are indigenous, but the majority (85%) are non-tribal (Egoavil 1992). These people practice agriculture, hunting, fishing and small-scale resource extraction (Padoch 1988). Bodmer (1995) acknowledges that the human population must be the key to the conservation of mammals in these forests.

Bodmer (1995) compared the threats of hunting, deforestation and international trade to mammal populations in the Amazonian state of Loreto in northeast Peru. Overall, Bodmer found that hunting removed more animals each year than deforestation, but also concluded that different pressures affected species differently. Small-bodied primates are infrequently hunted, and 85-96% of the removal of small primates from the population in Loreto is from the clear-cutting of habitat. Large-bodied primates on the other hand are widely hunted and hunting accounts for 45-89% of the removal of large primates from Loreto. Deforestation was also important and accounted for between 11 and 55% of individuals removed from the primate population. In Loreto, the trade in primates for biomedical research is monitored in accordance with CITES (Convention on International Trade in Endangered Species). The trade is minimal and has little or no effect on primate populations (Bodmer 1995). Hunting was more important than deforestation in terms of the annual numbers of animals removed from the populations, and is the primary concern for mammalian conservation in the Peruvian Amazon. Thus, Bodmer (1995) advocates a shift towards the sustainable hunting of mammalian populations as the most effective way of conserving them. Since primates show particularly poor resistance to hunting (e.g. Bodmer *et al.* 1997), cessation of hunting of large-bodied primates in most areas is a key conservation strategy (Puertas and Bodmer 1993).

1.4 Why the red uakari monkey?

Different primate species in Amazonia are threatened by different pressures. For the larger-bodied primates, the major threat is often hunting, which affects small-bodied primates less. For smaller species habitat degradation and deforestation are more important (Bodmer 1995). Furthermore, some primates are more at risk than others due to patchy populations or restricted ranges. Habitat specialists or specialist feeders, such as seed predators, might also be more sensitive to habitat modification (Plumptre and Grieser Johns 2001), whilst complex life histories or social systems might influence a species' ability to survive in small fragmented populations, or to recover after a reduction in population size.

The red uakari monkey (*Cacajao calvus ucayalii*) has a number of characteristics that make it suitable for a case study of primate conservation biology. With its restricted geographical range (Chapter 1.5.6) and low population densities it is perhaps the most endangered primate species in lowland Amazonian Peru (Chapter 1.5.7). Within its range the species is patchily distributed. Potential threats to the species include those which are common to many Amazonian primates, including logging, non-timber resource extraction and hunting. Hunting within the range of *Cacajao calvus ucayalii* has been studied for many years (e.g. Puertas and Bodmer 1993; Bodmer 1995; Bodmer *et al.* 2003), and the red uakari is of such a size that it is regularly, but not preferentially, hunted for subsistence (Puertas and Bodmer 1993). The ability of a species to sustain a certain level of hunting depends largely on its life history characteristics and to a certain extent its social, ranging and reproductive behaviour, which can have clear demographic consequences (Veiga

2004). *Cacajao calvus* has unusual 'fission-fusion' grouping behaviour, and forms very large groups (Ayres 1986).

There are other reasons why the red uakari monkey is worthy of study. The species belongs to the Pitheciidae (Mivart 1865), a primate family that has a degree of evolutionary uniqueness in terms of its dietary specialisation and unusual social behaviour. Even within this family, *Cacajao calvus* is evolutionarily unique in that it has a bald, bright-red head and face. The social and reproductive behaviours that have lead to the evolution of this remarkable feature are intellectually interesting. Finally, it is this red face, along with the bright orange fur, that makes the species visually striking, if not appealing to all observers. This makes it particularly appropriate as a flagship species for the conservation of the wildlife and habitats within its range.

1.5 An introduction to the red uakari monkey

1.5.1 Historical descriptions of *Cacajao calvus*

Red uakari monkeys were recorded in European literature as early as 1743 by Charles Marie de La Condamine on his journey down the Amazon River after his expedition to Ecuador to measure the length of a degree of meridian at the Equator. His was one of the first scientific accounts of the Amazon, which he published as *Journal du voyage fait par ordre du roi a l'équateur* (1751), but this did not include a formal description of the uakari monkey. The first description of the genus *Cacajao* was of the black uakari *Cacajao melanocephalus*, which was originally given the name *Simia melanocephala* by Alexander Von Humboldt (1811). The genus was renamed *Brachyurus* by Spix (1823) and then *Cacajao*, when Lesson (1840) realised that *Brachyurus* was preoccupied by a genus of rodent. White uakari and red uakari monkeys were originally described as separate species, using the names *Brachyurus calvus* (Geoffroy 1847) and *Brachyurus rubicundus* (Geoffroy and Deville 1848) respectively. Geoffroy and Deville were obviously unaware of Lesson's change to the name of the genus. Perhaps the most famous account of *Cacajao calvus* appears in Henry Walter Bates' (1863) *The Naturalist on the River Amazon*, possibly the first scientific record of the species in English. Bates described captive white uakaris as "monkeys of the most grotesque appearance" and recounted some local knowledge of the ecology of the species, but never saw them in the wild.

Hershkovitz (1972) united red and white uakaris as subspecies of the same species; *Cacajao calvus calvus* and *Cacajao calvus rubicundus*, because they were only superficially different. Later Hershkovitz (1987a) described a further two subspecies *Cacajao calvus novaesi* and *Cacajao calvus ucayalii* in the most recent revision of the species. The subjects of this study are of the subspecies *Cacajao calvus ucayalii* (Hershkovitz 1987a), which was first described by Thomas (1928) as *Cacajao rubicundus ucayalii* from a locality near Contamana on the east bank of the Ucayali River.

1.5.2 The current taxonomy of the Pitheciines

Since the 1990s primate taxonomists working with living primates have been moving away from the 'Biological Species Concept' as the definition of a species towards the 'Phylogenetic Species Concept'. This concept was originally introduced by Cracraft (1983), and elaborated on by Nixon and Wheeler (1990). It was adopted in a major work on primate taxonomy by Groves (2001). Using this concept, a species is simply a diagnosable entity with fixed heritable differences from other species. The taxonomy of many primate families has recently been revised (see Groves 2001 for a review), but the family Pitheciidae has only been partially revised in recent years.

Horovitz *et al.* (1998) and Groves (2001) conclude that *Callicebus* (the titi monkeys) are associated with *Pithecia, Cacajao* and *Chiropotes* and unite them in a single family; the Pitheciidae. Based on β_2-Microglobulin DNA sequences, Canavez *et al.* (1999) determined that the Pitheciidae branched into clades that Groves (2001) separates at subfamily level; the Callicebinae (including the genus *Callicebus*) and Pitheciinae (including the genera *Pithecia, Cacajao* and *Chiropotes*).

Within the Pitheciinae, Schneider *et al.* (1996) concluded that *Cacajao* and *Chiropotes* were more closely related to each other than to *Pithecia,* and Boubli and Ditchfield (2000) analysed mitochondrial DNA and estimated the time of divergence between *Chiropotes* and *Cacajao* at around nine million years. Goodman *et al.* (1998) combined *Chiropotes* and *Cacajao* in a single genus (with *Chiropotes* taking priority), but Groves (2001) accepted the older arrangements of Hershkovitz (1985, 1987a,b), explaining that more evidence and consensus are required before the proposals of Goodman *et al.* can be accepted.

1.5.3 The current taxonomy of *Cacajao*

In the latest revision of the genus by Hershkovitz (1987a), there are two uakari species; *Cacajao melanocephalus* and *Cacajao calvus*. The two species share a short tail, long thick straight hair, a broad muzzle and widely separated nares. There is some sexual dimorphism, males being larger than females with larger canines and a conspicuously more massive mandible. Sexual dimorphism is more pronounced in *Cacajao calvus* than in *Cacajao melanocephalus* (Hershkovitz 1987a). There are limited data for the bodyweight of *Cacajao*. One adult male *Cacajao calvus calvus* at Lake Teiú weighed 3450g and two adult females weighed 2750g and 3000g (Ayres 1986). A captive male *Cacajao calvus ucayalii* weighed 4100g and a captive female 3550g (Fontaine (1981). Three wild female *Cacajao melanocephalus ouakary* weighed 2660g, 2790g and 2820g (Ayres 1986). In terms of head and body measurements, *Cacajao melanocephalus* is smaller than *Cacajao calvus*, the average male *Cacajao melanocephalus* being smaller in all dimensions than a male or female *Cacajao calvus* (Hershkovitz 1987a). *Cacajao melanocephalus* has a correspondingly smaller skull, with less elongate incisors (Hershkovitz 1987a). The tail is proportionately longer in *Cacajao melanocephalus* than in *Cacajao calvus* (39-41% of the head and body length compared with 34-36%). Most obviously, apart from the differences in pelage described below, the head and face of *Cacajao melanocephalus* are pigmented blackish and covered on the forehead and crown with blackish hairs, whereas *Cacajao calvus* has a virtually unpigmented and almost hairless face, forehead and crown (Hershkovitz 1987a). Specialised vascularisation in the facial skin of *Cacajao calvus* means that the face and head appears blood-red (Hill 1965). In *Cacajao calvus* the genitalia are naked and blackish in colour (Hershkovitz 1987a), whereas some male *Cacajao melanocephalus* may have whitish external genitalia (A. Barnett pers. com.). Boubli and Ditchfield (2000) analysed mitochondrial DNA and estimated the time of divergence between *Cacajao melanocephalus* and *Cacajao calvus* at around 5 million years.

Cacajao melanocephalus is split into two subspecies; the black-backed uakari (*Cacajao melanocephalus melanocephalus*), and the golden-backed uakari (*Cacajao melanocephalus ouakary*). These are distinguished by the pelage colour. *Cacajao melanocephalus melanocephalus* has a blackish head, beard, nape, arms, legs, chest, and mantle to midback, while the midback is reddish brown and the belly is either blackish or reddish brown (Hershkovitz 1987a). *Cacajao melanocephalus ouakary* differs from *Cacajao melanocephalus melanocephalus* in the colour of the midback, which is golden or pale red, and the lower back and thighs, which are reddish brown to chestnut (Hershkovitz 1987a).

Cacajao calvus is split into four subspecies (*calvus, rubicundus, novaesi* and *ucayalii*), again distinguished by pelage colour:

- *Cacajao calvus ucayalii* is reddish orange. Neither the nape nor the midback contrast sharply with the overall colour. Hershkovitz (1987a) wrote that the dorsal side of the tail is black in colour with the rest of the tail being reddish, but no individuals at Lago Preto were observed with black on the tail. The beard is reddish orange proximally becoming blackish distally (Hershkovitz 1987a). At Lago Preto, the amount of black on the beard varied between individuals.

- *Cacajao calvus rubicundus* is reddish or reddish chestnut, with the area from the nape to between the shoulders buffy or whitish. From the midback to the rump, the tips of the hairs are buffy or pale orange. The tail is reddish or reddish orange often mixed with pale golden tipped hairs. The beard is reddish proximally and becomes darker, often blackish, distally.

- *Cacajao calvus novaesi* is orange with paler orange, buffy, or whitish hairs from the nape to the tip of the tail. The sides of the trunk and the ventral side are reddish orange, and the beard ranges from orange to brownish orange (Hershkovitz 1987a).

- *Cacajao calvus calvus* is pale orange, buffy, greyish or whitish. The ventral surfaces are orange to yellowish, and the tail can either be pale or have an orange colour like the ventral surfaces. The beard is reddish or reddish brown and becomes darker distally (Hershkovitz 1987a).

The possibility that a fifth subspecies of *Cacajao calvus* exists was raised when Sousa e Silva Júnior and Martins (1999) discovered a new population of white uakari monkeys on the Juruparí River. This population is separated from the known distribution of *Cacajao calvus calvus* by 700km with *Cacajao calvus novaesi* distributed between them. There was some disagreement between Hershkovitz and Perez as to whether this new population was of a new subspecies (their comments were recorded by Sousa e Silva Júnior and Martins 1999). Perez argued that the range is not necessarily disjunct with *Cacajao calvus calvus*, but Hershkovitz concluded that the Juruparí uakaris were an undescribed subspecies, convergent with *Cacajao calvus calvus* in colour (Sousa e Silva Júnior and Martins 1999). Sousa e Silva Júnior and Martins are currently conducting morphometric and DNA analysis to determine whether the Juruparí uakaris have affinity with *Cacajao calvus novaesi* or *Cacajao calvus calvus.*

The subspecies of *Cacajao calvus* appear to grade into each other to some extent, and Groves (2001) points out that more distributional data is required for *Cacajao* to substantiate the status of some taxa as subspecies rather than species. It is clear that the genus *Cacajao* and the subfamily Pitheciinae are due reorganisation, and it seems likely that the white and red forms of *Cacajao* might one day be recognised as separate species, as they were originally described by Geoffroy (1847) and Geoffroy and Deville (1848), but the newly-discovered population of white uakaris may complicate the classification further. Speaking at the 'Pitheciins: Ecology and Conservation' symposium at the XXI Congress of the International Primatological Society in 2006, Russell Mittermeier of Conservation International highlighted the need for revision in the taxonomy of the Pitheciins as *the* priority for future research. The classification of Pitheciin taxa is the first step in identifying conservation and research priorities.

1.5.4 Common names

Monkeys of the genus *Cacajao* are known in English by the common name 'uakari' or 'uacari' (pronounced wah-kar-ee) which was originally written 'ouakary' by Spix (1823). Barnett (2004) provides a good account of the origins of the words '*uacari*' and '*Cacajao*', which both appear to be derived from onomatopoeic native Amazonian local names. A. Barnett (pers. com.) favours 'uacari' over 'uakari', because it conforms to the Portuguese spelling of the word, but the spelling 'uakari' appears to be more common than 'uacari' in English language scientific publications (e.g. Bates 1863; Fontaine 1981; Ayres 1986; Groves 2001, but also see Hershkovitz 1987a) and particularly in the popular press (e.g. Goulding 1989; Emmons and Feer 1997; MacDonald 2001; ARKive 2006). The Portuguese language journal of the Institute of Sustainable Development Mamirauá is even called 'Uakari'. However, the IUCN (2006) gives both spellings of the word in its list of common names for *Cacajao*, and both spellings are used on different pages of CITES (2006) web pages.

Since the spelling 'uakari' appears more commonly published, and was used in all the grant proposals and project updates for this project's fieldwork, this spelling is used throughout this thesis. Since some co-authors and editors have just cause for preferring 'uacari', publications derived from this research use either of the two spellings (e.g. Bowler 2003; Bowler *et al.* 2006; Setz *et al.* 2006; Veiga *et al.* 2006, and several papers in preparation).

Cacajao calvus is known by several common names. The white subspecies *Cacajao calvus calvus* is generally known as the 'white uakari monkey' (e.g. Ayres 1986), and the three red subspecies *Cacajao calvus novaesi, Cacajao calvus rubicundus* and *Cacajao calvus ucayalii* are all most known as the 'red uakari monkey', as used in this thesis. When referring to *Cacajao calvus,* inclusive of both red and white subspecies, 'bald uakari' is commonly used, but various permutations of red, white, bald, bald-headed, uakari and uacari occur. The name 'Ucayali bald-headed uacari' is suggested for *Cacajao calvus ucayalii* by the IUCN (2006), but this name is rarely used and the subspecies are generally differentiated using their scientific names. The name 'Ucayali red uakari' was frequently used (but not spelled) for *Cacajao calvus ucayalii* during the 'Pitheciins: Ecology and Conservation' symposium at the XXI Congress of the International Primatological Society, 2006.

The local Peruvian name for *Cacajao calvus ucayalii* is '*huapo rojo*' or '*huapo colorado*'. On the Yavarí River, the Brazilian name '*Macaco inglês*' meaning 'English monkey' is also used by Brazilian residents, and occasionally by Peruvians (often in jest whilst conversing with English researchers).

1.5.5 Morphology

Cacajao calvus ucayalii are medium-sized New World monkeys, males weighing up to about 4.1kg and females 3.5kg (see Chapter 1.5.3). They are striking in appearance, with a number of unusual physical characteristics. Hershkovitz (1987a) gives a detailed account of the morphology of *Cacajao*. The most obvious features are the thick red-orange fur, the bald, bright red head and face, the enlarged highly specialised dentition, and the short non-prehensile tail. The short tail and red face of *Cacajao calvus* are discussed in Chapter 7. The enlarged and specialised dentition of the red uakari monkey has long been recognised as an adaptation for feeding on hard-shelled fruits, termed 'sclerocarpic foraging' by Kinzey and Norconk (1990). The adaptations of uakari teeth to their diet are discussed in Chapter 5.3.10.

1.5.5.1 Red fur

Few authors have published views on why red uakaris have their red-orange fur. Several other primate species have red or orange fur; orangutan (*Pongo pygmaeus*), golden lion tamarin (*Leontopithecus rosalia*), buffy saki (*Pithecia albicans*), red howler (*Alouatta seniculus*), Javan langur (*Trachypithecus auratus*) and Sichuan snub-nosed monkey (*Pygathrix roxellana*) among others, including some individuals of our own species. Sumner and Mollon (2003) discussed primate pelage and skin colour in a range of orange primates, considering the possible costs and benefits to primates in terms of camouflage, signalling and mate choice. Sumner and Mollon (2003) point out that if pelage colour does not have a cost, then we do not need to find an advantage. The obvious potential cost of having bright orange fur is that it may be conspicuous to predators. Big cats, snakes and large raptors are all potential predators of *Cacajao calvus.* Big cats are probably dichromatic or monochromatic (Jacobs 1993), so the orange colour would be cryptic to these animals. Snakes may be trichromatic or tetrachromatic (Bowmaker 1998), but since big snakes are generally 'lie-in wait' or nocturnal predators, prey selection is unlikely to revolve around colour. The main predators of medium-sized monkeys, like *Cacajao calvus,* are almost certainly the two largest raptors in the area; the crested eagle (*Morphnus guianensis)* and the harpy eagle (*Harpia harpyja)* (Robinson 1994). One attack by a large eagle on *Cacajao calvus ucayalii* at Lago Preto was observed during data collection for this study (Chapter 6.4). While the colour vision of neither *Morphnus guianensis* nor *Harpia harpyja* has been tested, virtually every other diurnal bird that has been tested is tetrachromatic (Hart 2001). Sumner and Mollon (2003) point out that raptors may have sacrificed a certain amount of colour vision in favour of improved special acuity, but we do not know if orange primates are more conspicuous than brown or black primates to large eagles.

Richard Bodmer (pers. com.) suggests that *Cacajao calvus ucayalii* is more camouflaged against attacks from large eagles when it is feeding on racemes of its preferred food, aguaje palm fruits (*Mauritia flexuosa*). These dark-red fruits grow on large racemes that are exposed in the relatively open canopy of *aguajal* palm-swamps. The only eagle attack observed during this study occurred in the *aguajal* palm-swamp habitat, but to the human eye *Cacajao calvus ucayalii* appears a lighter and more conspicuous orange than the dark red aguaje fruits. Bodmer points to the absence of the *Mauritia flexuosa* palm in the range of the white-furred *Cacajao calvus calvus* as evidence for his theory. *Cacajao calvus novaesi* is an even paler orange than *Cacajao calvus ucayalii*, however, and the newly-discovered populations of white uakaris (Sousa e Silva Júnior and Martins 1999) occur in an area where there is no reason to suspect that *Mauritia flexuosa* is locally absent. These paler subspecies do not support this idea.

The existence of white uakaris, which are conspicuous even to monochromatic vision, makes the colour vision of crested and harpy eagles less relevant. Either there is no cost in being conspicuous, or there is also a significant advantage to uakari monkeys in being red or white. It is possible that harpy eagles are so good at detecting prey by movement or other means, that fur colour does not make a difference in terms of their prey selection when feeding on monkeys. Some of the harpy eagle's favourite prey items are extremely cryptic, such as the sloths *Bradypus* spp. and *Choloepus* spp., and these are still taken in preference to conspicuous monkeys in some areas (Galetti and de Carvalho Jr. 2000).

If there is no cost to the red or white colours, then there is no need to infer a selective advantage to the red or white pelage, and genetic drift might be responsible. *Cacajao calvus* lives in riparian habitats prone to fragment into riverine islands, as with the current population of *Cacajao calvus calvus* in Mamirauá. White-water rivers typically shift in their courses, repeatedly opening and closing rainforest corridors. The apparently naturally patchy distribution of *Cacajao calvus* (discussed in Chapter 9) may also demonstrate that the species is prone to isolation in smaller populations that might be more prone to genetic drift, potentially affecting the pigmentation of the pelage. This idea was first proposed by Hershkovitz (1987a) who also noted that the largest geographic range belongs to the most saturate subspecies *Cacajao calvus ucayalii*, and the progressively smaller ranges belong to progressively more bleached subspecies. The newly discovered population of white uakaris appears to fit this pattern.

Whether there is a cost to having a red or white pelage or not, there are other possible functions for the red or white pelages in *Cacajao calvus*. Sumner and Mollon (2003) suggest that in other orange primate species, possible advantages lie in being conspicuous to other members of the group or to other groups. Sumner and Mollon (2003) point out that *Cacajao calvus* is polymorphic in its colour vision. All males, and many of the females, are dichromatic and are therefore likely to find the orange pelage colour of *Cacajao calvus ucayalii* difficult to detect amongst foliage, while some females are trichromatic and able to distinguish orange from green. While orange pelage is inconspicuous against foliage to dichromatic individuals, it is distinguishable from all other primate pelage colours (Sumner and Mollon 2003). Discrimination between orange and other pelages is therefore possible and a social function for the pelage colour cannot be ruled out on this basis.

1.5.6 Geographic distribution of *Cacajao*

None of the ranges of the various subspecies of the two species of *Cacajao* overlap significantly (Figure 1.1), although there may be a contact zone between *Cacajao calvus calvus* and *Cacajao calvus rubicundus* where the ranges meet (Ayres 1986). *Cacajao melanocephalus melanocephalus* is distributed on the upper Orinoco-Casiquiare River basin in Amazonas, Venezuela, and on the Serra do Imeri on the Brazil-Venezuela border (Hershkovitz 1987a). *Cacajao melanocephalus ouakary* is distributed in eastern Colombia from the Guaviare River south to the Apaporis River in the departments of Guainía, Guaviare and Vaupés. In Brazil it is distributed in the basin of the Negro and upper Solimões west of the Araçá River and north of the Japurá and Solimões Rivers (Hershkovitz 1987a).

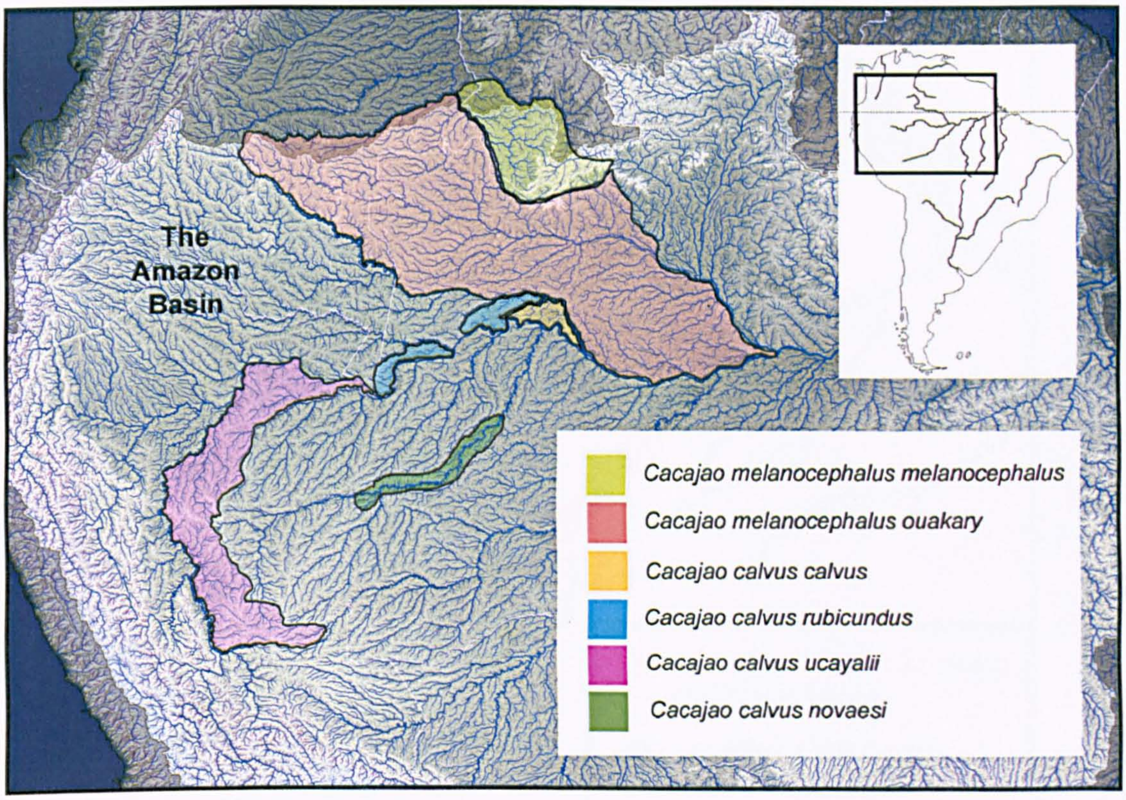

Figure 1.1 Geographic distributions of the described subspecies of *Cacajao*. Ranges from Hershkovitz (1987a) and Sousa e Silva Júnior and Martins (1999). (Map adapted from http://earthobservatory.nasa.gov).

Cacajao calvus rubicundus is distributed on the north bank of the Solimões River in Amazonas, Brazil from opposite São Paulo de Olivença to the mouth of the Içá River (Hershkovitz 1987a). *Cacajao calvus rubicundus* also occurs south of the Solimões, west of the Jutaí River at the Jutaí-Solimões Ecological Station (Nogueira-Neto 1992). *Cacajao calvus calvus* occurs from above the junction of the Japurpá and Solimões Rivers, between the two rivers up to the connecting Paraná Yauala or the Paraná da Aranapa (Hershkovitz 1987a). The discovery of a new population of white uakaris by Sousa e Silva Júnior and de Sousa Martins (1999) on the Juruparí River (Chapter 1.5.3) may result in an extension of the known range for *Cacajao calvus calvus* if the population is found to be of this subspecies rather than of a new undescribed one (Figure 1.2). Sousa e Silva Júnior and Martins (1999) also summarised observations by Peres (1990, 1997) and A. Perequillo of *Cacajao calvus calvus* south of the Solimões at various locations on the west bank of the Juruá River.

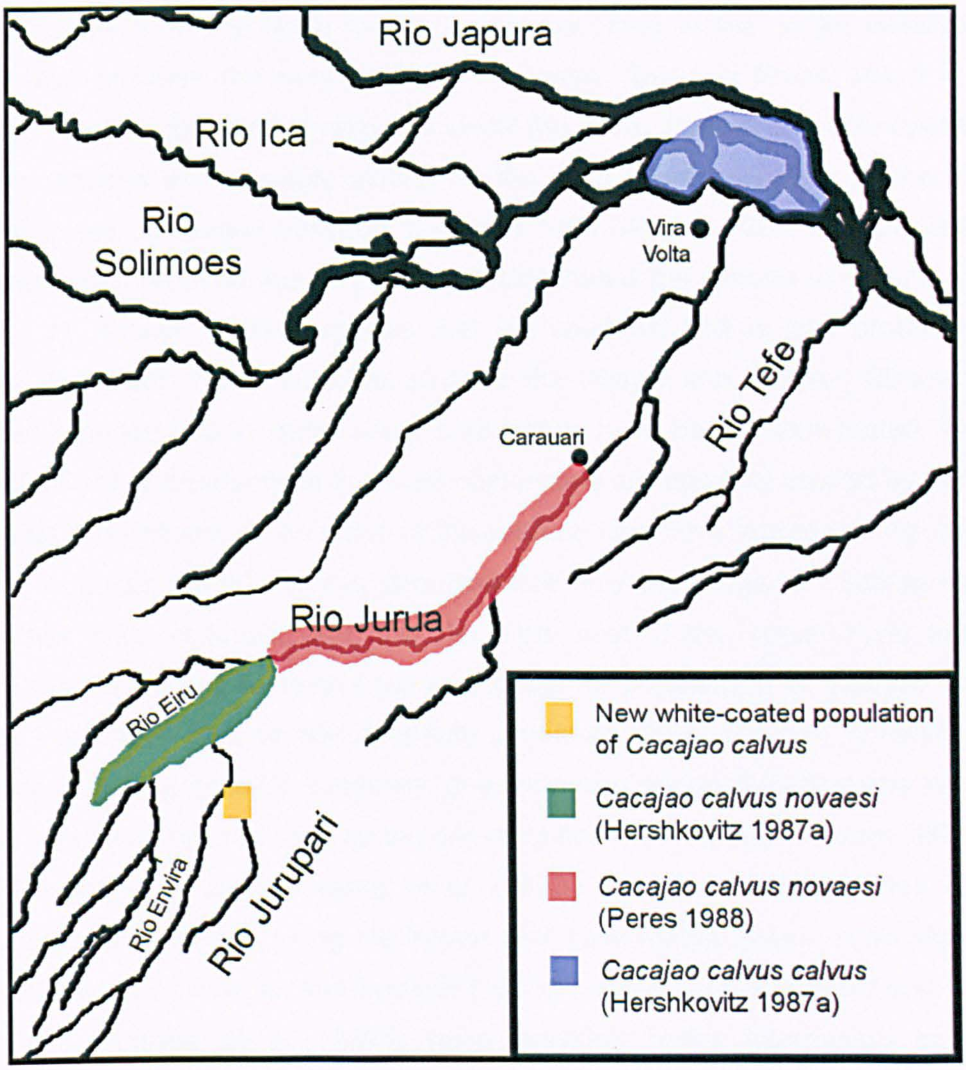

Figure 1.2 Range extension for *Cacajao calvus novaesi*, and the range of a new population of white uakaris (from Sousa e Silva Júnior and Martins 1999).

The distribution of *Cacajao calvus novaesi* has been updated since first described by Hershkovitz (1987a), when it was known only on the south bank of the upper Juruá River between the Tarauacá and Eirú Rivers. Sousa e Silva Júnior and Martins (1999) summarised new range information, largely from Peres (1988, 1990, 1997) who found it to the north-east of the range described by Hershkovitz (1987a), on the left bank of the Juruá and at Lago da Fortuna, Carauari to the north (Figure

1.2). Peres also recorded *Cacajao calvus* on the right bank of the upper Juruá River at Sobral, but this population could have been either *Cacajao calvus novaesi* or *Cacajao calvus ucayalii.*

Cacajao calvus ucayalii is found south of the Amazon River in Peru between the Ucayali and Yavarí Rivers. According to Hershkovitz (1987a) it was distributed from the east bank of the Ucayali in an easterly direction to the Yavarí River and from the Amazon River in the north to the Urubamba River in the south. Hershkovitz (1987a) also includes the east bank of the lower Yavarí in Brazil, but it is not confirmed whether the current range includes this area. Populations also appear to be much reduced and possibly extinct on the west (Peruvian) bank of the lower Yavarí. Surveys conducted between 1979 and 1986 (Aquino 1988) showed that the range was much reduced, hunting having exterminated the species in several areas (Figure 1.3). Aquino (1988) suggests that the southern limit is now probably the Sheshea River, and that populations close to the Ucayali and Amazon Rivers have also been reduced and in some areas populations have been exterminated. These local extinctions and reductions in uakari populations are certainly caused by hunting and habitat disturbance. While some of these areas may have lacked census data at the time, Aquino's (1988) surveys demonstrated how the range of *Cacajao calvus ucayalii* has been reduced, and how the area west of the Yavarí River and its tributary the Yaquerana represent the stronghold for populations of *Cacajao calvus ucayalii.* Population decline has probably continued since Aquino's surveys, with increasing human population pressure, and dwindling populations of game animals close to population centres such as the city of Iquitos (Puertas and Bodmer 1993).

Census work by Salovaara *et al.* (2003) has given a better idea of the distribution of this species along the Yavarí and Yavarí-Mirín Rivers, while sightings and census work by Puertas and Bodmer (1993), Heymann (1992), Ward and Chism (2003) and Bennett *et al.* (2001) have provided better information on local populations in the areas around the Tamshiyacu-Tahuayo Communal Reserve and on the Tapiche River. These surveys cover around 25% of the current known range of *Cacajao calvus ucayalii.* South of the Gálvez River, the range is even more poorly known, and few reports have been published since Aquino (1988). One detailed survey in the Sierras de Contamana by Aquino *et al.* (2005) has recorded groups of *Cacajao calvus ucayalii* at relatively high abundances.

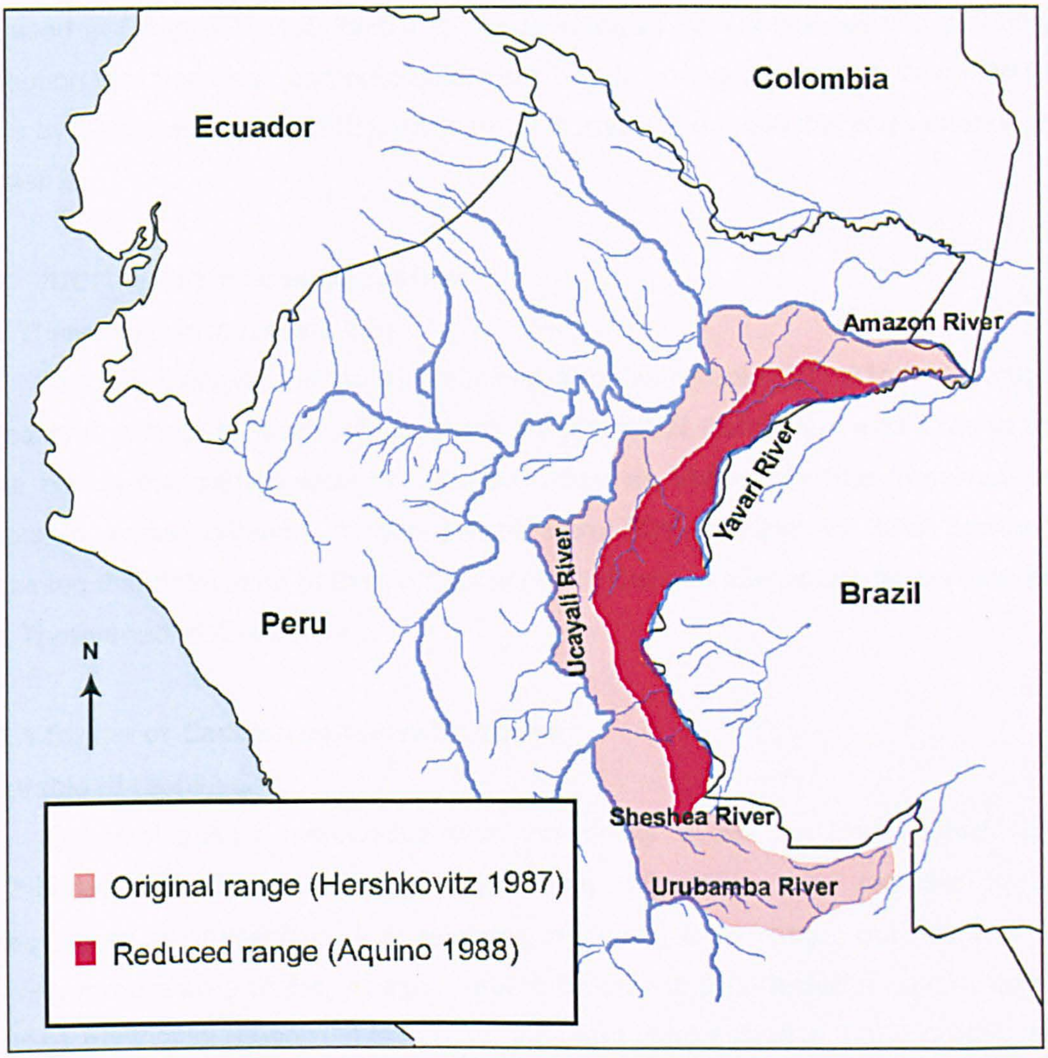

Figure 1.3 The original distribution of *Cacajao calvus ucayalii* and the distribution in 1986. Map adapted from Aquino (1988).

Populations of *Cacajao calvus* observed by Peres on the upper Juruá and unconfirmed reports by Fernandes (1990) in the Brazilian state of Acre on the upper Juruá and Purus are either of *Cacajao calvus novaesi* or *Cacajao calvus ucayalii*, which would extend the known ranges of either of these subspecies. Since it is not confirmed that *Cacajao calvus ucayalii* survives on the lower Yavarí in Brazil, this could extend the current range of *Cacajao calvus ucayalii* into a country where it is currently unconfirmed. Isolated reports of red uakari monkeys west of the Ucayali on the Yanayacu River, a tributary of the Marañon, running more or less parallel to the Ucayali River, in the Pacaya-Samiria National Reserve have occurred for a number of years (R. Bodmer pers. com.). These reports are unconfirmed, but would extend the known range of *Cacajao calvus ucayalii*; investigations to confirm or refute these reports, and the implications of finding a population of uakaris in this reserve, are discussed in Chapter 9.11.3. Within its range *Cacajao calvus ucayalii* has a patchy distribution that has been demonstrated most clearly on the Yavarí and Yavarí-Mirín Rivers by Salovaara *et al.* (2003). An attempt is made to explain this phenomenon in Chapter 9.

1.5.7 IUCN Status of *Cacajao calvus*

Near Threatened (assessed 2003).

In 1996 *Cacajao calvus* was assessed as Vulnerable (VU A1cd). Although hunted and subject to local extirpation, the 2001 IUCN Categories and Criteria no longer permit the classification of *Cacajao calvus* as Vulnerable (the threshold for Vulnerable under criterion A was raised from 20% decline to 30% decline). Combining the distribution of the four subspecies, *Cacajao calvus* can be considered Near Threatened (IUCN 2006).

1.5.7.1 Status of *Cacajao calvus rubicundus*

Vulnerable (B1ab(iii); C1).

Cacajao calvus rubicundus was previously listed as Endangered (EN B1+2abcde), but new information about this subspecies has resulted in its reassessment as Vulnerable. It is relatively restricted in its range, but occurs in a relatively remote area of the Amazon, and in at least one protected area (the Jutaí-Solimões Ecological Station). It is hunted, but there is no evidence that it is seriously threatened at present (IUCN 2006).

1.5.7.2 Status of *Cacajao calvus calvus*

Vulnerable (B1ab(iii); C1).

Cacajao calvus calvus was listed as Endangered in 1996 and 2000 (EN B1+2abcde), but was down-listed to Vulnerable as a result of an improvement in the taxon's status due to successful protection and monitoring in the Mamirauá State Sustainable Development Reserve. It has a very restricted range, but the area is entirely covered by the Reserve (IUCN 2006).

1.5.7.3 Status of *Cacajao calvus novaesi*

Vulnerable (B1ab(iii); C1).

Cacajao calvus novaesi was previously listed as Endangered, but new information on the range of this subspecies (see 1.5.6) has resulted in its reassessment as Vulnerable (IUCN 2006).

1.5.7.4 Status of *Cacajao calvus ucayalii*

Vulnerable (A2cd)

Precise information is lacking concerning the area of occupancy and rate of extirpation of *Cacajao calvus ucayalii* in Peru (IUCN 2006). Assessors and evaluators Rylands, A.B., Heymann, E.W. and Mittermeier, R.A. (Primate Red List Authority) must have based their classification partially on surveys conducted between 1979 and 1986 by Aquino (1988) on the Ucayali. These surveys indicated that this subspecies had disappeared from many areas, while in other parts of its range populations had diminished due to strong hunting pressure and habitat destruction. Up-to-date survey data are needed in many areas. More recent surveys have shown that there are some good populations of *Cacajao calvus ucayalii* on the Yavarí and Yavarí-Mirín Rivers (Salovaara *et al.* 2003; Puertas and Bodmer 1993). The conservation of *Cacajao calvus ucayalii* is discussed in Chapters 8 and 9.

1.5.8 Previous studies on the ecology and behaviour of *Cacajao*

Cacajao is the least known of Neotropical primate genera. Fontaine's (1981) review of the genus was based largely on observations on a captive population of *Cacajao calvus ucayalii.* Kinzey (1997) reviewed the biology of *Cacajao* and Barnett and Brandon-Jones (1997) reviewed the ecology, biogeography and conservation of the genus.

Barnett (2005) reviewed the literature for *Cacajao melanocephalus*, and survey work on the species was completed by Lehman and Robertson (1994), Barnett *et al.* (2000) and Boubli (1993). Boubli (1994, 1997, 1998, 1999) made a long-term ecological study of *Cacajao melanocephalus melanocephalus* in the Pico de Neblina National Park, Brazil. Ecological studies on *Cacajao melanocephalus ouakary* have been carried out by Barnett and da Cunha (1991), Setz (1994) and Barnett *et al.* (2005). T.R. Defler made one of the most complete studies on *Cacajao melanocephalus ouakary*, accumulating more than 1800 hours of observation on the subspecies at the Caparú Biological Station, but because much of his data was destroyed in the field there have been relatively few publications (but see Defler 1991, 1999, 2001). Defler remains one of the authorities on the species and many of his insights on the species come across in his review of primates in Colombia (Defler 2003).

Of the four subspecies of *Cacajao calvus*, only *Cacajao calvus calvus* has been studied in any detail. Ayres (1986, 1989) made a long-term study at Lake Teiú in Brazil that was followed by a short study on the positional behaviour of *Cacajao* *calvus calvus* (Walker and Ayres 1996). Ayres work has been the most complete source of information on *Cacajao calvus* since it was published.

Early census work specifically on *Cacajao calvus ucayalii* was completed by Fontaine (1979) and Aquino (1988). *Cacajao calvus* has also been recorded in more general census work by Puertas and Bodmer (1993), Bodmer *et al.* (1994), Bodmer *et al.* (1997), Salovaara *et al.* (2003) and Peres (1988, 1990, 1997). There have been few successful behavioural studies on any of the red subspecies. Fontaine (1977, 1981) made a study of semi free-ranging *Cacajao calvus ucayalii* in Florida. This remained the only source of information on the development and social behaviour for the species until research began at Lago Preto in 2003. A detailed year-round ecological study on red uakaris (subspecies *rubicundus, novaesi* and *ucayalii*) has never been completed, largely because attempts to establish a site where sufficient observations are assured have consistently failed. The patchy distribution and large home ranges of the red uakari have made data collection for the species difficult. A number of short studies have been published, first by Bartecki and Heymann (1987) and Heymann (1990, 1992), then a study was set up by S. Leonard on the Quebrada Blanco adjacent to the Tamshiyacu-Tahuayo Communal Reserve in northeastern Peru. Over 270 contact hours were recorded over 14 months completing 151.5 hours of scan data in 1994. The results of this study are published in Leonard and Bennett (1996), and in Aquino (1995, 1998). These data are also used in Aquino's (1999) short study of 95.2 hours of data, which includes a small amount of data collected at Lago Preto on the Yavarí. Prior to the start of this project R. Bodmer and P. Puertas of DICE and WCS had already established an area where large groups of red uakaris were easily encountered and sufficiently unafraid of human observers to collect good ecological data. Two short undergraduate studies have been completed at Lago Preto by students from The Durrell Institute for Conservation and Ecology (Garrett 2002; Barton 2006), and the pilot study for this research was completed in 2002 (Bowler 2003).

1.6 The aims in this study

With its restricted geographical range and low population densities, *Cacajao calvus ucayalii* is perhaps the most endangered primate in the lowland Peruvian Amazon. It is also probably the least known. The aim is to apply ecological and behavioural information to the conservation problems faced by red uakaris. In particular, one aim is to understand why uakaris regularly occur at such high densities at Lago Preto, and at low densities in other areas, and to make predictions regarding the impact of current logging practices on the species.

In Chapter 2 the environment and history of the Yavarí River basin, the main area considered in this study, is described. The Yavarí is a stronghold for red uakari monkeys, and is the only place known where this species can be encountered regularly. The study site 'Lago Preto' on the Yavarí, where the ecological data for this project were collected, is also described. The general methods used to collect behavioural and ecological data on the red uakari monkeys at Lago Preto are given in Chapter 3. These methods are relevant to several of the following Chapters. The statistics used to analyse these data and the reasons for using them are also given. More specific methods are given within the relevant Chapters. In Chapter 4, the composition and diversity of the main habitats found at Lago Preto are determined. The vegetation of the habitats were characterised, and the parameters most likely to affect the primates were measured. Fruit production in each of the habitats was measured and the seasonal variation in fruit availability discussed. These data are used throughout the thesis, to explain the ecology and behaviour of red uakari monkeys in the context of their environment, and to answer the questions: Does diversity vary between the habitats at Lago Preto? Which habitats are most diverse? Does productivity vary between habitats? Does productivity vary on a monthly basis between habitats?

Perhaps the most important component to this research was recording the diet and feeding ecology of the red uakari monkey. These results are presented and discussed in Chapter 5, answering the following research questions: What plant parts were most commonly eaten? What species, genera and families were most commonly eaten? Did uakaris select some plant genera in their diet in preference to other genera eaten? Was there seasonal variation in the proportion of different plant parts in the diet? Was there seasonal variation in the proportions of different genera in the diet? Is there a correlation between monthly fruit production and the proportion of different plant parts in the diet? Did uakaris feed on harder-shelled fruits in preference to softer fruits? Was there a difference between uakari age-sex classes in the proportion of harder-shelled fruits in the diet? Did uakaris associate with other primate species? Is there a correlation between densities of uakaris and other mammals with similar diets at various sites on the Yavarí River? The results of this Chapter are important in understanding many other facets of uakari biology, and are used in the Chapters that follow.

One of the most interesting aspects of uakari ecology is their unusually-flexible grouping patterns, where group size varies from a few individuals to several hundred. This 'fission-fusion' grouping system could have direct impacts on the ability of the species to inhabit certain areas. Using results on resource availability and feeding ecology from Chapters 4 and 5, the effect of the distribution of resources on grouping patterns and ranging behaviour through the different habitats at Lago Preto is examined in Chapter 6. The following research questions are posed: How long do uakaris spend performing various activities during the day? What is the home range of the uakaris? How far do the uakaris range each day? Do the uakaris use the habitats at Lago Preto in different proportions relative to their availability within the home range, and does this use of habitat vary on a monthly basis? Do group sizes vary on a monthly, daily or hourly basis at Lago Preto? Are average group sizes different when uakaris range through different habitats? Using the theories of Ayres (1986), predictions are made and then tested on the grouping patterns of *Cacajao calvus ucayalii* in *terra firme* and *várzea*.

The large groups and flexible grouping patterns observed in *Cacajao calvus ucayalii* have consequences for the social behaviour of red uakaris. The population growth of a species, and its ability to recover from changes in population size caused by hunting or habitat degradation, depend on its life history characteristics and to a certain extent its social, ranging and reproductive behaviour (Veiga 2004). The social behaviour of *Cacajao calvus ucayalii* is investigated in Chapter 7, with emphasis on testing existing theories on the social organisation. Uakari calls are recorded within the social context for the first time in wild uakaris, and births and mating behaviour are recorded to determine the seasonality of breeding at Lago Preto. The function of the shortened tail and red face are then discussed in the light of new evidence for the social organisation of uakaris.

The effect of timber and non-timber resource extraction on red uakaris is considered in Chapter 8. Since the extraction of resources through much of the range of red uakaris is selective, the effect that extraction has on the uakaris will depend on the diet and habitat use of the monkeys, as well as the presence and extraction of economically-important resources in the environment. Data on the diet of *Cacajao calvus ucayalii* and information on logging practices and the extraction of other resources in key areas of the monkeys' range is used to determine the degree of overlap in the species removed and the species eaten by uakaris. Predictions are then made on the effects of these activities on uakari populations. Within its range the red uakari monkey is patchily distributed. This phenomenon is discussed in Chapter 9 using data on the composition of habitats within the range of *Cacajao* *calvus ucayalii*, including the detailed analysis of the vegetation at Lago Preto. The question is posed: does the distribution of uakaris coincide with relatively high abundances of favour food species or with soil types? The location of protected areas in relation to the occurrence and abundance of the red uakari in Loreto, Peru is then discussed. Finally, under the heading of 'Conclusions' in Chapter 10, all the preceding Chapters are discussed in terms of their contribution to the understanding of red uakari biology and how this affects the conservation of the species in Peru. The lessons learnt by this case study for the wider field of conservation biology are also considered.

Chapter 2

The Yavarí and Lago Preto

2.1 Introduction

The environment and history of the Yavarí River basin are described in this Chapter, and the choice of the area as a site to study red uakari monkeys is explained. The geology, hydrology and climate are briefly described, as are the most important features of the habitat types found in the area. The forests between the Yavarí and Ucayali Rivers have perhaps the highest mammalian diversity in the world (Valqui 2001), but many other animal groups have barely been studied. The work that has been done on the fauna of the Yavarí is briefly reviewed in this Chapter.

It is important to understand the considerable influence that human populations have had, and still have on the Yavarí. The history of the area is reviewed, leading on to a description of the current population, and their subsistence lifestyle. Commercial activities have been of particular importance in the Yavarí, and continue to shape the area. The changing emphasis on the exploitation of different natural resources along the Yavarí is traced through the years, finishing with a brief outline of the current situation, particularly with regard to the extraction of timber.

The Yavarí River was chosen for this study because of the abundance of red uakari monkeys and the relative ease of studying them there, especially at the Lago Preto Conservation Concession. Sites on the Yavarí and Yavarí-Mirín have the highest known densities of *Cacajao calvus ucayalii* (Chapter 1.5.6, Salovaara *et al.* 2003, Puertas and Bodmer 1993), and several key areas for the conservation of the species are within this area (Figure 2.1). These include the Tamshiyacu-Tahuayo Communal Reserve, the Lago Preto Conservation Concession, the 'Iquitos-Yavarí' Logging Concessions and a large area between the Yavarí and Yavarí-Mirín Rivers that is the subject of several proposals to make it a reserved zone. The focus in this thesis is therefore largely on these areas, the Yavarí river basin, and particularly on the Lago Preto Conservation Concession where the ecological data on red uakari monkey were collected.

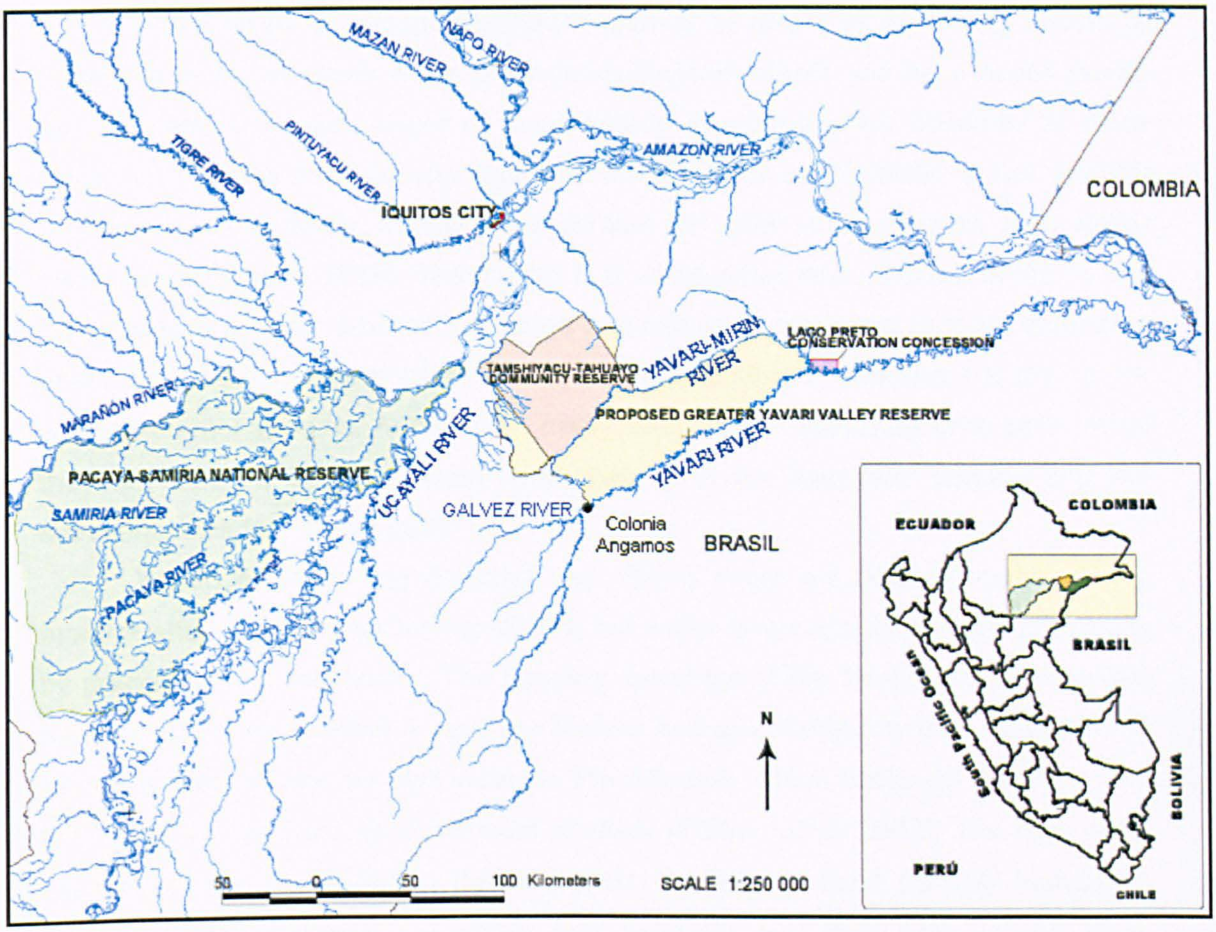

Figure 2.1 Map of the Yavarí River and key areas for the conservation of *Cacajao calvus ucayalii.*

2.2 The Yavarí River

The Yavarí River winds through the Amazonian lowlands, forming the border between Brazil and northeast Peru. It is over 500km long and is one of the larger tributaries of the Amazon River. The Yavarí meanders greatly and is flanked by many oxbow lakes formed when the river cuts between these meanders. The river changes course slowly in comparison with other Amazonian rivers. Pitman *et al.* (2003) compared satellite images from 2002 with maps produced in 1979 and found that the oxbow lakes and river bends were basically identical after 23 years. The courses of many other rivers in the Peruvian Amazon change much more rapidly (Pitman *et al.* 2003).

There are two types of water in the rivers of western Amazonia, white-water and black water. White-water rivers are so called because of the high sediment content that gives the water an opaque light-brown colour. This sediment is brought down from the Andes, and the water is high in nutrients as a result. Black water occurs either where sediment has had a chance to settle, as frequently occurs in floodplain lakes, or where rivers originate in lowland forests and have never picked up sediment. The black colour of these waters is orange when observed at close range, and comes from tannins leached from leaf-litter as the water drains through the topsoil in the forest. These rivers contain far lower nutrient levels than white-water rivers (Prance 1985). The Yavarí is a white-water river, since it is fed by the Yaquerana and other smaller tributaries originating in some low foothills extending east from the Andes. Many of the smaller rivers and streams draining into the Yavarí are black-water streams. Additionally, many lakes on the Yavarí become black when they are isolated from the main river channel in the low-water season and the sediments sink to the lake beds.

Water levels on the Amazon and Yavarí rivers are at their lowest during months when there is also lowest rainfall, but water levels are determined principally by precipitation in the Andes. The flooding dynamics of the Yavarí are intermediate between upper and central Amazonian Rivers, and are affected by both rainfall in the Yavarí watershed and by high water in the Amazon, which backs up the current of the Yavarí by reducing its elevational gradient (Pitman *et al.* 2003). The high water season on the Yavarí, when the floodplain forest is at least partially inundated, generally starts between December and February and lasts until around June. Flooding periods can vary greatly depending on rainfall locally and in the Andes. Water levels generally peak around April, but are also affected by local rainfall, particularly in the upper reaches of the Yavarí and Yavarí-Mirín Rivers. Flash floods caused by heavy rainfall control water levels in the floodplain forests of the Yavarí-Mirín to a greater extent than the water levels on the Yavarí and Amazon Rivers.

2.3 Geology and climate on the Yavarí

The Yavarí River basin is relatively homogeneous in geology, being dominated by the 'Pebas formation'; a thick deposit of clays and sands laid down in ancient lakes and rivers (Räsänen *et al.* 1998, Sánchez *et al.* 1999, de la Cruz *et al.* 1999). The 'Iquitos Arch', an uplifted geological feature that extends several hundred kilometres through Loreto and Colombia, crosses the area and is identifiable on satellite images as a band of steep low hills. Several of the region's major rivers flow from this feature. Soil-types vary between clays and sand, and patches of different soil types occur throughout the area. Most of these soils are acidic and low in nutrients (Pitman *et al.* 2003).

Three weather stations in the area give an approximation of the climate on the Yavarí. These are at Angamos (ONERN 1976), Jenaro Herrera (Gautier and Spichiger 1986) and Iquitos (Marengo 1998). Total annual precipitation is 2000mm to 3000mm. While the climate is not very seasonal (Pitman *et al.* 2003), average rainfall peaks between December and March with drier months in May, June, July and August. Mean temperatures are between 24 and 26°C and are fairly constant throughout the year, except during short climatic phenomena in the drier months, when winds coming north from Antarctica can produce minimum temperatures as low as 10°C.

2003 was a fairly typical year in terms of rainfall, while in 2004 high rainfall kept water levels higher than usual on the Yavarí during the low water season. Rainfall and water levels were unusually low in 2005, coinciding with the worst drought in Amazonia for 40 years (Marengo 2006).

2.4 Flora on the Yavarí

The region between the Ucayali and Yavarí Rivers contains the most diverse tree communities in the world (Vásquez-Martínez and Philips 2000). The forest can be divided fairly clearly into those which do not flood, known as 'upland' or '*terra firme*' forests, and floodplain forests that are inundated seasonally generally known as *várzea* (Pires and Prance 1985; Encarnación 1993). Within these two 'classes' of forest there is much variation in the structure and composition of the vegetation. Encarnación (1993) divided *terra firme* forest in the Peruvian Amazon into 7 formations with 14 sub-formations, and seasonally-inundated forests into 7 formations with 10 sub-formations. Ruokolainen and Tuomisto (1998) assert, however, that the concept of 'forest types' is a human abstraction, used to describe and understand what is actually continuous variation in these forests. Many of Encarnación's formations, which are defined variously by their soil type, drainage and the presence or dominance of key indicator species, appear to grade into each other. The extremely high plant-species richness of Amazon areas makes habitat classification difficult. Salovaara *et al.* (2004) devised a method for large-scale vegetation inventories in complex rainforest landscapes using the species composition of pteridophytes, resulting in the classification of 4 forest types in the Yavarí-Mirín: 1) inundated forests, 2) terrace forests, 3) intermediate *terra firme* forests and 4) Pebas Formation forests. This method requires relatively skilled identification of pteridophytes and results in the classification of just four forest types. Although forests vary continuously, the distinction between *terra firme* and floodplain forests is clear, and there are a number of other clearly-distinct forest types that can be distinguished by their vegetation structure. These forest types tend to be defined by their fertility, drainage, flood dynamics and water type.

The area between the Ucayali and Yavarí Rivers is dominated by vast tracts of upland *terra firme* forest, which shows a high degree of small-scale heterogeneity in its floral composition (Ruokolainen and Tuomisto 1998). Encarnación (1993) divided *terra firme* forest into two sub-classes; those with poorly-drained soils and those with well-drained soils. *Terra firme* forests with poorly-drained soils consist of just two of Encarnación's formations; '*yarinal de altura*', characterised by the dominance of the 'yarina' palm *Phytelephas macrocarpa* and '*aguajal de altura*', characterised by the dominance of the 'aguaje' palm *Mauritia flexuosa*. These *aguajal* palm-swamps within *terra firme* forest are common on the Yavarí and are clearly distinct from the surrounding *terra firme* forest. They can be clearly identified from the air, and on satellite images.

Floodplain forests in Amazonia are divided into two types. These are *igapó* forests that are inundated seasonally with black water, and *várzea* forests that are seasonally-inundated with white-water. Large quantities of sediment are deposited in white-water flooded forests when they are inundated; making the soils far more fertile than in *igapó* forests (Pires and Prance 1985). The floodplain forests in the Iquitos-Yavarí region are white-water *várzea* forests. Within these forests several types of flooded forest occur and grade into one another to some extent. This makes classification difficult (Pitman 2003). Much of the forest is flooded for six months of the year, but in the upper reaches of many of the smaller rivers there are forests that flood for shorter periods dependent on local rainfall. In areas flooded continuously during the high water season, forest types vary largely depending on their topography and the time they spend underwater. Areas of higher ground occur largely in strips along riverbanks where sedimentation is highest. These are true levees, known locally as *restingas*. These high areas grade into lower areas of *várzea* which are deeper and flooded for longer, but still have a closed canopy. Even lower areas, often around lakes or along larger low-lying streams, have an open canopy and are characterised by low, scrubby and thick vegetation. The Brazilian term '*chavascal*' is used for this habitat in this thesis, because it is commonly used in the scientific literature (e.g. Ayres 1986).

Palm-swamps, with permanently-waterlogged soils, dominated by *Mauritia* and *Euterpe* palms, are common on the Yavarí making up 25-50% of the floodplain

(Pitman *et al.* 2003). This habitat is known as '*aguajal*' in Peru and '*buritizal*' in Brazil. Pires and Prance (1985) separated this vegetation type as a special type of *várzea*. Encarnación (1993) also separated *aguajal* into a sub-class of white-water *várzea* along with '*pungal*', a habitat dominated by the species *Pseudobombax munguba*. Floodplain *aguajal* is a common habitat in the floodplain of the Yavarí, and varies from mixed stands dominated by *Euterpe precatoria*, *Mauritia flexuosa* and *Virola* spp. to almost pure *Mauritia flexuosa*. *Aguajal* occurs in higher areas of the floodplain that do not flood particularly deeply, but which are depressed and do not dry out during the low water season. While floodplain and upland *aguajal* palm-swamps appear very similar, and are dominated by the same species, the classification systems used by both Encarnación (1993) and Pires and Prance (1985) classify floodplain *aguajal* essentially as *várzea*, while upland *aguajal* is classified as *terra firme* forest. Although both are dominated by *Mauritia* and *Euterpe* palms, upland *aguajal* swamps are generally smaller in area than floodplain *aguajal* swamps, and they have different plant communities.

Because the different types of *terra firme* and *várzea* forest defined by other authors intergrade and are not clearly defined, in this thesis habitats are divided into the broad categories of *terra firme*, *várzea* and *aguajal*. The term *terra firme* in this thesis is used to include all forest types at Lago Preto which do not flood, or become waterlogged for long periods. The term *várzea* describes all habitats that flood seasonally and dry out for part of the year, and includes areas of *chavascal* and *restinga*. Although upland and floodplain *aguajal* habitats are shown to be different in species composition in Chapter 4 of this thesis, they are similar in that they are dominated by common palm species. These palm species also produce the most fruit within the habitat (see Chapter 4). For this reason both types of *aguajal* are generally considered together in this thesis. The floral composition of *terra firme*, *várzea* and *aguajal* habitats is discussed in Chapter 4.

2.5 Fauna on the Yavarí

Richard Bodmer and colleagues from DICE and WCS have been conducting expeditions to the Yavarí and the Yavarí-Mirín Rivers since 1990. Their research has been principally on mammal populations and economically-important species (e.g. Bodmer *et al.* 2003). As a result the mammal communities here are among the most studied in Amazonia. In contrast, many other animal groups are poorly studied on the Yavarí, though DICE-WCS have also studied some groups of birds, fish, reptiles, amphibians and butterflies. The focus of their work has been on endangered species and species that are commercially important for their eggs, meat or skins. Selected species that can be used to monitor the health of the environment are also monitored. Notably, the populations of commercially important fish, caiman, river turtles, land tortoises, macaws, game birds, giant river otter, dolphins and all large terrestrial and arboreal mammal species are monitored.

During a 'Rapid Biological Inventory' on the Yavarí, conducted by Pitman *et al.* (2003), inventories on fish (Ortega *et al.* 2003), reptiles and amphibians (Rodríguez and Knell, 2003) and birds (Lane *et al.* 2003) were made, while Salovaara *et al.* (2003) censused large mammals. The results of these inventories highlighted the paucity of research conducted in the area. Around one in ten of the fish collected by Ortega *et al.* (2003) was a new record for Peru, and ten of these were new to science. The combined work of Pérez *et al.* (2004) and Rodríguez and Knell (2003) on the amphibian and reptile communities on the Yavarí have registered five new species of frog to date.

With the exception of the Cracidae, Psophiidae and Tinamidae, which have been studied alongside mammals as important game species (Flores 2006), birds have not been well-studied on the Yavarí or even elsewhere on the interfluvium between the Amazon, Yavarí and Ucayali Rivers. Lane *et al.* (2003) list expeditions that collected some samples from the area, ranging from Castelnau and Deville's collections in 1846, to some unpublished surveys on the Yavarí-Mirín by A. Begazo. These collections and surveys do not appear to be particularly detailed. The best record of species appears to be the list made by Lane *et al.* (2003) on the upper Yavarí. Mist-netting for understory birds by DICE and WCS-Peru has further extended the bird list for the Yavarí River. Lane *et al.* (2003) also wrote of the possibility of finding *Crax globuosa*, listed as 'vulnerable' by BirdLife International (2000), on the upper Yavarí. This species is found in *várzea* on the lower Yavarí, but was not recorded during censuses at sites upriver from the mouth of the Yavarí-Mirín. Flores (2006) studied Cracidae at the Lago Preto study site, and did not record this species, but an observation of a single *Crax* with an obvious curly crest during data collection on red uakari monkeys for this study may have been this species (personal observation).

Valqui (2001) conducted the most detailed inventory of mammals in the Iquitos and Yavarí regions in the Tamshiyacu-Tahuayo Communal Reserve. Valqui found that this reserve, which extends to the Yavarí-Mirín River on its southern boundary, harbours one of the highest non-volant mammal diversities in the world. Based on Valqui's study and on censuses on the Yavarí and Yavarí-Mirín Rivers, Salovaara *et al.* (2003) estimate that around 150 mammal species occur in the Yavarí river basin.

In addition to the red uakari monkey, several other species considered at risk by the IUCN are present on the Yavarí. Three mammals classified as 'endangered' occur on the Yavarí; the giant armadillo (*Priodontes maximus*), the giant otter (*Pteronura brasiliensis*) and a species of spiny mouse (*Scolomys ucayalensis*). The status of the spiny mouse *Scolomys ucayalensis* on the Yavarí is unknown, but studies have shown that healthy populations of giant armadillos occur at Lago Preto (Drage 2003). The giant river otter has recently recolonised the area after a period of absence or extreme rarity following intensive hunting for its skin between the 1940s and 1970s. Populations of this species are increasing as a direct result of the ban on hunting this animal and the CITES restriction on trade in its fur (Recharte and Bodmer 2004). Species listed as 'vulnerable' include the bush dog (*Speothos venaticus*), the giant anteater (*Myrmecophaga tridactyla*), Emilia's short-tailed opossum (*Monodelphis emiliae*) and the pink river dolphin (*Inia geoffrensis*). The presence of the vulnerable Amazonian manatee (*Trichechus inunguis*) has not been confirmed in the area and, if present, is very rare. The lowland tapir (*Tapirus terrestris*), globally vulnerable due to hunting and habitat loss, is occasionally seen on the Yavarí and Yavarí-Mirín, and local populations would appear to be healthy. The 'near threatened' jaguar (*Panthera onca*) and the short-eared dog (*Atelocynus microtis*), for which data are deficient both occur. Red and grey brocket deer (*Mazama americana* and *Mazama gouazoubira*) are listed by the IUCN, because there are insufficient data on them, but they seem to have healthy populations on the Yavarí (Salovaara *et al.* 2003).

2.6 Primates on the Yavarí

Fifteen non-human primate species occur in the forests between the Amazon, Yavarí, Ucayali and Gálvez Rivers. One of these, Goeldi's monkey (*Callimico goeldii*) has only been observed on the Gálvez River and another, the black-capped squirrel monkey (*Saimiri boliviensis*), is also absent from the Yavarí and Yavarí-Mirín. The remaining 13 species have all been recorded during censuses on the upper Yavarí and Yavarí-Mirín (Salovaara *et al.* 2003) (Table 2.1). This represents one of the world's highest primate diversities (Puertas and Bodmer 1993).

Although not listed as threatened, heavy hunting has reduced populations of large-bodied primates in much of the Peruvian Amazon (Bodmer 1997), but on the upper Yavarí and Yavarí-Mirín Rivers, populations of the large-bodied black-faced black spider monkeys (*Ateles chamek*) and woolly monkeys (*Lagothrix lagotricha*) are healthy. At some sites on these rivers, groups of these species mob researchers, indicating that they are rarely hunted. Salovaara *et al.* (2003) calculated that 40% of the crude biomass and over 50% of the metabolic biomass of the mammalian community was made up of primates. Furthermore, two thirds of the primate biomass is accounted for by woolly monkeys.

Table 2.1 Primate species present on the Yavarí and Yavarí-Mirín Rivers. Density and abundance data from Salovaara *et al.* (2003).

Species	Density (ind./km^2)			Abundance (ind./100 km)		
	Yavarí	Lower Yavarí-Mirín	Upper Yavarí-Mirín	Yavarí	Lower Yavarí-Mirín	Upper Yavarí-Mirín
Black-faced black spider monkey *Ateles chamek*[1]	4.06	n/a	1.58	28.39	1.24	7.24
Woolly monkey *Lagothrix lagothricha*	32.68	27.61	24.5	181.78	114.26	28.31
Red howler monkey *Alouatta seniculus*	n/a	0.77	0.76	1.77	3.83	3.94
Brown capuchin monkey *Cebus apella*	4.01	5.01	10.20	22.85	25.56	35.78
White-fronted capuchin monkey *Cebus albifrons*	2.63	2.23	5.58	19.47	13.40	28.43
Red uakari monkey *Cacajao calvus*	n/a	4.94	n/a	14.79	47.33	6.07
Monk saki monkey *Pithecia monachus*[2]	7.18	4.41	10.51	23.86	23.76	33.12
Dusky titi monkey *Callicebus cupreus*	11.84	5.08	11.72	23.85	12.72	23.55
Common squirrel monkey *Saimiri sciureus*	18.63	33.07	45.9	54.23	199.05	192.96
Black-chested moustached tamarin *Saguinus mystax*	30.49	22.63	28.52	97.6	70.15	80.1
Saddleback tamarin *Saguinus fuscicollis*						
Night monkey *Aotus nancymae*	n/a	n/a	n/a	n/a	n/a	n/a
Pygmy marmoset *Cebuella pygmaea*	n/a	n/a	n/a	n/a	n/a	n/a

[1] The black spider monkeys on the Yavarí are *Ateles chamek*, which was previously considered a subspecies of *Ateles paniscus* and are still referred to as this species by many authors, including Salovaara *et al.* (2003). Here we follow the IUCN Red List (Rylands *et al.* 2003a).

[2] L. Marsh is currently reviewing the genus *Pithecia*. This population has been known as *Pithecia monachus* for many years following the classification by Hershkovitz (1987b). Marsh, having reviewed photographs taken on the Yavarí and Yavarí-Mirín Rivers, suspects that individuals photographed might not actually be *Pithecia monachus*, but has yet to determine the identity of this population.

The red uakari monkey, *Cacajao calvus ucayalii,* is the only primate in the region listed as threatened by the IUCN, who consider the subspecies vulnerable (Rylands *et al.* 2003b). The red uakari is a flagship species for conservation in the Yavarí region with populations on many parts of the river. Census work (Puertas and Bodmer 1993; Salovaara *et al.* 2003) has revealed a patchy distribution for *Cacajao calvus ucayalii.* The species is unusually abundant in the Lago Preto area on the Yavarí close to the mouth of the Yavarí-Mirín, but elsewhere group sizes are smaller and are encountered more rarely. *Cacajao calvus ucayalii* is absent for a long stretch of the Yavarí upriver from Lago Preto, from above the mouth of the Yavarí-Mirín perhaps as far as Quebrada Curacinha, close to the town of Colonia Angamos, where a group was observed by Salovaara *et al.* (2003). The species is only present on the Peruvian side of the Yavarí River. On the Yavarí-Mirín, the species is present in the upper and lower reaches of the river, but is absent from the middle section, and from the south side of the river, except in the very upper reaches. Chapter 9 attempts to explain this patchy distribution.

2.7 Human population

2.7.1 The history of the Yavarí

People have featured prominently in the history of the Yavarí River valley since the first description of the river in the account of an expedition made by Don Pedro de Texeira (D'Acuna 1698). During the 1800s two major expeditions by Spix and Martius (1823-31) and Castelnau (1850-51) documented the fauna and flora on the river, as well as the indigenous tribes living there. Spix and Martius in particular described the dominance of the Mayorunas or Matís (Matsés), whose ferocity prevented the Portuguese from entering the river. The Mayoruna, known for their skills as hunters, do not traditionally practice agriculture. This demonstrates the relative abundance of large mammals on the Yavarí (Bodmer *et al.* 2003). In 1866, a joint expedition lead by the Secretaries of State of Peru and Brazil, Dr Manuel Rouaud y Paz-Soldán and Dr João Soares Pinto, was mounted to determine the boundary between the two nations (Raimondi 1874-79). The expedition, travelling on the steamship *Napo,* took 35 days to travel the length of the Yavarí to the confluence of the Gálvez and Yaquerana Rivers. The expedition entered the larger tributary, the Yaquerana, in smaller canoes and frequently noticed signs of indigenous people, who they called the Matapis. The indigenous people eventually attacked the expedition, killing Pinto and wounding Paz-Soldán, who fled and returned to the mouth of the Yavarí in the steamship.

At the end of the nineteenth century the 'rubber boom' drew people from all over the world to the Amazon. Being rich in natural rubber trees (*Hevea* spp.), the Yavarí became an important source of this valuable commodity. In 1903 there were 55 rubber estates along the Peruvian side of the Yavarí, serviced by 22 steamships and 107 smaller steamboats (Larrabure y Correa 1905-09). This influx of people pushed the Mayoruna back to the upper reaches of the Yavarí, but violent conflict between the rubber tappers and the Mayoruna continued throughout the rubber boom period (e.g. Lange 1912). The decline of the rubber boom started around 1912 and by 1920 rubber extraction on the Yavarí was minimal.

Extraction of other resources continued, and timber, rosewood oil and animal pelts were all exploited. In the 1940s and 1950s the population was still high, and the creation of the Peruvian military base of Angamos swelled numbers further. The upper Yavarí-Mirín was the site of an industrial rosewood plant, and families lived on every bend of this river, with a total population of over 1000 people (Bodmer and Puertas 2003). Resource extraction peaked in the 1970s and then started to decline. Rosewood oil and the most valuable *Cedrela* timber were becoming scarce, and the market for animal skins was all but eliminated as Peru entered CITES (Bodmer and Puertas 2003). In the early 1990s timber extraction dominated the area around Angamos, but a logging ban implemented by the Peruvian National Institute of Natural Resources (INRENA) in 1996 ended this industry. Similarly in 1990 there were three logging operations and a population of around 400 people on the Yavarí-Mirín, but the increasing scarcity of timber trees was making extraction difficult (Bodmer and Puertas 2003).

Malaria had always been a problem on the Yavarí since the arrival of non-indigenous people. In 1995 an epidemic of deadly cerebral malaria hit the region and the timber companies left. Many inhabitants of the Yavarí and Yavarí-Mirín Rivers died in this outbreak and several communities disintegrated or moved closer to the mouth of the Yavarí to look for government support (Bodmer and Puertas 2003).

At the start of the data collection for this thesis in 2003, human population levels on the Yavarí were probably at their lowest levels in recorded history. 179 inhabitants lived in the town of Esperanza, 18 in Buen Jardin, 17 civilians and 7 policemen in Carolina, and 5 people in San Francisco de Mercedes (Bodmer and Puertas 2003). These communities live largely by subsistence agriculture and hunting, while also trading in wild meat and peccary skins to buy items such as soap and salt. The population has swelled since 2003 with the incursion of several timber companies who have been awarded new logging concessions in the Yavarí and Yavarí-Mirín Rivers.

Logging on the Yavarí is a commercial activity with an economic return likely to exceed that of the sale of wild meat and peccary skins (Bodmer *et al.* 2006). The forest concessions were offered as plots by the government through INRENA in September 2004 for the exploitation of timber, and are subject to the regulations of the government. The concessions are to be managed as 'forests of permanent production', and the extraction of timber must be carried out under a 'Sustainable Forest Management Plan' that should include the approval of the INRENA. This document should guarantee the sustainability of extraction of the wood in the forest concessions. The forest concessions are offered for a time period of 40 years, after which they are renewable (PERU 2001).

More recently, concessions for the exploration and extraction of oil have been announced by the Peruvian government. Full details were not available at the time of writing, but the concession areas cover the entire area of the Yavarí and Yavarí-Mirín Rivers, as well as much of the rest of Loreto. The concessions overlap with logging concessions, communities and protected areas including the Lago Preto Conservation Concession (Chapter 2.9).

2.7.2 Communities on the Yavarí

Indigenous people are still present on the Yavarí. Much of the land on the Brazilian side of the upper Yavarí consists of the 'Vale do Javari Indigenous Area' where there may be as many as 1,350 uncontacted indigenous people, possibly the largest concentration anywhere in the world (Wallace 2003). Close to the Yavarí there are many more contacted indigenous people, whose villages can be seen as one travels up the Yavarí. On the Peruvian side, presence on the mid-lower Yavarí was limited to a single family who abandoned their house at some point during the data collection for this thesis. There are a number of Matsés communities on the upper Yavarí and on the Gálvez, where an area of 452,735ha was given legal titling of 'The Matsés Native Community' in 1993, and where Matsés communities are proposing an additional protected area; the Matsés Communal Reserve' (del Campo *et al.* 2003). There are over 2100 people in the Matsés Native Community, who practice small-scale agriculture and sell game meat in Angamos to buy basic products. The communities remain close to Angamos to take advantage of medical centres and schools (del Campo *et al.* 2003).

Most of the people on the Yavarí are non-tribal people known in Loreto as '*ribereños*'. These people practice fishing, agriculture and game hunting, and collect forest products. Like the indigenous groups, the *ribereños* on the Yavarí have a great knowledge of hunting and fishing methods, and of forest plants. The origins of *ribereños* are diverse and include detribalized Indians, and various mixtures of Indians, Europeans and Africans (Lima 1991). The transformation of the Yavarí from tribal groups to ribereños began largely with the influx of immigrants during the rubber boom period (Bodmer and Puertas 2003).

Very few people live on the upper Yavarí River between the communities close to Angamos and the mouth of the Yavarí-Mirín, but there are four communities on the Yavarí-Mirín. The people in these communities are largely descendants from the Yagua and Cocama peoples (del Campo *et al.* 2003). While they were legally recognised by the government, these communities did not hold legal rights to their land until the designation of the Yavarí-Mirín logging concessions in 2004, when Esperanza and Carolina were awarded their own concessions. All residents have the right to hunt and fish in the area, and the community members make informal agreements about where they will hunt and fish. Each household also cultivates a plot of land primarily for their own consumption (del Campo *et al.* 2003). Goods brought from Islandia in the mouth of the Yavarí are purchased from one of three members of the community who regularly travel downriver to sell meat and skins, and to buy other supplies to sell in Esperanza. These return trips take 7 days or more, and the distance to market is one of the key economic problems facing the community (del Campo *et al.* 2003). As on other parts of the Yavarí, malaria is probably the biggest health problem facing the communities. There is a high mortality rate from malaria on the river and, since the disease is fully treatable in most cases, this has to be a direct result of the isolation of the community. WCS-Peru has started a health programme to assist with this issue and other heath problems, but this is still in its early stages.

Four bends downriver from the mouth of the Yavarí-Mirín is the Brazilian military base of Estirón de Ecuador. Downriver from Estirón de Ecuador there are more communities and large villages. Ribereños still live in these areas, but increasingly towards the mouth of the Yavarí there are a number of more recent immigrants, including a large number of people from a religious group known as Israelites. These people practice agriculture and timber extraction, and some areas on the lower Yavarí have been cleared for livestock production (R. Bodmer pers. com.).

Towards the mouth of the Yavarí are the towns of Atalaia do Norte and Benjamin Constante in Brazil, and Islandia, a Peruvian town on an island towards the

Brazilian side of the river. Around the towns there are several sawmills on both sides of the river, and commercial boats travelling to Iquitos leave from Islandia every day.

2.7.3 Agriculture on the Yavarí

Communities on the upper Yavarí use a traditional Amazonian system of agriculture known locally as 'chacra'. Padoch and De Jong (1987) describe how indigenous and non-indigenous populations in the Peruvian Amazon create economically enriched fallows. In these systems the people cut down the forest leaving species they can use, and plant other useful species in the spaces. The forest then effectively re-grows giving a different mix of crops each year. This form of agriculture effectively mimics the forest (Beckerman 1983), and because plots are cut on a long-term basis, soils recuperate in a way non-traditional methods do not allow.

On the Yavarí-Mirín the staple crops are yucca and plantain, but a number of strains of sweet banana, lemons and limes, ginger, pineapples and others are also grown. Aguaje palms (*Mauritia flexuosa*), which tend to spring up almost by accident from discarded aguaje palm seeds, are also incorporated into the agricultural system. Although aguaje is not a staple, it is the most valuable fruit in the Peruvian Amazon (Padoch 1988). On the Yavarí and Yavarí-Mirín, long distances to markets prevent large-scale commercial exploitation of aguaje and most other agricultural and non-timber plant forest products (see Chapter 8).

2.7.4 Hunting on the Yavarí

Hunting for wild meat provides an important source of protein in rural areas throughout Amazonia, and the Yavarí basin is a major area for wildlife production (Robinson and Bodmer 1999). Some of this meat is sold illegally in the city of Iquitos, but the majority (94%) is consumed legally in the smaller villages and towns of Loreto (Bodmer and Pezo 2001). Around 25% of the wildlife hunted in the department comes from the headwaters of the Orosa, Maniti, Tamshiyacu, Tahuayo, Yarapa, Gálvez, and Yaquirana rivers (Bodmer *et al.* 2003). The Yavarí-Mirín valley acts as a source area for headwater rivers, and is extremely important in the socio-economics of rural Loreto (Bodmer *et al.* 2003).

Bodmer *et al.* (2003) analysed the sustainability of the hunting of large mammals in the region, using data collected on the Yavarí-Mirín and Quebrada Blanco between 1992 and 2003. Data were collected with the participation of the hunters. This approach allows researchers to collect direct data on hunting pressure, but also develops relationships between hunters and researchers. This is essential for the future management of wildlife resources. Bodmer *et al.* (2003) found that the most frequently hunted animals in the Yavarí-Mirín were collared and white-lipped peccary (*Tayassu tajacu* and *Tayassu pecari*), and to a lesser extent red brocket deer (*Mazama americana*) and lowland tapir (*Tapirus terrestris*). Primates, rodents, edentates, marsupials and carnivores were more rarely hunted. In comparison, these species were frequently hunted on the Quebrada Blanco. Bodmer *et al.* (2003) calculated that the catch-per-unit-effort (CPUE) of preferred species, particularly peccaries, is much higher in the Yavarí-Mirín than on the Quebrada Blanco, suggesting that the hunting is more sustainable on the Yavarí-Mirín. Bodmer *et al.* used a harvest model to show that all species in the Yavarí-Mirín were hunted within sustainable levels, even the lowland tapir, which is a species very susceptible to over hunting.

Bodmer (2000) and Bodmer *et al.* (2003) described how the Yavarí-Mirín area acts as a source area for the Tamshiyacu-Tahuayo Communal Reserve and the surrounding areas, highlighting its importance and describing how a source-sink strategy could be used to conserve wildlife populations. Both papers stress the importance of community-based conservation in managing wildlife in these areas. Bodmer and Puertas (1999) highlighted the importance of co-management between conservationists and communities, describing the success of these methods in the Tamshiyacu-Tahuayo Communal Reserve, where harvests of primates decreased between 1991 and 1995. In the Yavarí-Mirín, DICE and WCS have been working with hunters from Esperanza and Carolina since 1990, and are in the early stages of implementing a wildlife management plan. In Carolina residents have already made the decision not to hunt red uakari monkeys. In Esperanza the species is still taken very occasionally for subsistence.

Several other non-mammalian species are also hunted on the Yavarí-Mirín. Game birds, Cracidae, Psophiidae and Tinamidae are hunted only for subsistence, but Cracidae and Psophiidae can be particularly vulnerable to over hunting (Begazo and Bodmer 1998). Populations on the Yavarí and Yavarí-Mirín appear to be healthy (Flores 2004). Caiman are occasionally hunted for subsistence and, while hunting pressure does not appear to be high, numbers of black caiman (*Melanosuchus niger*) are low compared with other areas, such as the Samiria River in the Pacaya-Samiria National Reserve (Swan 2006). This may be because the species has not yet recovered from intensive hunting for its skins before trade became strictly controlled in the 1970s, or because the black caiman was exported illegally as a substitute for paiche fish (*Arapaima gigas*) between 2001 and 2003 (Swan 2006). Turtles and tortoises are particularly sought after on the Yavarí and Yavarí-Mirín Rivers. Land tortoises (*Geochelone denticulata*) are collected opportunistically or in baited traps, while river turtles (*Podocnemis* spp.) are caught in fishing nets or collected as they lay their eggs at night. These species can be kept alive for long periods, and have a high value in towns downriver. They are often sent downriver to be sold alive in Islandia. Turtle eggs are also collected intensively when the nesting beaches are exposed in the low-water season.

Hunting levels on the Yavarí-Mirín and on parts of the Yavarí have changed since 2004, when logging activities increased the human population on the river. Logging workers are permitted to hunt wild meat in logging concessions as long as they produce and implement a hunting management plan. The hunting of primates is not permitted. More wild meat *per capita* was consumed in a commercial forest concession on the Yavarí than is consumed *per capita* in the rural communities (Bodmer *et al.* 2006). This was because logging workers did not have sources of carbohydrate, such as rice, plantains or yucca. Logging workers also consumed more small game species, often shooting the first animal they encountered to secure a meal as soon as possible. Bodmer *et al.* (2006) found that the hunting of peccaries, deer, woolly monkeys and agouti (*Dasyprocta fuliginosa*) appeared sustainable in a commercial lumber concession on the Yavarí-Mirín, but since the hunting of primates is relatively easy compared to hunting ungulates, it is likely to increase. Primates are more susceptible to over-hunting and local populations might be under threat while logging operations are active in the area.

2.7.5 Fishing on the Yavarí

Residents on the Yavarí-Mirín fish largely for subsistence using hooks, spears and nets. While fishing is easier during the low-water seasons, community members are able to find fish in the lakes, rivers or flooded forests year-round. Excess catch is preserved by salting or smoking. Larger species of fish, including some of the larger catfish like *Pseudoplatystoma tigrinum* and *Pseudoplatystoma fasciatum,* gamitana (*Colossoma macropomum*) and paiche (*Arapaima gigas*), are preserved for sale in markets downriver.

Commercial fishing boats occasionally make expeditions to the Yavarí and Yavarí-Mirín Rivers with large iceboxes to keep their catch fresh until they return to markets. The most sought-after fish in the Yavarí is the extremely large paiche (*Arapaima gigas*), which is commercially very important. It is over-fished in many areas, where it has become extremely rare. When the water levels are falling and the paiche become trapped in the lakes, the entrances of the lakes are often crowded with people competing to catch this valuable fish. The fish come to the surface to breathe every 20 minutes, so fisherman can quickly estimate how many fish are left in the lakes. Ruck and Montreuil (2004) surveyed paiche in many of the lakes on the Yavarí River, and while the censuses showed that there were still good numbers of paiche in the area, paiche were extremely rare in lakes with easy access to fisherman, including most of the larger lakes.

Some collection of ornamental fish occurs on the Yavarí and Yavarí-Mirín Rivers. Smaller fish are occasionally taken (e.g. *Corydoras* sp.), but the lucrative trade in the fry of arahuana fish *Osteoglossum bicirrosum* is probably the most important. Fry fetch $1 each in markets at the mouth of the Yavarí, and are collected from the father fish that guards the young in his mouth. Fry can be removed from the parent without harming the adult which can be released, but on the Yavarí the adults are generally killed. This is either because the correct techniques are not followed, or because the adults are large and valued as a food fish. Arahuana are over-fished in many areas close to Iquitos, but the species appears relatively abundant in some of the lakes on the Yavarí (Newman 2006).

2.8 Lago Preto

Lago Preto (S04°27.5' W071°45.9') is one of a system of several oxbow lakes in the floodplain forests on the Peruvian side of the Yavarí River, close to the mouth of the Yavarí-Mirín River. Lago Preto is the Portuguese name for the lake used by Brazilians living on the Yavarí, and means 'Black Lake'. This refers to the colour of the water, which drains from the surrounding floodplain forest and upland terraces. The Spanish name for the Lake 'Lago Paredón' means 'fenced lake' and probably refers to the dense *várzea* forest one has to canoe through to get to the lake in the high-water season. The Brazilian name was adopted by researchers, because they were first introduced to the area in 1990 by a Brazilian family, who were still tapping rubber in the area.

Lago Preto now gives its name to the Lago Preto study area and the Lago Preto Conservation Concession. The Lago Preto study area is the only site known where large numbers of red uakaris are easily observable throughout the year. The area of the study site was defined largely by the trail system and the areas to which uakaris were followed during the study, but also by the topography of the habitat. The study area was bounded on much of its west side by *aguajal* and *chavascal* swamps that are difficult to travel through, and on the east side by a long wide strip of impenetrable *chavascal* on the banks of a stream.

2.9 The history of the Lago Preto area

Rubber was extracted from the Lago Preto area during the rubber boom, and a Brazilian family living on the other side of the river continued to collect rubber from the area up until the early 1990s. All adult rubber trees (*Hevea* sp.*)* and some *Rhigospira quadrangularis* in the area are scarred with neat parallel furrows where they have been tapped for their latex. There is only one point where *terra firme* forest can be reached from the *várzea* seasonally-inundated forest without passing through palm or *chavascal* swamp. At this site a bottle inscribed 'New York' dating from around the 1920s was found, and there was a stand of large *Pourouma* trees (Cecropiaceae), a fast-growing pioneer genus associated with recolonisation. This suggests the site was inhabited during the rubber-tapping era.

DICE and WCS involvement with Lago Preto began when R. Bodmer and P. Puertas discovered the site in 1990, after they were advised that the area was a good place to see red uakari monkeys. Red uakari monkeys have since been seen on every subsequent expedition made by WCS-Peru and DICE to Lago Preto, something that cannot be said of any other site. It became apparent that an ecological study on red uakari monkeys would be possible at this site. The Lago Preto study area's population of red uakari monkeys is unique. The species has never been encountered with such consistency or in such high numbers in other areas and, consequently, other attempts to study the species have met with limited success.

WCS-Peru and DICE have made various studies on a range of fauna at Lago Preto, and have been working with red uakari monkeys since 1990. They have looked at primate densities (Puertas and Bodmer 1993; Pascoe 2002) and conducted short ecological studies (Garrett 2002). A pilot study for this long-term project was conducted at Lago Preto in June and July 2002, supported by WCS and DICE. During this time, groups of up to 200 uakari monkeys were followed through *aguajal* palm-swamps, *várzea* and *terra firme* forests. A variety of methods was used to determine which would be best employed for a long-term project, and the many logistical problems involved in working at Lago Preto were considered. From the work of WCS and DICE, and from the work completed on the pilot study, it was clear that Lago Preto presented an opportunity to collect good year-round ecological data on uakari monkeys. Previous studies had been concentrated, however, in the months of June, July and August, and it was not clear if monkeys would be as easy to find at other times of the year. Year-round fieldwork for this thesis was completed between April 2003 and July 2005.

In August 2003 a logging survey team surveyed timber trees at Lago Preto and, in 2004, logging concessions were designated on the north bank of the Yavarí-Mirín and on the Yavarí downriver from the mouth of the Yavarí-Mirín (Figure 2.2). Originally the Lago Preto area was included in the area slated for logging concession, but efforts by WCS-Peru and DICE led to this area being excluded, and proposals were submitted, and subsequently approved, to designate the Lago Preto area as a 'Conservation Concession'.

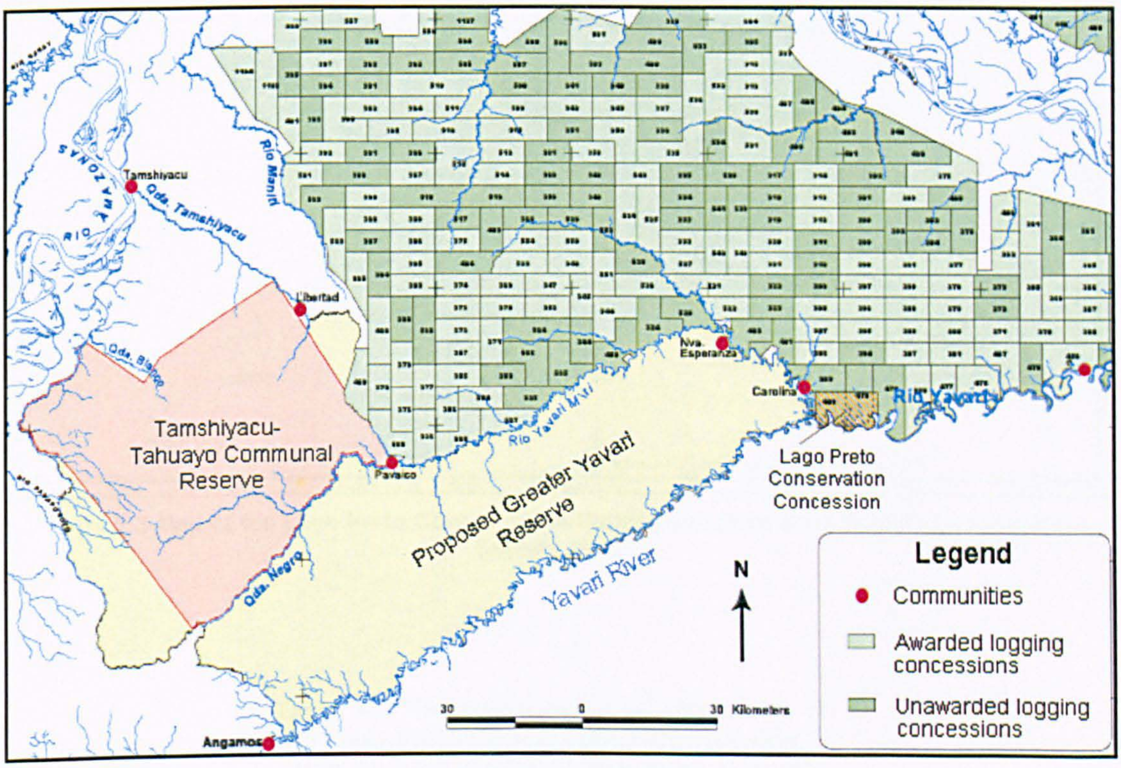

Figure 2.2 Logging concessions on the Yavarí and Yavarí-Mirín Rivers (Figure adapted from INRENA).

2.10 The Lago Preto Conservation Concession

In August 2006 the Lago Preto Conservation Concession (LPCC) was awarded to WCS-Peru, who will manage the area in collaboration with DICE. It is situated about 175km south-east from the city of Iquitos on the Yavarí River, and is 9926.19ha in area. The Yavarí River forms the southern border of the concession, while the north, east and west borders are formed by straight lines (Figure 2.3; Table 2.2). The concession is bordered to the north and east by the Iquitos-Yavarí logging concessions.

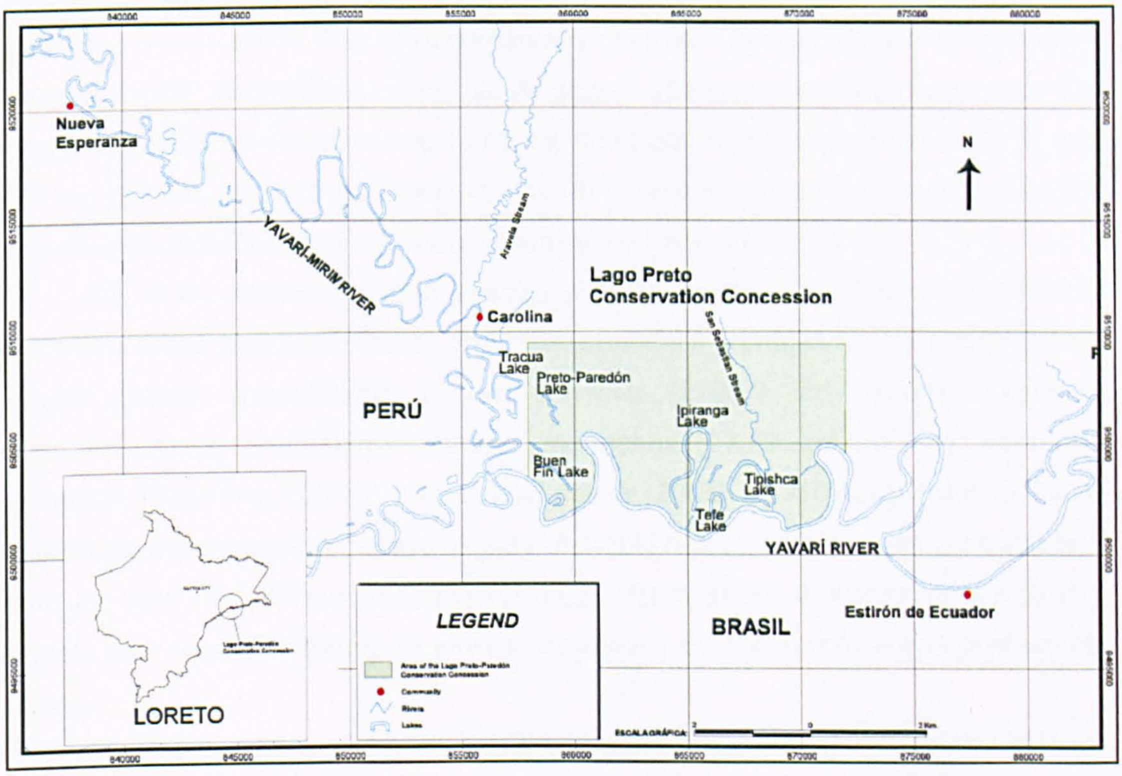

Figure 2.3 Map of the Lago Preto Conservation Concession (Map from Wildlife Conservation Society (WCS).

Table 2.2 The coordinates of the limits of the Lago Preto Conservation Concession. Datum Horizontal WGS 84 Projection UTM. SIG: CIF-IFFS-IANP-INRENA (taken from Puertas *et al.* 2006).

Point	UTM	
	East	North
1. SW corner	857949	9503866
2. NW corner	857943	9509773
3. NE corner	872019	9509711
4. SE corner	872005	9504831

2.11 Fauna at Lago Preto

The species present at Lago Preto are typical of the animal communities on other parts of the Yavarí and Yavarí-Mirín. The community of mammals at Lago Preto is similar to that recorded by Salovaara *et al.* (2003) on other parts of the Yavarí and Yavarí-Mirín. The collared peccary (*Tayassu tajacu*) is the most abundant ungulate (4.83 ind./100km). The black agouti (*Dasyprocta fuliginosa*) and the Amazonian squirrels (*Sciurus* spp.) are the most abundant large rodents (3.45 and 2.76 ind./100km, respectively), and the South American coati (*Nasua nasua*) is the most abundant carnivore (11.72 ind./100km) (Puertas *et al.* 2006).

All 13 non-human primate species present on the Yavarí and Yavarí-Mirín Rivers are present at Lago Preto. The most abundant primates are: *Cacajao calvus ucayalii* (308.97 ind./100km), *Saimiri sciureus* (226.90 ind./100km), *Saguinus fuscicollis* (38.62 ind./100km), *Pithecia monachus* (27.59 ind./100km), *Lagothrix lagotricha* (24.83 ind./100km) and *Cebus apella* (20.69 ind./100km). Prior to 2004, black-faced black spider monkeys (*Ateles chamek*) had only been seen once at Lago Preto in 1998 (WCS-Peru *unpublished data*). From 2004, a single female spider monkey was seen and heard on several occasions travelling with a group of woolly monkeys.

The most striking and important thing about the mammal community at Lago Preto is that the area has by far the highest known densities of *Cacajao calvus ucayalii*. The abundance of *Cacajao calvus ucayalii* at Lago Preto is many times higher than at other sites on the Yavarí and Yavarí-Mirín Rivers (Table 2.3). It was largely for this reason that proposals were made to designate the area a conservation concession. It is also this abundance of red uakari monkeys which made it possible to study the species at a single study site year-round. The methods used at Lago Preto to collect behavioural and ecological data on the large population of monkeys there, are discussed in the next Chapter.

Table 2.3 Abundance of *Cacajao calvus ucayalii* at Lago Preto and other sites in the Yavarí and Yavarí-Mirín (From Salovaara *et al.* 2003).

Abundance (ind./100 km)			
Yavarí	Lower Yavarí-Mirín	Upper Yavarí-Mirín	Lago Preto
14.79	47.33	6.07	308.97

Chapter 3

General Methods

3.1 Introduction

This Chapter describes the Lago Preto study area, where the botanical and behavioural data were collected, and the general methods used to collect and analyse this data. Only methods that apply to multiple Chapters are given here, while more detailed methods are given in the appropriate Chapters. The Lago Preto study site is remote; although it is only 180km from Iquitos, it is separated by thick forest. To get there from Iquitos one has to first travel 483km downriver (362km in a straight line) on the Amazon to Santa Rosa where the borders of Peru, Colombia and Brazil meet, and then a further 493km upriver on the Yavarí (202km in a straight line). The bends on the Yavarí more than double the length of this section of the journey.

During the data collection for this project, the first leg of this journey, from Iquitos to Santa Rosa, was either accomplished on large commercial passenger boats that complete the trip in around 48 hours downstream or 60 hours upstream, or on commercial speedboats that complete the trip in around 12 hours. The second leg of the trip, from Santa Rosa to Lago Preto, was made far more frequently because supplies were obtained from the towns of Benjamin Constante (Brazil), Tabatinga (Brazil) and Leticia (Colombia) close to the mouth of the Yavarí. These supply runs were made in a 6m wooden boat with an 8hp 'peque-peque' motor. Supply runs were made every two to three months and took 7 to 10 days (including around 3 days travel each way) when there were no logistical problems.

A research camp was built at Lago Preto during the early stages of the research. It was a simple structure with no walls, a raised floor and a thatched roof. Rainwater was collected with plastic sheeting, cooking was done on a gas stove and there was a pit toilet 40m from the house. This camp was left to revert to natural vegetation after April 2005. From this date all researchers were based on boats moored on the Yavarí River on the edge of the concession, as required by the rules of the new Lago Preto Conservation Concession. The research camp was positioned on the edge of the *terra firme* forest on the shores of Lago Huapo. It was reached during high water by manoeuvring a large boat through the *várzea* forest, and during low water by making many trips on foot through the forest to bring supplies from the from the river.

3.2 The study area and trails

The behavioural and ecological data for this thesis were collected within an area of around 2200ha on the west side of the Lago Preto Conservation Concession, extending several kilometres north of the northernmost reserve boundary. The area includes around 1400ha of *terra firme*, around 500ha of *várzea* (including *Chavascal*) and around 300ha of *aguajal* (Figure 3.1). The study area did not have clearly delimited boundaries, because attempts were made to follow monkeys as far as they ranged. In this respect the boundaries of the study area were determined in part by the home range of the monkeys. The area was limited on some borders by areas of near impenetrable vegetation such as *aguajal* or *chavascal*. The study area includes two lakes; Lago Preto, which is 1900m long, and the much smaller Lago Huapo, which is 410m long.

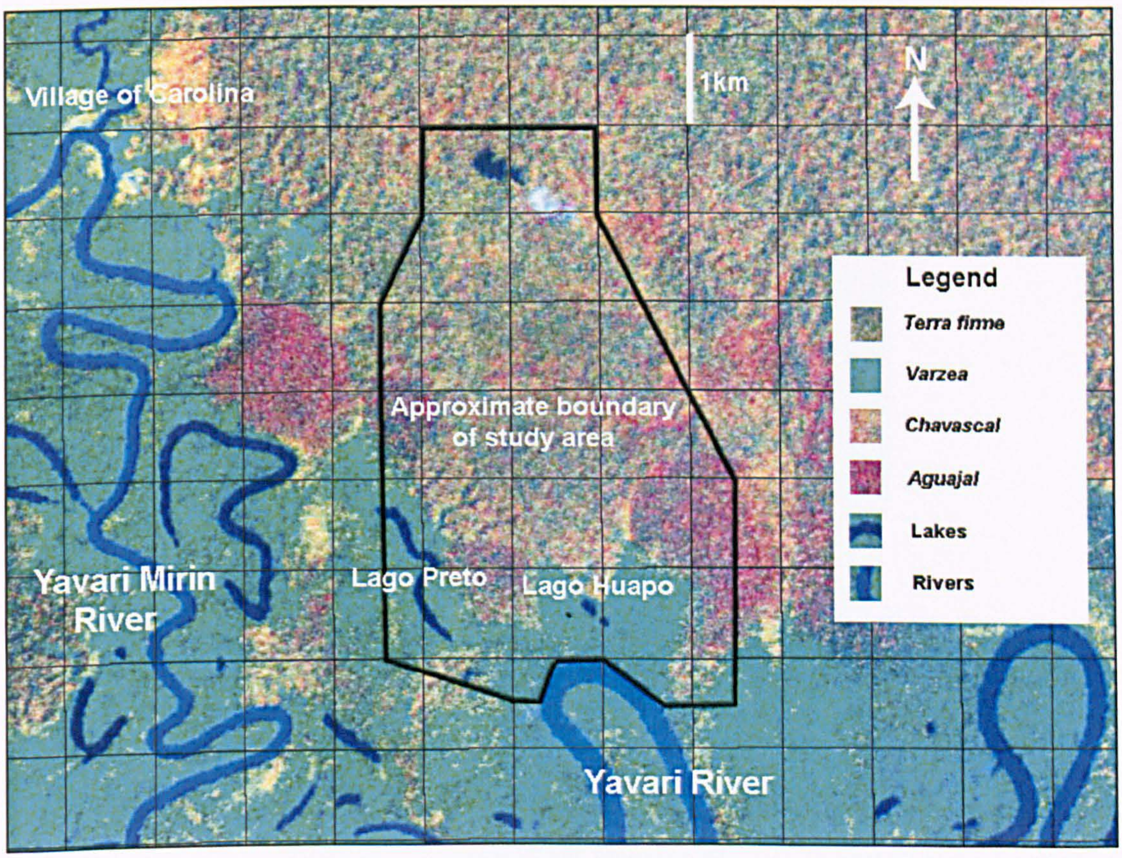

Figure 3.1 Satellite image of the study area at Lago Preto, showing the distribution of habitat types.

At the start of the project there was already a basic trail system, cut by WCS and DICE to census mammals. This was extended and accurately mapped during the early stages of the project. Parallel trails 200m apart were cut in one of the larger mixed *aguajal* swamps, because *aguajal* is a dense habitat that it is difficult to move through without a trail, and it was known that the uakaris were frequently sighted in this swamp. In other habitats, with the exception of *chavascal*, monkeys can be followed without trails. In total the study site has over 30km of trails (Figure 3.2).

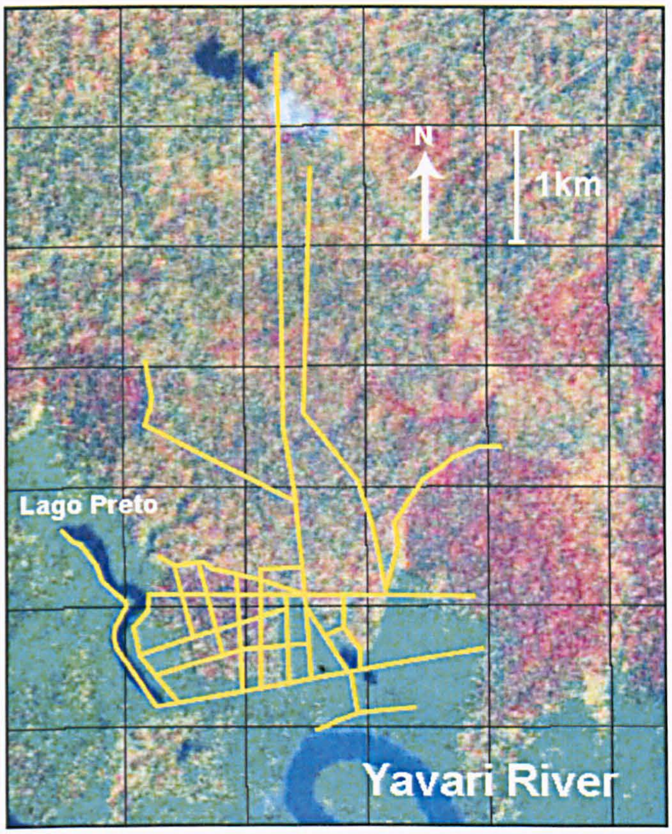

Figure 3.2 The trail system at Lago Preto.

3.3 Following monkeys

Monkeys were located each day by walking the trail system, or searching the *várzea* by canoe. They were followed until they settled into their sleeping trees at dusk, or the group was lost. When the group was successfully followed to their sleeping trees, they were relocated before dawn the following day. Between December and June, when the *várzea* forest was flooded, the monkeys were often followed by canoe. In these months, monkeys were often lost when they entered flooded areas where no canoe was available, or when they crossed areas of dry land where the canoes could not pass.

Groups of 1 to 150+ uakaris were followed for a total of 945 hours and 10 minutes between April 2003 and July 2005. Data were collected in all calendar months (Table 3.1).

Table 3.1 Hours of data collection at Lago Preto.

Month	Number of scans	Hours of data collection	
		h	m
January	233	38	50
February	199	33	10
March	363	60	30
April	519	86	30
May	457	76	10
June	604	100	40
July	648	108	0
August	743	123	50
September	511	85	10
October	605	100	50
November	537	89	30
December	252	42	0
Total	**5671**	**945**	**10**

3.4 Habituation

Uakari groups at Lago Preto were habituated to varying degrees, but the groups never completely ignored researchers at all times. In many cases the monkeys tolerated the presence of researchers at ranges of around 30m, but would flee from, or mob, researchers at closer range. Researchers could not generally observe the monkeys from directly below the group without disturbing them, unless the canopy was thick enough to avoid detection.

When it was possible to follow the same groups for extended periods, the monkeys became more tolerant of researchers, particularly when only one researcher was present. This was the case for the majority of the study. The fission-fusion nature of the groups meant that some groups were followed more than others, and became more habituated than others. Breaks in the research programme often meant that the monkeys were less tolerant of researchers after a period away. Males, particularly those in all-male groups following behind the rest of the group, habituated more than females and young, possibly because researchers generally also followed at the back of the groups.

3.5 Scan sampling

Point scan sampling was used (Altmann 1974), collecting data at ten-minute intervals and allowing one minute to complete the scans; 5671 scans were obtained during the study period.

In each scan the following parameters were recorded:

- Group size (see Chapter 2.27)
- Group spread (an estimate of the maximum diameter of the group)
- Habitat
- Location (using a GPS with external antenna, or where no signal was available, the position in relation to trails or other landmarks)
- The presence of any groups of other primate species and their location in relation to the uakari group.
- Weather (using the broad categories: full sun, light cloud, heavy cloud, light rain, medium rain and heavy rain along with the presence or absence of strong wind)

For each visible uakari monkey, the age-sex class (see Chapter 3.7) was recorded with the individual's behaviour from the categories in Chapter 3.8. Monkey sightings in which neither the age-sex class or the behaviour could be determined were discarded from the scans.

3.6 Age-sex classes

It was not possible to recognise individuals consistently, so for each individual the age-sex class were recorded. Ages were defined following Fontaine (1981) as closely as possible. In the field, it is often difficult to be sure that subadult or even adult females are not juvenile or subadult males, because the genitalia are cryptic. Defler (2003) describes the sexes of *Cacajao melanocephalus* as indistinguishable up to 4 years old, and similar difficulties are found in *Cacajao calvus ucayalii*. Fontaine (1981) reported that, in captivity, two juvenile male *Cacajao calvus ucayalii* entered a subadult phase lasting 2 to 3 years in which the uakaris displayed physical characteristics typical of adult females, including pendulous scrotal alae resembling female labia. The following age-sex classes were used:

Infant one (1-3 months)
- 10-25% length of the mother.
- Face grey/brown with a trace of pink around the nose.

Infant two (3-12 months)
- 25-60% length of the mother.
- Face pink/red, not as saturated as in adult females.
- Thick grey scalp hair.

Juvenile (12 to 36 months)
- Includes Fontaine's 'Juvenile one' and 'Juvenile two'.
- Face pink/red to red.
- Thick grey scalp hair is retained through most of this period.

Subadult
- Where the sex was not determined.

Subadult male
- Similar size or larger than an adult female.
- Lacks the bulging cranial muscles of an adult male.
- Scrotum usually visible, but superficially resembles adult female labia.

Adult male
- Large size.
- Characteristic bulging cranial muscles of an adult male.
- Scrotum always visible.
- Face usually a more intense scarlet than other classes.

Adult female
- Little or no grey scalp hair.
- Lack the bulging cranial muscles of an adult male.
- Smaller than a male.

3.6.1 Adult females carrying dependent young

Where females were recorded carrying young (either *infant one* or *infant two* age classes), the size of the young was recorded as a percentage of the size of the female. The colour of the face and the position of the young were also recorded.

3.7 Behavioural categories

Behavioural categories were based on the three main categories used by Ayres (1986). Because the focus of this study was largely ecological, many of the more subtle social behaviours were not defined, although some of the more obvious ones were added to Ayres' categories. More complex social behaviours, recorded during the study, are described in Chapter 7.

Feed

Feed was recorded when an animal was ingesting or processing food, including masticating, swallowing or carrying food items. Where possible, the plant species, plant parts (seeds, pulp, arils, flowers, leaves or otherwise) and the maturity of the fruit eaten by the individual were recorded (by observation and by collecting discarded parts).

Ayres (1986) included breaking apart branches, leaves and twigs for insects in this category, and presumably also included individuals turning over leaves or inspecting foliage. In this study these behaviours were subcategorised as *searching*.

Rest

Ayres (1986) broadly defined *rest* as when the animal was stationary or engaged in auto-grooming or allo-grooming. In this study auto-grooming and allo-grooming were categorised as separate behaviours. *Rest* was recorded whenever the animal was stationary and not involved in other behaviour.

Move

Move was recorded for animals engaged in locomotion. Following Ayres (1986), no distinction was made between 'rapid' (between trees) and 'local' movements (defined as movements directly associated with feeding, such as between fruits within a tree or when looking for a place to sleep in the sleeping trees in the evening), as is common in studies of primates. This is because uakaris often forage in large groups, moving steadily through the canopy and often feed on small patches of food. To determine each individual's destination (food item within a tree or the next tree) is not practical in the field for large groups of this species.

Social grooming

Social grooming was subcategorised into *give groom* (the age-sex class of the recipient was also recorded) and *receive groom* (the age-sex class of the giver was also recorded).

Display

Display was subcategorised into *arm raising, branch slapping, branch shaking, urine washing, branch breaking, straight legged strut, branch swaying, vertical hanging, hindquarters bounce* and other behaviours that were described when they were recorded. These behaviours are described as part of the results of Chapter 7, following the definitions of Fontaine (1981) where possible.

React to researchers

React to researchers was recorded when *flee* or *display* behaviours were observed in response to the presence of researchers.

Other

Including *auto-grooming, ano-genital rubbing* and other rare behaviours that were described when they were recorded.

3.8 Feeding records

Varying degrees of habituation often meant that researchers were not close enough, or did not have a clear enough view, to identify food items eaten by individuals during instantaneous scan sampling. Trees with open canopies or with large, easily identified fruits may have been disproportionately represented in the scan samples. Fruits with longer processing times were also disproportionately represented, whereas insects and smaller fruits with short processing times are disproportionately rare in the data. For these reasons 'one-zero' sampling (Altmann 1974) was employed in addition to the scan-sampling methods. A '1' was recorded for each food item if it was used during a ten-minute period. The one-zero data probably underestimates the importance of certain species that had crowns full of fruit that were fed on intensively by large groups of uakaris. This method ensured that all plant species observed being eaten were recorded.

3.8.1 Identifying fruits

For each new tree or vine species consumed, the first two or more examples were tagged and the location noted. Field notes on the characteristics of the tree were taken, and fruit or plant parts were collected, photographed and preserved for identification.

Where identification of plant species was not possible in the field, samples and photographs were preserved and identified by professional botanists from the Herbarium at the Universidad Nacional de la Amazonía Peruana (UNAP), Iquitos. Further identifications were made from photographs and descriptions by C. Vriesendorp and R. Foster of the Chicago Field Museum, and others.

3.8.2 Hardness categories

Each fruit eaten was given a subjective score for the hardness and puncture resistance of the fruit, which took into account the thickness of the wall of the fruit. In effect this was a measure of the difficulty of opening the fruit using the fingers or a knife. These categories ranged from fruits with no physical protection to those requiring a knife to open, and used similar criteria to Boubli (1999). Five categories were defined rather than Boubli's three; further subdividing the harder fruits. Hardness was measured at the stage at which the fruit was eaten by the uakaris.

Hardness categories:

1. Soft; fruits as soft as grapes, crushable with the fingers.
2. Medium; fruits with husks comparable to those of avocados.
3. Medium-hard; fruits with tougher skins requiring moderate pressure with a knife to open.
4. Hard; requiring heavy pressure with a knife to open.
5. Very hard; requiring heavy 'hammer action' pressure with a large knife to open.

3.9 Counting monkeys

There are a number of difficulties in determining primate group sizes in dense forest, and with large widely spread groups of uakari monkeys these problems are exacerbated (Defler 1999). For many of the 'instantaneous' scan samples few individuals were visible and the monkeys did not call. To avoid underestimating the size of groups, and overestimating the frequency of fission-fusion behaviour, estimates of group sizes were taken from repeat counts and calls heard throughout the 10-minute period preceding the scan. If necessary, estimates were taken from previous scans, and exact counts of groups taken earlier in the observation period (if the group was known not to have split or fused with other groups). These methods approximate the recommendations made by Chapman *et al.* (1993).

The size of large groups of uakari monkeys was often estimated using calls and partial counts. While collecting other ecological data it was not practical to get ahead of a foraging group repeatedly to count the groups, since they could be spread over several hectares.

3.10 Group composition

When an entire group, or large part of a group, passed through the same part of the canopy, it was sometimes possible to obtain an exact count. Where possible the age-sex class of every individual was recorded in the order in which they passed.

3.11 Nearest neighbour distances

During scan sampling, one 'focal individual' was randomly selected for each scan. The age-sex class of this individual was recorded, along with the age-sex classes of the nearest neighbour, if the nearest neighbour could be seen clearly. Additionally, if the age-sex class of other nearest neighbours within 10m of the focal individual could be determined, these were also recorded in the order of closeness to the focal individual. When it was clear that the focal individual had no neighbours closer than 30m, this was recorded.

3.12 Uakari calls

Calls were recorded using a digital recorder and directional microphone. Several samples of each type of vocalization were collected. When individuals were seen calling, the age-sex class and mode of behaviour were recorded *ad libitum*

(Altmann 1974). During August 2003, a research assistant recorded the frequency of each type of call during one minute at the start of each scan sample.

3.13 Informal interviews

Informal interviews were conducted with people living on the Yavarí and Yavarí-Mirín Rivers whenever opportunity arose. Many people were keen to talk about red uakari monkeys when they heard that researchers were interested in this species. Interviews were not structured, but focused on determining the distribution of the species on the rivers. In the communities of Esperanza and Carolina on the Yavarí-Mirín River, subjects included hunting practices and game preferences, as well as anecdotal accounts on the biology of uakaris.

3.14 Analysis of the data

A variety of statistical tests were used to determine the significance of results. Some statistical methods were only used in one Chapter, and are described in the Chapter they are relevant to. Other tests were common to various Chapters. Relationships between variables were tested using Pearson correlations. The chi-square test was used to analyse variation of observed frequencies from expected frequencies in count data. Where counts were obtained with unequal sample sizes, Medians were compared with the Mann-Whitney U-test. Where more than two samples were compared, ANOVA was used to compare means. The data were normalized where necessary, using arcsinh transformation when zeros were observed in count data. Where the means of groups of samples differed, the Tukey test was used to determine the significantly different means within the group.

Chapter 4

Vegetation and Habitats at Lago Preto

4.1 Introduction

The flora on the Yavarí is poorly known. Gentry, Revilla, Prance and Lleras made collections on the Lower Yavarí in the 1970s and Zapater Carlín made collections on the lower Yavarí-Mirín (noted in Pitmen *at al.* 2003). Salovaara (2005) made a survey of ferns at sites along the Yavarí-Mirín. Pitman *et al.* (2003) conducted the most recent and detailed work in the region, along the upper Yavarí River between the mouth of the Gálvez River and Lago Preto near the mouth of the Yavarí-Mirín. This work was conducted during a three-week 'Rapid Biological Inventory' at four sites on a 125km stretch of the upper Yavarí, using a range of techniques to characterise the flora in a number of forest types. Pitman *et al.* (2003) suggest that the upland vegetation on the Yavarí is compositionally and ecologically similar to the well-studied forests around Iquitos, but they noted that that they did not observe 'white-sand forests' during the inventories. Pitman *et al.* (2003) recorded around 1675 plant species during the expedition, which they estimate represents around half the flora along the upper Yavarí. This makes the Yavarí one of the more diverse sites within an already particularly diverse region (Vásquez-Martínez and Phillips 2000). One site inventoried by Pitman *et al.* (2003) proved to have one of the highest recorded tree diversities in one hectare of tropical forest. The diversity of woody plants in the understorey was also particularly high. Pitman *et al.* (2003) described family and genus level composition on the Yavarí as typical for Loreto, but identified families Sapotaceae, Myristicaceae and Lecythidaceae as especially diverse and abundant in their upland plots, accounting for 27% of all trees.

The geology of the sites surveyed by Pitman *et al.* (2003) ranged from steep hills on the Iquitos arch, where there were less fertile soils, to lower areas with more fertile soils. Pitman *et al.* (2003) noted a marked difference between *terra firme* forest on poor soils and on rich soils, but not between flooded forests at different sites. The soil changes were indicated by the frequencies of some palm species. *Oenocarpus bataua* and *Astrocaryum chambira* were more frequent on poorer soils and *Iriartea deltoidea* and *Euterpe precatoria* were more frequent on richer soils. Common trees throughout their four sites, regardless of soil type, were the palm *Astrocaryum murumuru* (Aracaceae), natural rubber *Hevea* sp. (Euphorbiaceae), and the trees *Senefeldera inclinata* (Euphorbiaceae), *Iryanthera macrophylla, Iryanthera juruensis, Virola pavonis* and *Osteophloeum platyspermum* (all Myristicaceae).

Plant composition at Pitman *et al.'s* (2003) poorer-soil upland forest at Quebrada Curacinha varied on a small spatial scale. Nearly 15% of the trees were

Myristicaceae, and half the trees in their one-hectare sample were from the families Myristicaceae, Sapotaceae, Moraceae, Euphorbiaceae, Lecythidaceae and Fabaceae. The commonest tree species were *Senefeldera inclinata* (Euphorbiaceae), *Rinorea racemosa* (Violaceae), *Oenocarpus bataua* (Aracaceae), *Ecclinusa* cf. *laneolata* (Sapotaceae), *Iryanthera macrophylla*, *Virola pavonis* and *Iryanthera tricornis* (all Myristicaceae). The understory in these forests was relatively species poor. Common understory species included a grass *Pariana*, a fern *Adiantum*, a treelet *Mouriri grandiflora* and several shrubs in the genus *Guarea*. Pitman *et al.*'s (2003) richer-soil upland forests at Quebrada Buenavista and Quebrada Limera were dominated by the same families as the poorer-soil site, but the families Meliaceae, Annonaceae and Aracaceae were much commoner. Myristicaceae was still the most abundant family, but the genus *Otoba* was common, in addition to *Iryanthera* and *Virola*. *Inga, Guarea* and *Trichilia* were also abundant genera. The commonest tree species were *Astrocaryum murumuru* (Aracaceae), *Iriartea deltoidea* (Aracaceae), *Anaueria* cf. *brasiliensis* (Lauraceae), *Nealchornea japurensis* (Euphorbiaceae), *Otoba parvifolia* (Myristicaceae), *Otoba glycycarpa* (Myristicaceae), *Pseudolmedia laevis* (Moraceae), *Eschweilera* cf. *coriacea* (Lecythidaceae), *Iryanthera laevis* (Myristicaceae) and *Iryanthera juruensis* (Myristicaceae). The understorey in these plots was more diverse, particularly in the families Marantaceae and Rubiaceae. The ferns *Didymochlaena truncatula* and *Adiantum pulverulentum* were common. Around a quarter of plant species and a third of tree species were recorded in both the poorer-soil and richer-soil plots.

Pitman *et al.*'s (2003) fourth site, Lago Preto was not surveyed in as much detail as the other sites. Lago Preto is the study site for this project, and Pitman *et al.* (2003) describe a special type of *terra firme* habitat on old alluvial terraces found there. These terraces are characterised by clay soils with poor drainage and deep ravines, and occur patchily on the Yavarí. The canopy composition observed by Pitman *et al.* (2003) at Lago Preto was similar to that of the poorer-soil site at Quebrada Curinha, but only 0.2 hectares of forest were inventoried. Large stands of the palm *Lepidocaryum tenue* grow in the understorey of the terraces, along with the small palms *Iriartella setigera, Bactris killipii* and *Itaya amicorum* (Pitman *et al.* 2003). More complete inventories of the *terra firme* at Lago Preto, incorporating those started by Pitman *et al.* (2003), are presented in this Chapter.

Pitman *et al.* (2003) did not inventory the trees in the periodically-flooded forests of the Yavarí, but characterised the habitat qualitatively. On the Yavarí itself successional forests were not as obvious as on other rivers in the Peruvian Amazon, perhaps because the Yavarí meanders more slowly. Close to the waterline, however, there is a fairly regular sequence of vegetation, starting with low shrubby vegetation consisting of *Alchornea castanaefolia, Adenaria floribunda, Tabernaemontana siphilitica, Annona hypoglauca* and *Marginataria nobilis*. Behind this Pitman *et al.* (2003) identified stands of the pioneering species *Cecropia latiloba, Triplaris weigeltiana* and *Acacuia* sp. The first large tree in the successional sequence is *Maquira coriacea* after which the vegetation is relatively stable and dominated by *Virola surinamensis*.

Pitman *et al.* (2003) distinguished two types of seasonally-inundated riparian white-water forest or *várzea*. The first type occurs on the Yavarí itself, and can be flooded for long periods during the high water season. The second type occurs on the banks of tributaries draining *terra firme* forests. The forests along tributaries were dominated largely by the palms *Astrocaryum murumuru*, *Iriartea deltoidea* and *Socracea exorrhiza* alongside typical floodplain species like *Spondias* cf. *mombin* and *Ficus insipida*. As is typical of floodplain forests, the composition of the *várzea* forests on the banks of the Yavarí varied continuously with relatively small changes in elevation corresponding to different lengths of time spent underwater. Obvious components identified by Pitman *et al.* (2003) from the river include the palms *Socratea exorrhiza* and *Euterpe precatoria* and the trees *Virola surinamensis* and *Pseudobombax munguba*. In higher areas of *várzea*, the common trees most obvious to Pitman *et al.* (2003) were *Vochysia* sp., *Sterculia* sp., *Socratea exorrhiza, Astrocaryum murumuru*, *Virola surinamensis* and *Hevea* cf. *brasiliensis*.

Swamp forests on the Yavarí, generally referred to as *aguajal*, show clearly on satellite images of the area. They are characterised by the almost complete or partial dominance of the aguaje palm *Mauritia flexuosa*. Purer stands of the palm show up on satellite images as denser blocks of colour than more mixed swamp forests. *Aguajal* palm-swamp forest occurs in two forms; large seasonally-inundated and permanently wet patches up to 200ha in area called floodplain *aguajal*, and in smaller inland patches, often along small streams or in depressions called upland *aguajal*. Both types are permanently wet, but upland *aguajal* are not inundated with floodwater, and are usually bordered on all sides by *terra firme* forest. Floodplain *aguajal* are generally bordered by *várzea* on at least one side. Pitman *et al.* (2003) inventoried trees in 0.5 hectares of a mixed floodplain *aguajal* in which *Mauritia flexuosa* made up only 8% of the trees. They found a relatively low diversity (52 species) typical of this type of habitat. *Symphonia globulifera* was the dominant species followed by *Euterpe precatoria, Mauritia flexuosa, Virola surinamensis, Attalea butyraceae* and *Eriotheca macrophylla*.

Pitman *et al.* (2003) also looked at the phenology and seedling biology at their sites. Since all observations were made in March 2003, this work provided a qualitative snapshot of patterns of fruiting, flowering and seedling germination. Few species were found flowering in any forested habitat during the inventory. Pitman *et al.* (2003) reported higher fruit and seedling production in flooded habitats than in *terra firme* sites at the time of the study. In areas of flooded forest, where water had receded, large carpets of seedlings were found from the species *Simarouba amara, Virola surinamensis, Bauhinia guianensis, Carapa guianensis* and *Tapura* sp.

Habitats at Lago Preto are broadly similar to those along much of the Yavarí, but the habitats are not uniform, and need to be characterised individually for any specific area. Because habitats intergrade, and are difficult to classify according to Encarnación (1993), habitats at Lago Preto were classified into easily distinguishable categories. The area has three main, clearly-distinct habitat types. There are *terra firme* forests, *várzea* forests and *aguajal* forests that can be divided up into upland and floodplain *aguajal* swamps.

Terra firme forest occurs inland from the river and the *várzea* forest, consisting in part of old alluvial terraces with clay soils, poor in nutrients. This habitat is very diverse and varies continuously. No distinction was made between types of *terra firme* forest. Instead specific areas were described in detail where necessary.

The *várzea* forest at Lago Preto is of the kind that floods for extended periods. It extends 1-5km inland from the Yavarí River on the southern border of the concession, and is generally flooded between January and June. This habitat can be divided further into *restingas*, lower forested *várzea* and *chavascal*. *Restingas* are only flooded at the peak of the high-water season, while lower forested *várzea* is flooded for longer periods. *Chavascal* is flooded for long periods and has an open canopy and a thick scrubby understorey. There are no clear boundaries between these habitat types.

4.2 Methods

4.2.1 Water levels in the *várzea* forest during the study period

Water levels were recorded during the study in two ways. Each day in which monkeys were followed, the water level on the *restingas* and lower forested *várzea* was recorded as dry, flooded or partially flooded. Additionally, between March 2004 and February 2005 water levels were recorded every 10m on all *várzea* transects used for monitoring tree fruiting. To reduce the effects of uneven ground, the depth of the water was taken at various points using a measured pole, and a mean was taken.

4.2.2 Tree species composition

To determine the trees species composition of the habitats at Lago Preto, and to assess tree diversity, vegetation transects were set up on randomly-selected trails in each of the main habitats at Lago Preto (Figure 2.9). Because the same transects were used to collect data on fruiting cycles, transects were preferred to plots for easier management of data collection. Transects were 5m wide except in the case of transect 'A' which was surveyed as part of the rapid biological inventory Pitman *et al.* (2003) and was 20m wide. Because of restrictions on the time available to sample tree species composition and fruiting cycles, transect lengths, and therefore areas sampled, were determined by the rate that new species were encountered. Sampling continued until the rate of encountering new species slowed, or in the case of *terra firme* until further sampling was impossible (Figures 4.2, 4.3, 4.4, and 4.5).

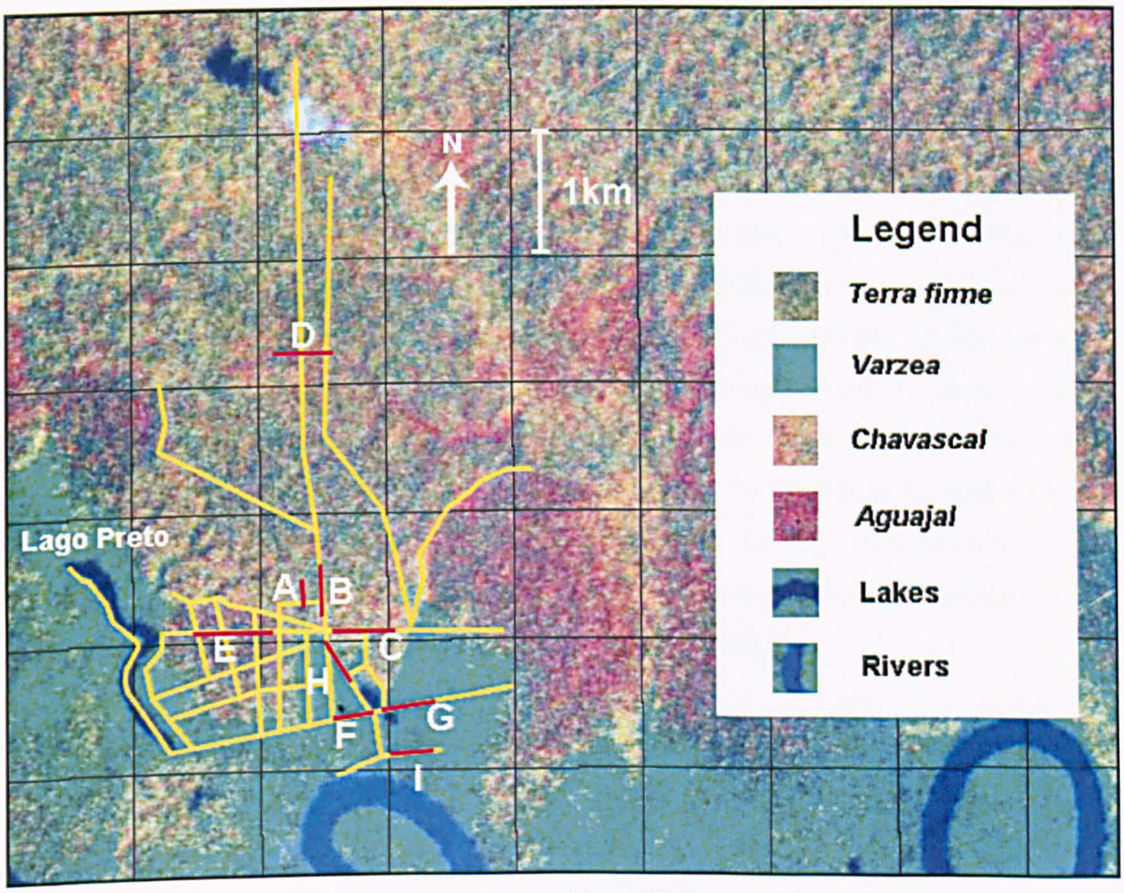

Figure 4.1 Positions of botanical transects and the trail system at Lago Preto (transects are marked in red).

- Transects A (100m x 20m), B (562m x 5m) and C (565m x 5m) were in upland '*terra firme*' forest.
- Transect D (489m x 5m) intended to sample *aguajal* in high forest. This habitat is patchy, often occurring in strips following small streams in low areas. Transect D therefore passes in and out of the *aguajal* through patches of high forest. Because the borders between the two habitats were very distinct, usually involving a step down into the swampy ground of the *aguajal*, and because the *terra firme* forest in these areas did not appear to differ greatly from other areas of *terra firme* forest, sections of transect D in high forest were analysed with the other *terra firme* transect data. Trees in *aguajal* on transect D were analysed separately. 222m of this transect were in *aguajal* and 267m were in *terra firme*.
- Transect E (808m x 5m) was in a large floodplain *aguajal*.
- Transects F (672m x 5m), G (299m x 5m) and H (300m x 5m) were in lower forested *várzea* ranging in depth from 0.7 to 3.5m at peak high water. Transect I (256m x 5m) was in *várzea* and included a length of higher restinga which in part formed the bank of the Yavarí and the bank of the stream which drains a small lake (Lago Huapo). The water depth on this transect ranged from 0.2 to 1.8m at peak high water.

Every tree within the transects with a diameter at breast height (DBH) above 10cm was tagged. Following Ayres (1986), every vine with a DBH above 7cm was also tagged on transects B to I. This is a relatively small sample of the vines at Lago Preto, but it was important to sample these fruiting components of the canopy, particularly as part of the tree fruiting observations. In total, 1600 trees and vines were tagged and measured along the transects, of which 1493 were trees or palms and 107 were vines. Trees on transect A were identified by R. García in April 2003 as part of a 'Rapid Biological Inventory' Pitman *et al.* (2003). Surviving trees on transects B to I were identified by M. Rios from the Universidad Nacional de la Amazonía Peruana (UNAP), at the end of the February 2005.

For each tagged tree and vine, the following were recorded:

- Diameter at breast height.
- The common name as given by a local guide.
- The basal area (estimated).

- The average diameter and the height of the canopy.
- Association with vines in the canopy.

Because species richness, measured as the total number of species present, is dependant on the sample size, the species richness was compared between habitats using Margalef's diversity index and Menhinick's index (Magurran 1988). Margalef's index (D1) was calculated as follows: $D_1 = (S - 1)/\ln(n)$, where S is the number of species and n is the total number of trees. The minimum value of Margalef's index is zero (when the number of species is 1), and the maximum value is $(n - 1)/[\ln(n)]$ (when each species is represented by one individual). Menhinick's index (D2) was calculated as follows: $D_2 = S/\sqrt{n}$. Menhinick's index approaches zero when there is a high number of individuals but few species and, like Margalef's index, approaches a maximum value when the number of species is equal to the number of individuals. D_1 and D_2 are sensitive to variations in sample size, so data were normalized by randomly removing individuals from each habitat sample until all sample sizes were equal to 372; the sample size for the aguajal habitat.

The Sorensen and Czekanowski indices of diversity were used to measure the similarity between habitats. The Sorensen index is an index of similarity that measures similarity based on species presence-absence. This measure does not, therefore, take species abundance into account. The Sorensen index is calculated by: $S=2C/(a+b)$, where C is the number of species shared by both sites, a is the number of species in site A and b is the number of species in site B. This measure gives a result between 0 (no similarity) and 1 (total similarity).

The Czekanowski similarity index calculates similarity according to the abundances of the species in the community. It is calculated by: $2w/(a+b)$, where w is the sum of minimum abundances of all the species which occur in both samples, a is the sum of species abundance in sample A and b is the sum of species abundance in sample B. This measure also gives a result between 0 (no similarity) and 1 (total similarity) (Magurran 1988). Habitats that are very different according to the Sorensen index sometimes share a few abundant species that may be particularly important in determining the structure of a habitat or that might be important for animal species. Where habitats share important abundant species, and are therefore similar in the way they are used by animals, but are different in the number of species they share, the Czekanowski similarity index deems them more similar than does the Sorensen index. The Czekanowski index was therefore used in conjunction with the Sorensen index.

4.2.3 Plant productivity

In order to make a quantitative assessment of fruit availability in the four habitats, all tagged trees and vines (including unidentified individuals) on transects A to G and transect I were surveyed as close to the third week in the month as possible. Transect H was not used for fruiting observations. Due to time constraints imposed by other data collection, fruiting observations were only made for one complete year between March 2004 and February 2005, and the majority of these observations were made by a research assistant.

Each tree or vine within a transect was examined with binoculars and a small telescope. Following Ayres (1986), the presence or absence of the following was recorded: Immature flowers, mature flowers, immature fruit (up to near full size), unripe fruit (near full size to nearly ripe) and ripe fruit. For unripe and ripe fruit, the number or density of the fruits was estimated by counting the number of fruits in $1m^3$ and multiplying by the area of the canopy, or by counting the fruits in the entire canopy (so far as the view of the canopy allowed). For palms, the number and size of racemes (of flowers or fruits) were recorded. Trees or vines which died during the course of the study where not included in the data set. Many flowers and fruits are difficult to spot in the canopy, particularly immature fruits which are often small or cryptically coloured. A telescope on a tripod was used to scan several sections of each canopy in detail to minimise error, but many of the vines included in the sample were almost entirely hidden in the canopy. Accuracy of fruit observations may have varied between different habitats due to changes in canopy heights and densities. The canopy in *terra firme* was typically higher than in other habitats, while *aguajal* habitats had a more open canopy relatively free from vines.

In $8970m^2$ of *terra firme*, 589 trees and vines were sampled. In $6135m^2$ of *várzea,* 387 trees and vines were sampled. In $1110m^2$ of upland *aguajal*, 98 trees and vines were sampled. In $4040m^2$ of floodplain *aguajal,* 286 trees and vines were sampled (of which 83 were palms), giving a total of 386 trees and vines in $5150\ m^2$ of *aguajal* habitat. Fruit traps, as used by Foster (1982) and Terborgh (1983) were not used in this study, partly because of the difficulty of using this method in swamps and flooded forests, but mainly because previous studies (e.g. Aquino 1999; Bowler 2003; Ayres 1986) have shown that unripe fruit is particularly important for the red uakari monkey, and fruit traps do not record unripe fruit. Productivity was estimated following Ayres (1986), in which the number of trees bearing fruit, expressed as a percentage of sampled trees, or as the number of trees bearing fruit per hectare, is used as a measure of productivity. Monthly estimates of productivity in each habitat were obtained from each month's transect, and an estimate of productivity for the year was obtained for each habitat from the mean of the monthly estimates.

4.3 Results

4.3.1 Water levels in the *várzea* forest during the study period

The water reached its highest level during the study in April 2004, when the depth of the water on the *várzea* transects ranged from 3.5m on the deepest parts of transects 'F' and 'G', to just 0.2m on the highest part of transect 'I' within restinga habitat. Water levels fluctuated on a daily basis depending on rainfall, often rising or falling very quickly. Between the 14th and 21st June 2003, for example, in a period not recorded in scheduled data collection, the water fell 2.1m at an average rate of 30cm/day. In 2004 the water level did not fall rapidly and fluctuated at a level that left the *várzea* partially flooded for a longer period (Figure 4.1).

Table 4.1 Flooded and dry periods in seasonally flooded várzea at Lago Preto.

Month	Coverage of floodwater in the *várzea*	
	Lower forested *várzea*	*Restinga*
Apr-03	flooded	dry
May-03	flooded	dry
Jun-03	partially flooded	dry
Jul-03	dry	dry
Aug-03	dry	dry
Sep-03	dry	dry
Oct-03	dry	dry
Nov-03	partially flooded	dry
Dec-03	flooded	dry
Jan-04	flooded	dry
Feb-04	flooded	dry
Mar-04	flooded	partially flooded
Apr-04	flooded	flooded
May-04	partially flooded	dry
Jun-04	partially flooded	dry
Jul-04	dry	dry
Aug-04	dry	dry
Sep-04	dry	dry
Oct-04	dry	dry
Nov-04	flooded	dry
Dec-04	partially flooded	dry
Jan-05	partially flooded	dry
Feb-05	partially flooded	dry
Mar-05	flooded	dry

4.3.2 Tree mortality

Twenty-nine tagged trees (including palms) died between being tagged at the start of the project and being identified at the end of the project. This included two large tree-falls in which larger falling trees killed a number of other trees on the transects. Data from these trees were not included in the analyses; 7 tagged vines also died during the study period, most of them because they were attached to falling trees.

4.3.3 Tree diversity

Of the 1464 surviving trees, 1372 were identified to species or morphospecies level. In total, 342 species or morphospecies were identified on the tree transects at Lago Preto (Appendix 1). The sample size for upland *aguajal* was low, because only a small area of this patchy habitat was sampled on the transects, but the rate of encountering new species in upland *aguajal* shows that few new species were encountered after 70 individuals were sampled (Figure 4.2). This suggests that the majority of species in the upland *aguajal* had been recorded. Similarly the curve for the rate of encountering new species in floodplain *aguajal* levels out after about 140 individuals have been sampled (Figure 4.3). The curve for the rate of encountering new species in *várzea* levels out at around 475 individuals. This suggests that the majority of species in this habitat have been sampled (Figure 4.4). The curve for the rate of encountering new species in *terra firme* does not level out, suggesting that the sample size of 505 individuals has not recorded all species in this habitat even though the largest area was sampled for this habitat. This indicates a higher diversity than the 199 species recorded (Figure 4.5).

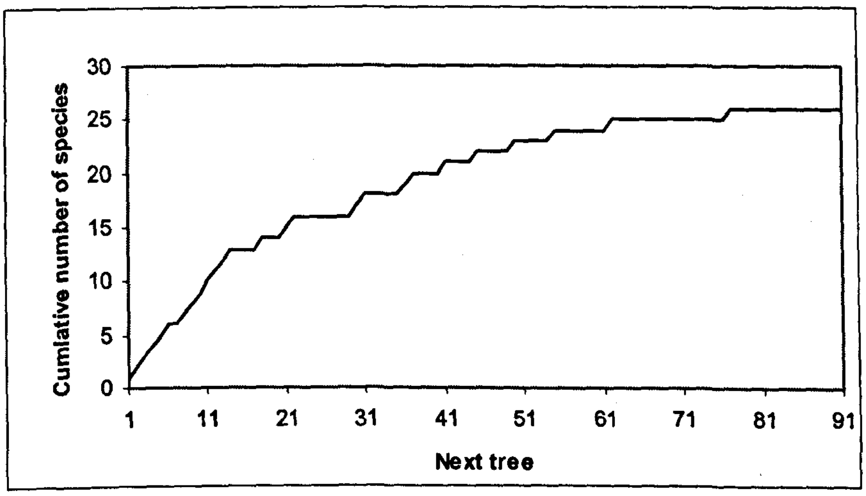

Figure 4.2 Rate of recording new species in upland *aguajal*.

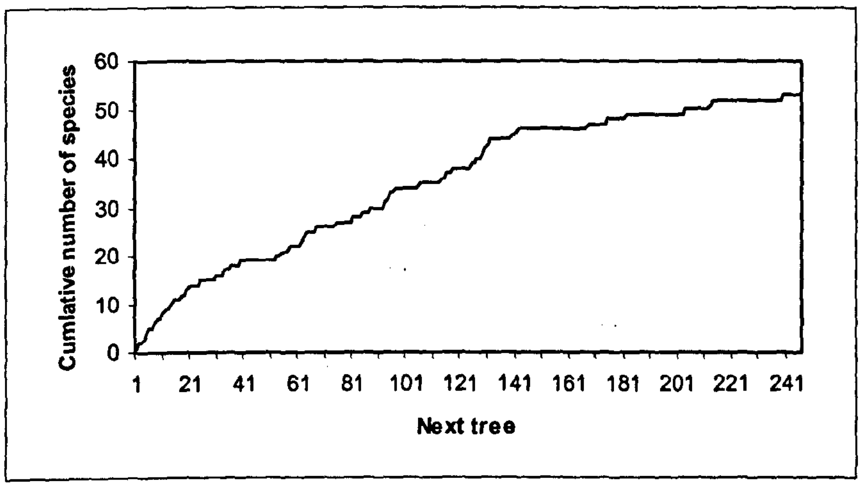

Figure 4.3 Rate of recording new species in floodplain *aguajal*.

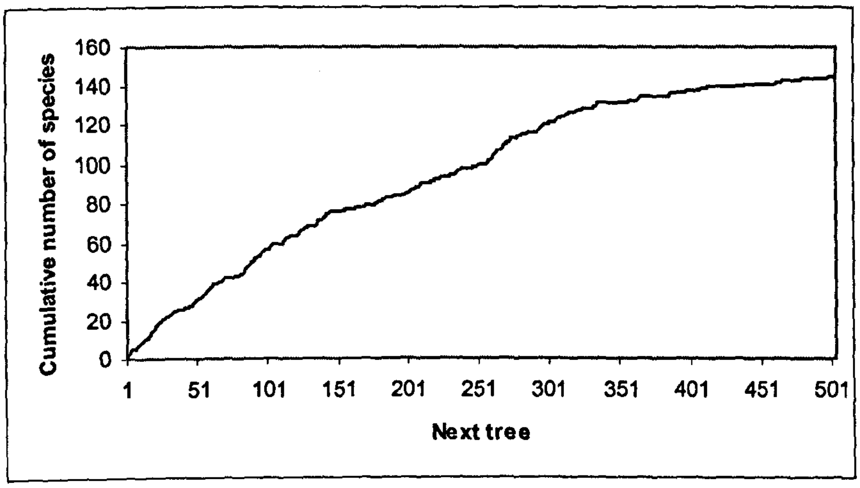

Figure 4.4 Rate of recording new species in *várzea*.

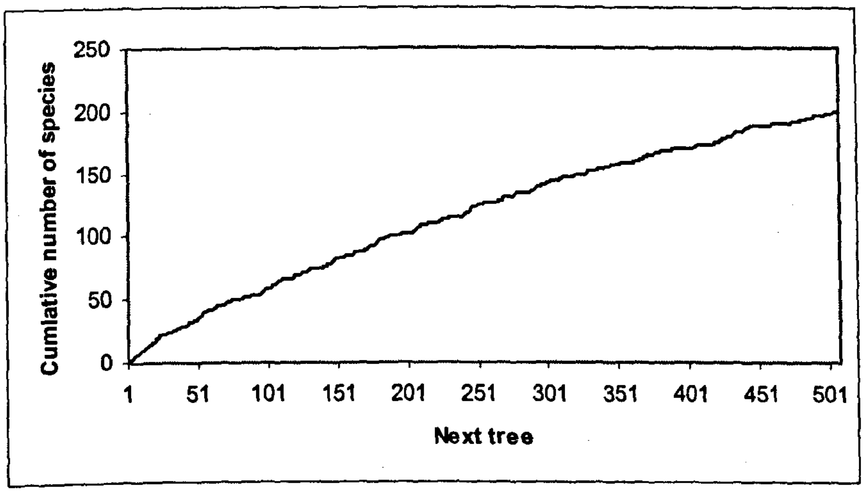

Figure 4.5 Rate of recording new species in *terra firme*.

The most species rich habitat was *terra* firme with 199 species, followed by 142 species in *várzea*, 60 in floodplain *aguajal*, and 25 in upland *aguajal*. The combined *aguajal* habitats had 78 species. Margalef's diversity index and Menhinick's indices gave similar results; *terra firme* is the most diverse habitat, followed by *várzea*, floodplain *aguajal*, and then upland *aguajal* (Table 4.2).

Table 4.2 Diversity of forest habitats at Lago Preto.

Habitat	Area sampled (m^2)	Number of individual trees and vines sampled	Number of individuals identified to species or morphospecies (n)	Number of species (S) (rank)	Number of species in a random sample of 372 individuals (rank)	Margalef's diversity index $D1=(S-1)/\ln N$ (rank)	Menhinick's index $D2=S/\sqrt{N}$ (rank)
terra firme	8970	558	505	199 (1)	169 (1)	28.4 (1)	8.8 (1)
várzea	7635	528	495	142 (2)	128 (2)	21.5 (2)	6.6 (2)
aguajal (combined)	5150	378	372	78 (3)	78 (3)	13.0 (3)	4.0 (3)
upland *aguajal*	1110	92	90	25	n/a	n/a	n/a
floodplain *aguajal*	4040	286	282	60	n/a	n/a	n/a

4.3.4 Tree species composition

4.3.4.1 *Terra firme*

Of the 558 trees sampled in *terra firme* forest, 46 families were identified. The commonest families were Myristicaceae (13.3%), Lecythidaceae (10.2%), Fabaceae (9.5%) and Chrysobalanaceae (8.1%) (Table 4.3). One-hundred and eight genera were identified, of which *Eschweilera* (9.9%), *Licania* (6.5%), *Virola* (6.3%) and *Iryanthera* (5.0%) were the commonest (Table 4.4). The commonest species were *Eschweilera coriacea, Licania heteromorpha, Eschweilera tessmanni, Hevea guianensis, Iryanthera tricornis* and *Oenocarpus bataua.*

Table 4.3 Commonest families in *terra firme* at Lago Preto.

Family	*Terra firme*	
	Freq	%
MYRISTICACEAE	74	13.3
LECYTHIDACEAE	57	10.2
FABACEAE	53	9.5
CHRYSOBALANACEAE	45	8.1
EUPHORBIACEAE	40	7.2
MORACEAE	30	5.4
SAPOTACEAE	29	5.2
CECROPIACEAE	20	3.6
ARECACEAE	19	3.4
BURSERACEAE	18	3.2

Table 4.4 Commonest genera in *terra firme* at Lago Preto.

Family	Genus	*Terra firme*	
		Freq	%
LECYTHIDACEAE	*Eschweilera*	55	9.9
CHRYSOBALANACEAE	*Licania*	36	6.5
MYRISTICACEAE	*Virola*	35	6.3
MYRISTICACEAE	*Iryanthera*	28	5.0
CECROPIACEAE	*Pourouma*	18	3.2
SAPOTACEAE	*Pouteria*	18	3.2
BURSERACEAE	*Protium*	14	2.5
EUPHORBIACEAE	*Hevea*	13	2.3
FABACEAE	*Inga*	13	2.3
ELAEOCARPACEAE	*Sloanea*	12	2.2
ARECACEAE	*Oenocarpus*	11	2.0
MELIACEAE	*Trichilia*	11	2.0
MORACEAE	*Naucleopsis*	11	2.0
FABACEAE	*Tachigali*	10	1.8
FABACEAE	*Marmaroxylon*	8	1.4
MORACEAE	*Helicostylis*	8	1.4
MYRISTICACEAE	*Osteophloeum*	8	1.4
EUPHORBIACEAE	*Hyeronima*	7	1.3
FABACEAE	*Parkia*	6	1.1
SAPOTACEAE	*Micropholis*	6	1.1

4.3.4.2 *Várzea*

Of the 528 trees sampled in *várzea* forest, 38 families were identified. The commonest families were Lecythidaceae (11.0%), Fabaceae (10.2%), Annonaceae (9.5%) and Myristicaceae (8.7%) (Table 4.5). 82 genera were identified, of which *Eschweilera* (8.9%), *Virola* (8.0%), *Pouteria* (5.5%) and *Licania* (4.7%) were the commonest (Table 4.6). The commonest species were *Eschweilera albiflora, Virola* cf. *peruviana, Micranda siphonoides, Pouteria gomphiifolia, Pseudoxandra polypheba* and *Tapura acreana.*

Table 4.5 Commonest families in *várzea* at Lago Preto.

Family	*Várzea*	
	freq	%
LECYTHIDACEAE	58	11.0
FABACEAE	54	10.2
ANNONACEAE	50	9.5
MYRISTICACEAE	46	8.7
CHRYSOBALANACEAE	37	7.0
MYRTACEAE	34	6.4
EUPHORBIACEAE	33	6.3
SAPOTACEAE	32	6.1
MORACEAE	30	5.7
CLUSIACEAE	19	3.6

Table 4.6 Commonest genera in *várzea* at Lago Preto.

Family	Genus	*Várzea*	
		Freq	%
LECYTHIDACEAE	*Eschweilera*	47	8.9
MYRISTICACEAE	*Virola*	42	8.0
SAPOTACEAE	*Pouteria*	29	5.5
MYRTACEAE	Unidentified Myrtaceae	28	5.3
CHRYSOBALANACEAE	*Licania*	25	4.7
MORACEAE	*Brosimum*	15	2.8
EUPHORBIACEAE	*Micranda*	14	2.7
ANNONACEAE	*Pseudoxandra*	13	2.5
DICHAPETALACEAE	*Tapura*	13	2.5
MORACEAE	*Pseudolmedia*	12	2.3
CLUSIACEAE	*Caraipa*	11	2.1
APOCYNACEAE	*Aspidosperma*	10	1.9
ANNONACEAE	*Duguetia*	9	1.7
ANNONACEAE	*Guatteria*	9	1.7
FABACEAE	*Macrolobium*	9	1.7
FABACEAE	*Zygia*	9	1.7
ANACARDIACEAE	*Tapirira*	8	1.5
ANNONACEAE	*Anonna*	7	1.3
CHRYSOBALANACEAE	*Hirtella*	7	1.3
FABACEAE	*Campsiandra*	7	1.3
FABACEAE	*Inga*	7	1.3
LECYTHIDACEAE	*Couratari*	7	1.3

4.3.4.3 *Aguajal* palm-swamps

In the *aquajal* palm-swamps, 378 trees were sampled; 92 in upland *aguajal* and 286 in floodplain *aguajal*. The same four families, Arecaceae, Clusiaceae, Myristicaceae and Fabaceae, were the commonest in both upland and floodplain *aguajal* palm-swamps (Tables 4.7 and 4.8). The palms (Arecaceae) make up 31.5% of the trees sampled in both these habitats. The next commonest families in the upland *aguajal* transects were Clusiaceae (20.7%), Myristicaceae (12.0%) and Fabaceae (9.8%). In the floodplain *aguajal* Fabaceae make up a higher proportion (18.2%), while Clusiaceae and Myristicaceae each make up 9.4% of the trees.

Upland and floodplain *aguajal* were both rich in *Mauritia, Euterpe* and *Virola* (tables 4.9 and 4.10), but in the upland *aguajal* sample *Caraipa* (Clusiaceae) was the commonest genus (19%). This genus did not occur in the floodplain sample. Similarly *Symphonia* was common in the floodplain *aguajal* sample (4.5%), but did not occur in the upland sample.

Table 4.7 Commonest families in upland *aguajal* at Lago Preto.

Family	Upland *aguajal*	
	Freq	%
ARECACEAE	29	31.5
CLUSIACEAE	19	20.7
MYRISTICACEAE	11	12.0
FABACEAE	9	9.8
EUPHORBIACEAE	6	6.5
SAPOTACEAE	6	6.5
APOCYNACEAE	2	2.2
BOMBACACEAE	2	2.2
STERCULIACEAE	2	2.2
ANNONACEAE	1	1.1

Table 4.8 Commonest families in floodplain *aguajal* at Lago Preto.

Family	Floodplain *aguajal*	
	Freq	%
ARECACEAE	90	31.5
FABACEAE	52	18.2
CLUSIACEAE	27	9.4
MYRISTICACEAE	27	9.4
ANNONACEAE	18	6.3
EUPHORBIACEAE	16	5.6
COMBRETACEAE	11	3.8
LECYTHIDACEAE	9	3.1
APOCYNACEAE	7	2.4
SAPOTACEAE	4	1.4

Table 4.9 Commonest genera in upland *aguajal* at Lago Preto.

Family	Genus	Upland *aguajal*	
		Freq	%
CLUSIACEAE	*Caraipa*	18	19.6
ARECACEAE	*Mauritia*	15	16.3
ARECACEAE	*Euterpe*	10	10.9
MYRISTICACEAE	*Virola*	6	6.5
SAPOTACEAE	*Ecclinusa*	6	6.5
FABACEAE	*Macrolobium*	5	5.4
MYRISTICACEAE	*Iryanthera*	5	5.4
ARECACEAE	*Oenocarpus*	4	4.3
EUPHORBIACEAE	*Hevea*	3	3.3
APOCYNACEAE	*Paranchornia*	2	2.2
BOMBACACEAE	*Eriotheca*	2	2.2
EUPHORBIACEAE	*Amanoa*	2	2.2
FABACEAE	*Inga*	2	2.2
STERCULIACEAE	*Theobroma*	2	2.2
ANNONACEAE	*Xylopia*	1	1.1
CLUSIACEAE	*Tovomita*	1	1.1
EUPHORBIACEAE	*Richeria*	1	1.1
FABACEAE	*Parkia*	1	1.1
FABACEAE	*Swartzia*	1	1.1
MYRTACEAE	Unidentified Myrtaceae	1	1.1
OCHNACEAE	*Cespedesia*	1	1.1
VOCHYSIACEAE	*Qualea*	1	1.1

Table 4.10 Commonest genera in floodplain *aguajal* at Lago Preto.

Family	Genus	Floodplain *aguajal*	
		Freq	%
ARECACEAE	*Euterpe*	66	23.1
MYRISTICACEAE	*Virola*	27	9.4
ARECACEAE	*Mauritia*	23	8.0
CLUSIACEAE	*Symphonia*	13	4.5
EUPHORBIACEAE	*Micranda*	12	4.2
FABACEAE	*Macrolobium*	11	3.8
FABACEAE	*Vatairea*	11	3.8
FABACEAE	*Inga*	10	3.5
LECYTHIDACEAE	*Couratari*	8	2.8
CLUSIACEAE	*Calophyllum*	7	2.4
ANNONACEAE	*Malmea*	6	2.1
COMBRETACEAE	*Terminalia*	6	2.1
ANNONACEAE	*Bocageopsis*	5	1.7
CLUSIACEAE	*Tovomita*	5	1.7
COMBRETACEAE	*Buchenavia*	5	1.7
FABACEAE	*Crudia*	5	1.7
ANNONACEAE	*Guatteria*	4	1.4
APOCYNACEAE	*Malouetia*	4	1.4
FABACEAE	*Zygia*	4	1.4
APOCYNACEAE	*Aspidosperma*	3	1.0
BOMBACACEAE	*Pachira*	3	1.0
ELAEOCARPACEAE	*Sloanea*	3	1.0
FABACEAE	*Pterocarpus*	3	1.0
MORACEAE	*Ficus*	3	1.0
STERCULIACEAE	*Sterculia*	3	1.0

4.3.5 Similarity of habitats

4.3.5.1 Species shared between habitats

Around a quarter (28%) of the species in the upland *aguajal* sample also occurred in the floodplain sample, whereas 56% of the upland *aguajal* species also occurred in *terra firme* forests. Similarly floodplain *aguajal* shared far more species with *várzea* forests than with upland *aguajal* (Table 4.11). The Sorensen index also suggests that upland *aguajal* is more similar to *terra firme* forest than it is to floodplain forest, and that floodplain forest is more similar to *várzea* than it is to upland forest (Table 4.12). This measure does not take species abundances into account.

Table 4.11 Percentage of species in each habitat which also occur in each of the other habitats.

		habitat (a)			
		terra firme (199 spp.)	*várzea* (142 spp.)	upland *aguajal* (25 spp.)	floodplain *aguajal* (60 spp.)
Habitat (b)	*terra firme*	-	24 (16.9%)	14 (56.0%)	12 (20.0%)
	várzea	24 (12.1%)	-	5 (20.0%)	35 (58%)
	upland *aguajal*	14 (7.0%)	5 (3.5%)	-	7 (11.7%)
	floodplain *aguajal*	12 (6.0%)	35 (24.6%)	7 (28.0%)	-

Table 4.12 Sorensen index similarity of the four habitats at Lago Preto.

	várzea (142 spp.)	upland *aguajal* (25 spp.)	floodplain *aguajal* (60 spp.)
terra firme (199 spp.)	0.1408	0.2258	0.1509
várzea (142 spp.)	-	0.0599	0.3465
upland *aguajal* (25 spp.)	-	-	0.1647

4.3.5.2 Habitat similarity and abundance of species

When considering habitat similarity, abundance of species can be an important factor. In the study area, the upland and floodplain *aguajal* are dominated by the same common species, and more individual trees in these habitats are of species that occur in both habitats (Table 4.13). According to the Czekanowski index, upland *aguajal* is more similar to floodplain *aguajal* than it is to either *terra firme* forest or *várzea* forest, but floodplain *aguajal* is more similar to *várzea* than it is to upland *aguajal* (Table 4.14). Neither of the similarity indices takes into account the structure of the canopy or the fruiting phenology of these habitats, which may be relevant to the similarity of plant communities as habitats for forest animals. Although the Sorensen index shows that, in terms of shared species, upland *aguajal* is not most similar to floodplain *aguajal*, the Czekanowski index shows that the similarity between the two *aguajal* habitats is greater when the abundances of common species are taken into account. Since the commonest species in these habitats are the highly fecund and structurally distinct palms, the two *aguajal* habitats are similar in terms of their resource distribution and canopy structure. These palm species are most likely to influence the use of the habitats by uakari monkeys. For this reason the upland and floodplain *aguajal* habitats were considered together as '*aguajal*' for many parts of this thesis.

Table 4.13 Number (and %) of individuals in habitat (a) of species which also occur in habitat (b).

		habitat (a)			
		terra firme **(n=505)**	***várzea*** **(n=495)**	**upland *aguajal*** **(n=90)**	**floodplain *aguajal*** **(n=282)**
Habitat (b)	***terra firme***	-	83 (16.8%)	41 (45.6%)	101 (35.8%)
	várzea	64 (12.7%)	-	21 (23.3%)	195 (69.1%)
	upland *aguajal*	49 (9.7%)	21 (4.2%)	-	122 (43.3%)
	floodplain *aguajal*	36 (7.1%)	172 (34.7%)	39 (43.3%)	-

Table 4.14 Czekanowski index of similarity for the four habitats at Lago Preto.

	várzea **(n=495)**	**upland *aguajal*** **(n=90)**	**floodplain *aguajal*** **(n=282)**
terra firme **(n=505)**	0.0760	0.0840	0.0508
várzea **(n=495)**	-	0.0376	0.2239
upland *aguajal* **(n=90)**	-	-	0.1935

4.3.6 Vines

107 vines of DBH > 7cm were tagged on all transects. The majority of vines were not identified, but thirteen species were identified to species or genus (Table 4.15). In addition, 28.1% of trees in *terra firme*, 31.8% of trees in *várzea*, 21.5% of trees in upland *aguajal* and 22.6% of trees in floodplain *aguajal* were associated with vines that reached the canopy (of DBH > 2cm).

Table 4.15 Vine species identified at Lago Preto.

Family	Species	Habitat
ANNONACEAE	*Anonna hypoglauca*	*várzea*
CELASTRACEAE	*Salacia macrantha*	*várzea*
CELASTRACEAE	*Cheiloclinium hippocrateoides*	*terra firme*
CONVOLVULACEAE	*Maripa* sp. (a)	*terra firme*
DILLENIACEAE	*Doliocarpus dentatus*	*terra firme*
FABACEAE	*Bauhinia guianensis*	*várzea*
FABACEAE	*Tachigali macbridei*	*terra firme*
GNETACEAE	*Gnetun nodiflorum*	*várzea*
LOGANIACEAE	*Strychnos asperula*	*terra firme*
MENISPERMACEAE	*Anomospermum reticulatum*	*terra firme*
MENISPERMACEAE	*Anomospermum solimoesanum*	*terra firme*
RUBIACEAE	*Uncaria guianensis*	*várzea*
TRIGONIACEAE	*Trigonia* sp. (a)	*várzea*
VERBENACEAE	*Petrea bracteata*	*terra firme*

4.3.7 Annual productivity of habitats

Productivity (the mean number of trees fruiting/hectare/month) for the year was different between habitats (ANOVA $F_{3,44}$=19.557 $p<0.0001$) (Figure 4.6 shows the differences between the medians). A pairwise multiple comparison (Tukey test) showed that the number of fruiting trees differed between all pairs of habitats ($p<0.05$) except between *terra firme* and *várzea*, and between upland *aguajal* and floodplain *aguajal* ($p>0.05$). Floodplain *aguajal* (mean 109.1 trees fruiting/hectare/month) and upland *aguajal* (mean 75.1 trees fruiting/hectare/month) were the most productive habitats, followed by *terra firme* (mean 20.7 trees fruiting/hectare/month) and *várzea* (mean 16.1 trees fruiting/hectare/month).

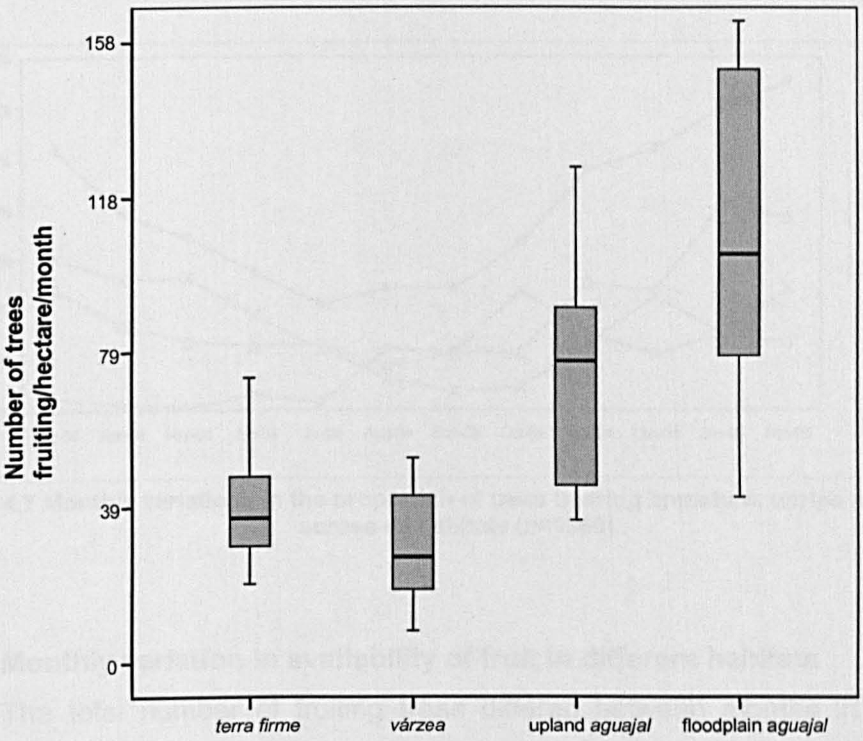

Figure 4.6 Productivity indicated by the median number of trees fruiting/hectare/month in habitats at Lago Preto.

4.3.8 Availability of fruit at Lago Preto

Over the course of the year, across all habitats, there were more fruiting trees bearing unripe or immature fruit than ripe fruit (ANOVA $F_{1,22}=4.969$ $p<0.05$). This is because immature and unripe stages generally last longer than ripe stages.

Across all habitats, the availability of different stages of fruit varied between months ($\chi^2_{22}=72.89$, $p<0.01$) (Figure 4.7). Availability of ripe fruit was highest between December and June, peaking in March. Ripe fruit availability was lower from July to November, and was at its lowest in September and October. Availability of unripe fruit was highest between November and April, peaking in January. Unripe fruit availability was lower from May to October, and was at its lowest in August. Availability of immature fruit was highest between August and February, peaking in October. Immature fruit availability was lower from March to July, and was at its lowest in May. Taking all stages of fruit into account, availability was greater from November to April, peaking in February, and lower from May to October (Figure 4.7).

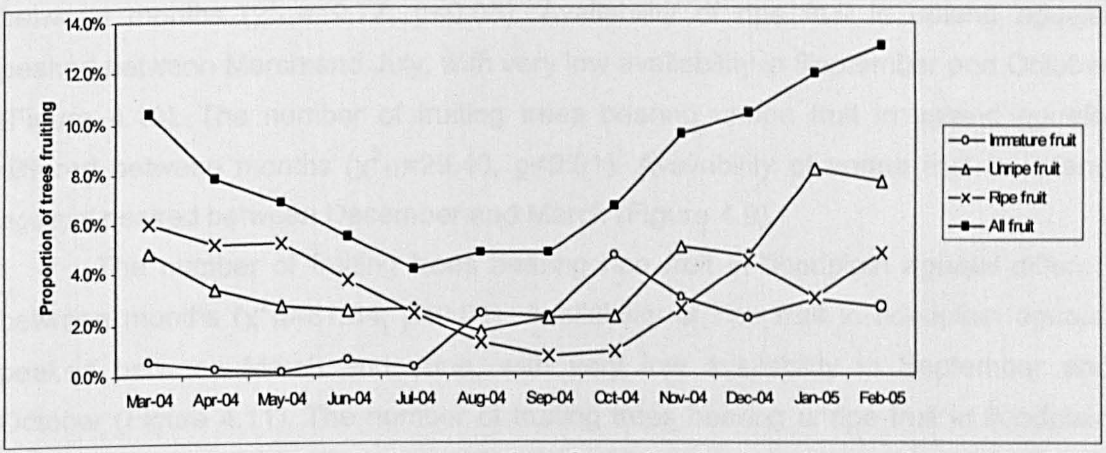

Figure 4.7 Monthly variations in the proportion of trees bearing immature, unripe and ripe fruit across all habitats (n=1360).

4.3.9 Monthly variation in availability of fruit in different habitats

The total number of fruiting trees differed between months in *terra firme* ($\chi^2_{11}=73.50$, $p<0.01$), indicating seasonality in fruit production in this habitat (Figure 4.8). Seasonality was also indicated by differences in the number of fruiting trees between months in *várzea* ($\chi^2_{11}=84.15$, $p<0.01$), and floodplain *aguajal* ($\chi^2_{11}=63.08$, $p<0.01$). In upland *aguajal*, there was no difference between the number of fruiting trees between months ($\chi^2_{11}=15.20$, $p<0.05$), but there was a difference between numbers of fruiting trees bearing ripe fruit between months in the upland *aguajal* habitat ($\chi^2_{11}=19.77$, $p<0.05$).

Two peaks in ripe fruit availability were seen in *terra firme*. One peak was in March and April, and a smaller peak occurred in December. The number of fruiting trees bearing ripe fruit in *terra firme* was different between months ($\chi^2_{11}=49.00$, $p<0.01$). The smallest numbers of fruiting trees bearing ripe fruit in *terra firme* were observed in August and September (Figure 4.8). The number of fruiting trees bearing unripe fruit in *terra firme* was different between months ($\chi^2_{11}=38.47$, $p<0.01$). Availability of unripe fruit peaked in January, February and March in *terra firme*, with lower availability in August, September and October (Figure 4.8).

The number of fruiting trees bearing ripe fruit in *várzea* differed between months ($\chi^2_{11}=35.27$, $p<0.01$). Availability of ripe fruit in *várzea* peaked in April and May, with very low availability between July and October (Figure 4.9). The number of fruiting trees bearing unripe fruit in *várzea* differed between months ($\chi^2_{11}=86.30$, $p<0.01$). Availability of unripe fruit in *várzea* peaked between November and February, with lower availability in other months (Figure 4.10).

The number of fruiting trees bearing ripe fruit in upland *aguajal* differed between months ($\chi^2_{11}=19.77$, $p<0.05$). Availability of ripe fruit in upland *aguajal* peaked between March and July, with very low availability in September and October (Figure 4.10). The number of fruiting trees bearing unripe fruit in upland *aguajal* differed between months ($\chi^2_{11}=29.40$, $p<0.01$). Availability of unripe fruit in upland *aguajal* peaked between December and March (Figure 4.9).

The number of fruiting trees bearing ripe fruit in floodplain *aguajal* differed between months ($\chi^2_{11}=81.84$, $p<0.01$). Availability of ripe fruit in floodplain *aguajal* peaked between March and June, with very low availability in September and October (Figure 4.11). The number of fruiting trees bearing unripe fruit in floodplain *aguajal* differed between months ($\chi^2_{11}=83.49$, $p<0.01$). Availability of unripe fruit in floodplain *aguajal* peaked between November and February (Figure 4.11).

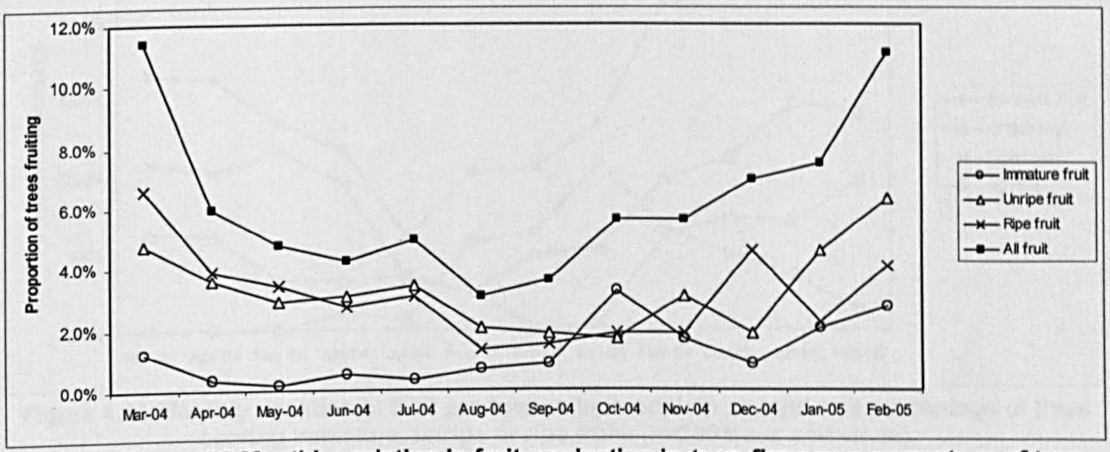

Figure 4.8 Monthly variation in fruit production in *terra firme* as a percentage of trees bearing immature, unripe or ripe fruits (n=589 trees and vines).

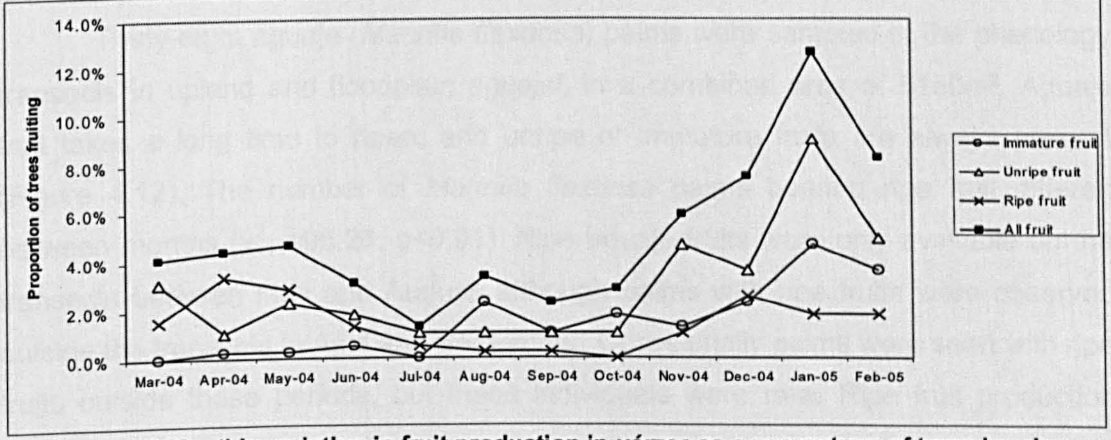

Figure 4.9 Monthly variation in fruit production in *várzea* as a percentage of trees bearing immature, unripe or ripe fruits (n=387 trees and vines).

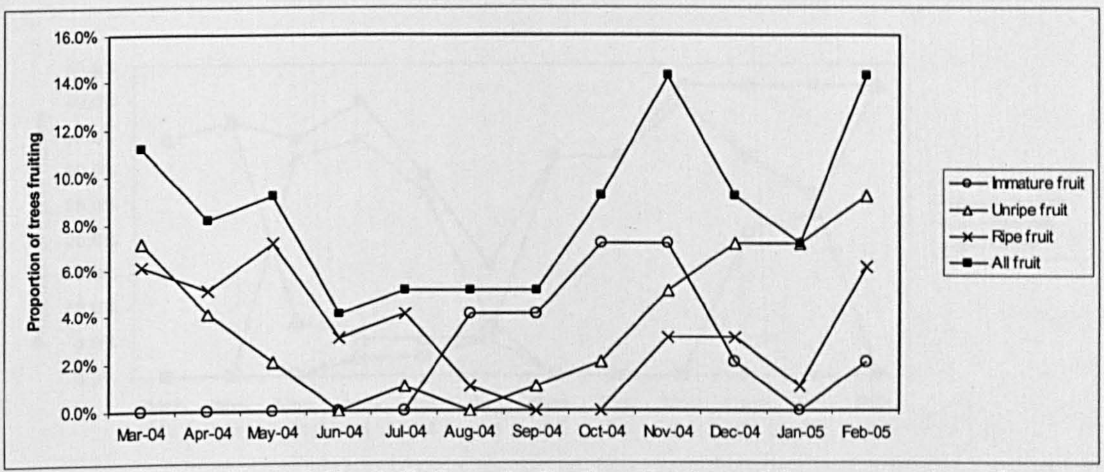

Figure 4.10 Monthly variation in fruit production in upland *aguajal* as a percentage of trees bearing immature, unripe or ripe fruits (n=98 trees and vines).

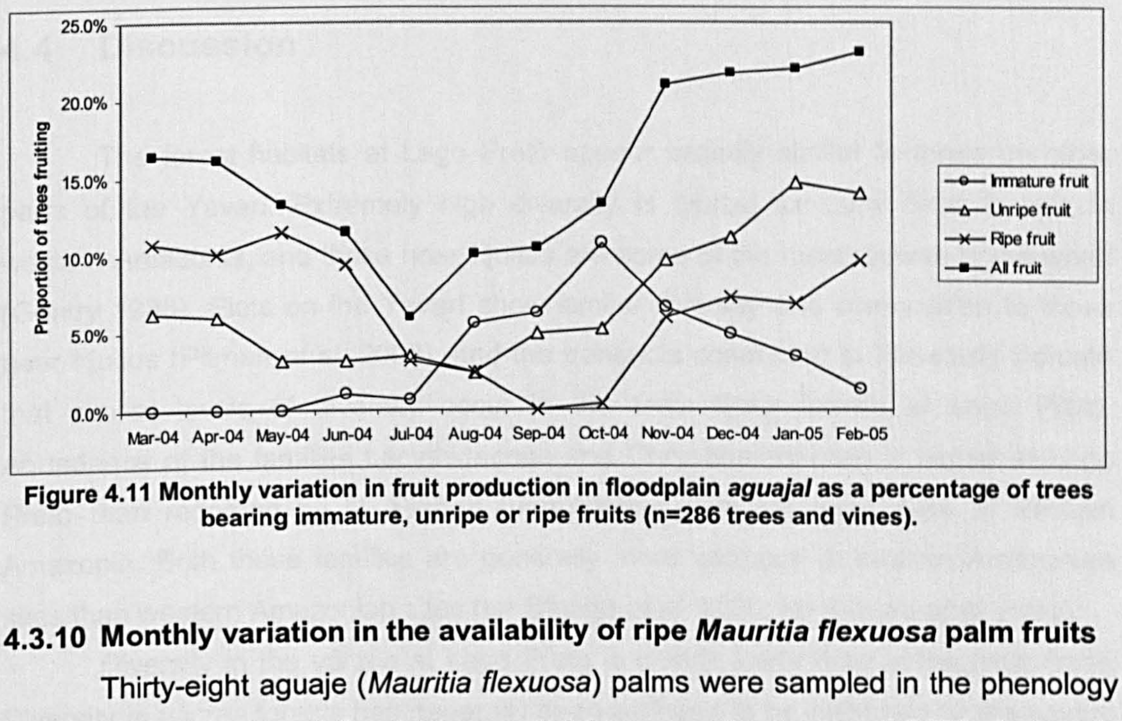

Figure 4.11 Monthly variation in fruit production in floodplain *aguajal* as a percentage of trees bearing immature, unripe or ripe fruits (n=286 trees and vines).

4.3.10 Monthly variation in the availability of ripe *Mauritia flexuosa* palm fruits

Thirty-eight aguaje (*Mauritia flexuosa*) palms were sampled in the phenology transects in upland and floodplain *aguajal*, in a combined area of 5150m². Aguaje fruit takes a long time to ripen, and unripe or immature fruits are always present (Figure 4.12). The number of *Mauritia flexuosa* palms bearing ripe fruit differed between months (χ^2_{11}=95.26, p<0.01). Ripe aguaje fruits were only available on the transects between May and August, although palms with ripe fruits were observed outside the transects in April and September. Occasionally palms were seen with ripe fruits outside these periods, but these individuals were rare. Ripe fruit production peaked in June.

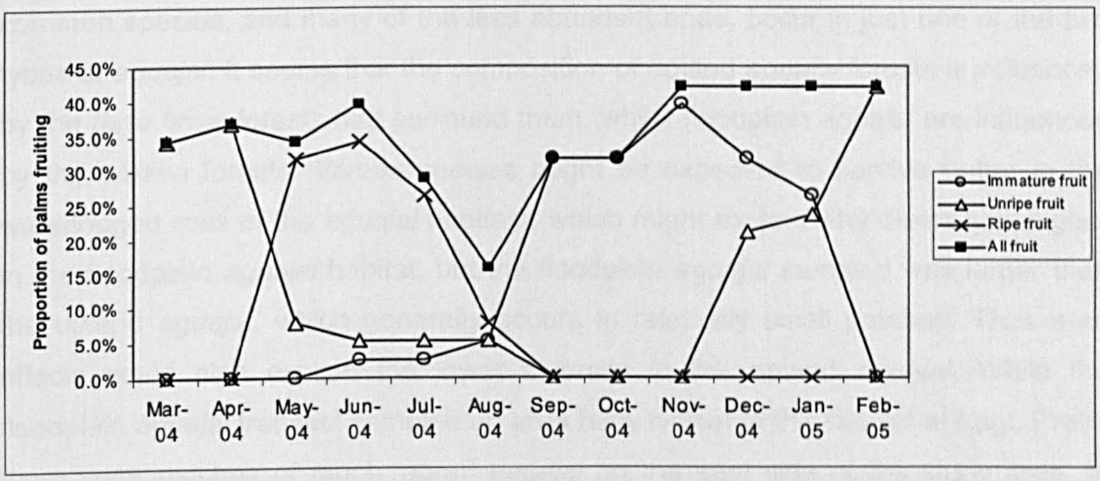

Figure 4.12 Monthly variation in fruit production for *Mauritia flexuosa* as a percentage of trees bearing immature, unripe or ripe fruits (n=38 trees).

4.4 Discussion

The forest habitats at Lago Preto appear broadly similar to those on other parts of the Yavarí. Extremely high diversity is typical for *terra firme* forests in western Amazonia, and those near Iquitos are some of the most diverse in the world (Gentry 1988). Plots on the Yavarí show similar diversity and composition to those near Iquitos (Pitman *et al.* 2003), and the transects conducted in this study indicate that similar levels of diversity occur in the *terra firme* forests at Lago Preto. Abundance of the families Lecythidaceae and Chrysobalanaceae is higher at Lago Preto than recorded by N. Pitman (unpublished data) at other sites in western Amazonia. Both these families are generally more common in eastern Amazonian sites than western Amazonian sites (ter Steege *et al.* 2000; ter Steege *et al.* 2006).

Diversity in the *várzea* at Lago Preto is clearly lower than in the *terra firme*. Diversity in *várzea* forests has generally been believed to be restricted by the severe physiological constraints imposed by regular flooding (e.g. Clinebell *et al.* 1995), but ter Steege *et al.* (2000) contend that the well-known effects of area on species diversity (e.g. Rosenzweig 1995) are more important. *Várzea* is a marginal habitat, covering smaller areas than *terra firme* and should therefore be expected to have lower diversity (ter Steege *et al.* 2000).

Upland and floodplain *aguajal* appear similar in appearance and structure, and the commonest species are abundant in both samples (appendix 1). The dominance of palms in both permanently waterlogged habitats gives the *aguajal* swamps a characteristic open canopy. Despite the similar appearance, some common species, and many of the less abundant ones, occur in just one of the two types of *aguajal*. It seems that the composition of upland *aguajal* forests is influenced by the *terra firme* forests that surround them, whilst floodplain *aguajal* are influenced by the *várzea* forests. *Várzea* species might be expected to survive better in the waterlogged soils of the *aguajal* habitats, which might explain why diversity is higher in the floodplain *aguajal* habitat, but the floodplain *aguajal* sampled was larger than the upland *aguajal*, which generally occurs in relatively small patches. Thus area effects could also explain the lower diversity in the upland *aguajal*. While the floodplain *aguajal* transect sampled an area fairly typical of this habitat at Lago Preto, there were patches of much 'purer' *aguajal* on the east side of the study area. In these patches *Mauritia flexuosa* was more dominant, the palms were more widely spaced, and there were relatively few trees of other species. Uakaris were not seen using these areas during the study, and this habitat may have been something of a barrier to the study groups.

All habitats at Lago Preto show some degree of seasonality, though the seasonal shortages appear most extreme in the *várzea* and *aguajal* habitats. The availability of ripe fruit peaks between March and April. The availability of unripe fruit peaks in January and February, before the peak for ripe fruit. The availability of immature fruit occurs in October and November before the peak for unripe fruit. Generally, across all habitats there is a scarcity of ripe fruit between August and October, but ripe *Mauritia flexuosa* and *Oenocarpus bataua* fruits, two species known to be eaten by *Cacajao calvus ucayalii* (Aquino 1999) are available in August and September.

As found in many other Neotropical forests (e.g. Foster 1982; Terborgh 1983) there were actually two small peaks in ripe fruit production in the *terra firme* forest, one in December at the start of the rainiest months, and a larger one in March towards the end of the wetter months. The *terra firme* in this region of western Amazonia, however, is generally less seasonal than other Neotropical sites (Bodmer 1989; Gentry 1990). Uakari monkeys are only found in this region of western Amazonia, and the lower seasonality of this habitat could be an important factor in their ecology.

The *várzea* forests also showed peaks in fruit production, and these were more pronounced than those in *terra firme* forests. Ripe fruit production peaked in April when water levels were at their highest, and there was a small peak at the start of the high water season. At other *várzea* sites fruiting has been shown to coincide with the onset of flooding in the forest and with peak high water levels (Ayres 1986).

This is because the seeds of many trees in the *várzea* are dispersed by floating or by seed-eating fish (Goulding 1980).

Both types of *aguajal* are dominated by palms *Mauritia flexuosa* and *Euterpe precatoria,* which have high fecundity (Kahn and Henderson 1999). Thus the fruiting phenology of these habitats is strongly related to the fruiting of these species. The fruiting cycle of the aguaje palm (*Mauritia flexuosa*) is of particular interest, because it is known to be an important species in the diet of *Cacajao calvus ucayalii* (Bowler 2003; Aquino 1999). The highest availability of aguaje occurs when there is low availability of other fruit in the forest. The lowest availability of fruit occurred between June and October. Aguaje began to ripen in April and was available until September. *Oenocarpus bataua* is also eaten by *Cacajao calvus ucayalii*, and has high fecundity (Kahn and Henderson 1999). *Oenocarpus bataua* has a similar fruiting cycle to the aguaje palm at Lago Preto, though ripe fruits were available on the phenology transects for a longer period than for aguaje. Because the process of seed maturation typically takes 3 to 5 months, ripe fruits are available for a shorter period than unripe and immature fruit. This pattern is clearly seen in the results from *várzea* and *aguajal* transects, but is less clear in the *terra firme*. This may be because the canopy in *terra firme* forest is higher and denser, making the detection of cryptic unripe fruits more difficult.

The results presented in this Chapter show the fruiting cycles of the habitats at Lago Preto during just one year. Many Neotropical trees have fruiting cycles of more than one year, and some years have higher production than others (Foster 1982). Variability in rainfall and flooding cycles may also influence fruit production. In 2004 high rainfall kept water levels higher than usual on the Yavarí during the low water season, and rainfall and water levels were unusually low in 2005, coinciding with the worst drought in Amazonia for 40 years (Marengo 2006). The monthly variations in fruit production suggest that there is seasonality in fruit production, particularly in the *várzea* and *aguajal* habitats. These data predict that there may be a seasonal shortage of fruit between June and October, but that between May and August shortages of fruit in *várzea* and *terra firme* habitats may be offset by large quantities of ripe palm fruits in *aguajal* habitats. The diet and use of habitat by *Cacajao calvus ucayalii* at Lago Preto may be expected to reflect these seasonal variations in resource distribution.

4.5 Summary

1. Forests at Lago Preto consist of *terra firme* forests that do not flood, and white-water *várzea* forests that flood seasonally. Within these broad categories are various forest types that are not clearly distinct and often intergrade with each other. In permanently waterlogged areas, a third clearly-distinct habitat type is recognised called *aguajal*. *Aguajal* habitats at Lago Preto occur in seasonally-flooded areas (floodplain *aguajal*) and non-flooding areas (upland *aguajal*).

2. In total, 342 species or morphospecies were identified on the tree transects at Lago Preto. *Terra firme* is the most diverse habitat, followed by *várzea*, floodplain *aguajal*, and then upland *aguajal*.

3. The Sorensen index shows that, in terms of shared species, upland *aguajal* is more similar to *terra firme* than to floodplain *aguajal*, and that floodplain *aguajal* is more similar to *várzea* than to upland *aguajal*. However, the Czekanowski index shows that the similarity between the two aguajal habitats is greater when the abundances of common species are taken into account. Since the commonest species in these habitats are the highly fecund and structurally distinct palms, the two aguajal habitats are similar in terms of their resource distribution and canopy structure. These palm species are most likely to influence the use of the habitats by uakari monkeys and the *aguajal* habitats can be treated as similar.

4. Using the number of trees in fruit as a measure of productivity, floodplain *aguajal* (mean 109.1 trees fruiting/hectare/month) and upland *aguajal* (mean 75.1 trees fruiting/hectare/month) were the most productive habitats, followed by *terra firme* (mean 20.7 trees fruiting/hectare/month) and *várzea* (mean 16.1 trees fruiting/hectare/month).

5. Across all habitats at Lago Preto, the availability of fruit of all stages was greater from November to April, peaking in February, and lower from May to October (Figure 4.7). Availability of ripe fruit was highest between December and June, peaking in March. Ripe fruit availability was at its lowest in September and October. Availability of unripe fruit was highest between

November and April, peaking in January. Unripe fruit availability was at its lowest in August.

6. Two peaks in ripe fruit availability were seen in *terra firme*. One peak was in March and April, and a smaller peak occurred in December. The smallest numbers of fruiting trees bearing ripe fruit in *terra firme* were observed in August and September. Availability of unripe fruit peaked in January, February and March in *terra firme*, with lower availability in August, September and October.

7. Availability of ripe fruit in *várzea* peaked in April and May, with very low availability between July and October Availability of unripe fruit in *várzea* peaked between November and February, with lower availability in other months.

8. Availability of ripe fruit in upland *aguajal* peaked between March and July, with very low availability in September and October. Availability of unripe fruit in upland *aguajal* peaked between December and March.

9. Availability of ripe fruit in floodplain *aguajal* peaked between March and June, with very low availability in September and October. Availability of unripe fruit in floodplain *aguajal* peaked between November and February.

10. Ripe *Mauritia flexuosa* fruits were available between April and September, and availability peaked in June.

Chapter 5

Diet and Feeding Ecology

5.1 Introduction

Primate diets have been shown to be correlated with a number of ecological traits, including density, ranging behaviour and group size (Clutton-Brock and Harvey 1977; Chivers and Hladik 1984; van Roosmalen 1984). Fruit is the principal component in the diets of many primate species (Chivers and Hladik 1984). Fruits are scarce, compared to other plant-resources and availability is often restricted by seasonal variation in production (Chivers and Hladik 1984; Chapter 4). Consequently, primate species have evolved different specialisations or strategies to cope with seasonal shortages of fruit (Terborgh 1983; 1986).

The Pitheciinae are unique among Neotropical primates in that they are specialised to feed on the seeds of hard-shelled fruit. This has been shown in *Pithecia* (e.g. Buchanan *et al.* 1981; Setz 1985; Johns 1986; Perez 1993), *Chiropotes* (e.g. van Roosmalen *et al.* 1988; Ayres 1994; Kinzey and Norconk 1993), and *Cacajao* (Ayres 1986; Aquino 1999; Boubli 1999). The enlarged and specialised dentition of the Pitheciinae has long been recognised as an adaptation for this diet (Kinzey 1992), and the morphology of the incisors and canines of these primates indicates that they process fruits differently to other seed-eating primates. The hard cases of fruits are opened with the canines, and the softer seeds are then consumed. This was termed 'sclerocarpic harvesting' by Kinzey and Norconk (1990). The enamel on the molars of the Pitheciins is thin, which is anomalous with other seed predators that characteristically have thick enamel and use their molars to crush hard seeds (Martin *et al.* 2003). This crushing function is replaced by the puncturing function of the canines to remove hard pericarps, while rear dentition is used to triturate relatively soft seeds. *Cacajao* has perhaps the most specialised morphology for this mode of feeding and its diet is also one of the least studied of Neotropical primates.

The aim in this Chapter is to identify important species in the diet of *Cacajao calvus ucayalii*, and particularly those that might be keystone species, vital to the persistence of *Cacajao calvus ucayalii* in the area. The relative importance of seeds, ripe pulp, flowers, leaves and animals in the diet of *Cacajao calvus ucayalii* is examined, considering differences in diet between age-sex classes that might be important in explaining the composition of feeding groups of the monkeys. Overlap in the diet of *Cacajao calvus ucayalii* with other species is clearly important in determining the density and distribution of the species. In this Chapter, dietary overlap and competition between *Cacajao calvus ucayalii* and other species is considered. Similarities and differences between the diet of *Cacajao calvus ucayalii* at Lago Preto and populations of *Chiropotes* and *Cacajao* in other areas are discussed, with particular reference to *Cacajao calvus calvus* at Lake Teiú (Ayres 1986). These differences and similarities in diet may explain differences observed in the densities and grouping behaviours of these related taxa. A detailed description of the diet of a primate can be invaluable in the conservation of the species. When the important food species are known, predictions can be made about the effects of habitat modification on primate populations. The data presented in this Chapter are used in following Chapters to explain habitat use, grouping patterns, social behaviour, and geographical distribution of *Cacajao calvus ucayalii*. The data are also used in Chapter 8 to predict the effects of habitat modification by timber and non-timber plant-resource extraction on the species on the Yavarí.

5.2 Methods

Feeding data were collected at the Lago Preto study site using the methods discussed in Chapter 3. Point-scan sampling (Altmann 1974) at ten-minute intervals was used to collect data on the different plant parts and stages of ripening of fruit in the diet, and on differences in diet between age-sex classes. Species composition in the diet was measured using feeding records recorded for each food item, if it was seen to be used during a ten-minute period. Items were recorded as used when an animal was ingesting or processing items, including reaching, masticating, swallowing or carrying. Where possible the species, plant parts and the maturity of the fruit eaten by the individual were recorded (by observation, and collecting discarded parts).

To calculate the percentage of the diet that each species made up, the number of feeding records for each species each month was multiplied by a 'correction factor' calculated for each month by dividing the mean number of feeding records collected each month by the number of feeding records collected for the month in question. The 'corrected' totals for each month were then summed to give the total proportions in the annual diet, thus controlling for differing amounts of data collected throughout the year.

Preferences for tree genera in the diet were calculated by Ivlev's index of Selectivity, which compares availability (A) with use (U) by (U-A)/(U+A) producing an index for each genera of between 1 (total selection) and -1 (total avoidance). (Ivlev 1961). Availability for each tree genus was calculated as a proportion of the total number of fruiting trees recorded on the phenology transects (Chapter 4). The number of fruiting trees of each genus in each habitat was adjusted by the proportion of the habitat within the home range of the uakaris to give a measure of availability of fruiting trees of each genera within the home range (home range is calculated in Chapter 6). Genera with fewer than 3 records of fruiting trees were discounted from the analysis.

5.3 Results

5.3.1 Plant and animal parts in the diet

The proportions of different plant and animal parts in the diet of uakaris at Lago Preto were different (ANOVA $F_{9,110}$=20.477 $p<0.0001$). When feeding records were adjusted to allow for different numbers of feeding records collected each month, 50.6% of the diet was made up of unripe seeds, 37.4% was ripe pulp including whole fruits, 3.7% was flowers and nectar, and the remaining 8.3% was made up of other animal material and plant parts, including mature seeds, unripe pulps, arils, leaves and gums (Figure 5.1).

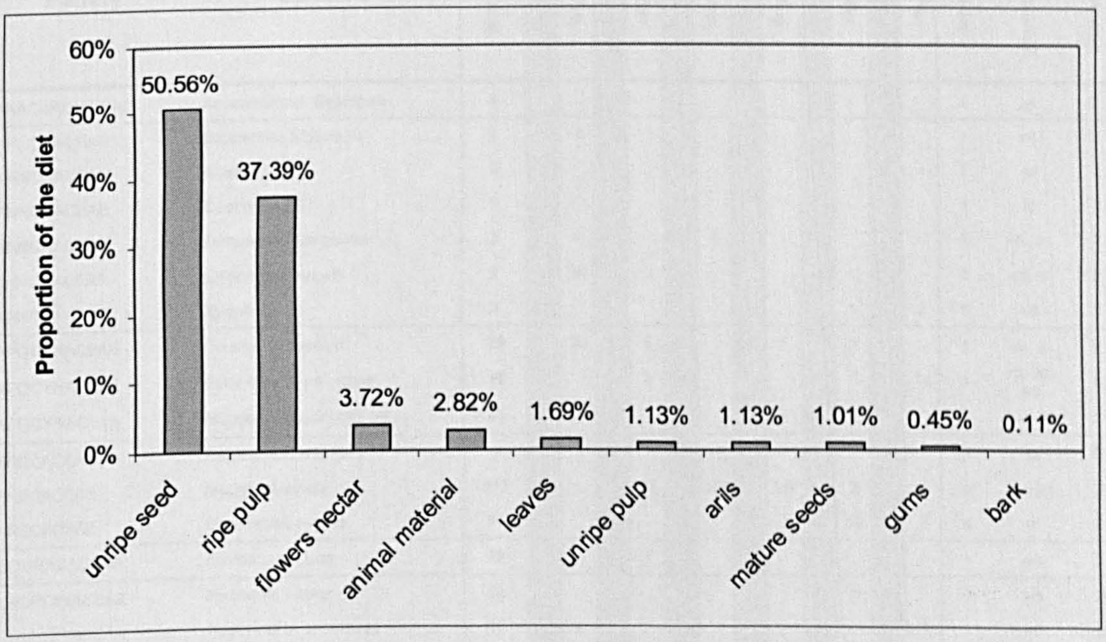

Figure 5.1 The proportions of plant parts and animal material in the diet of *Cacajao calvus ucayalii* at Lago Preto.

5.3.2 Plant species in the diet

One-hundred and sixty-four plant species were identified in the diet of *Cacajao calvus ucayalii* from feeding records, including several unidentified morphospecies (Table 5.1). In 122 feeding records, not enough of the plant was collected to enable identification, often because uakaris would carry items into other trees and only drop fragments of the fruit. While it is estimated that these additional feeding records could add 20 to 40 additional species to the diet list, the majority of them were only recorded on a small number of occasions.

Uakaris at Lago Preto fed on species in different proportions (ANOVA $F_{163,1804}$=2.922 p<0.0001). Only 22 plant species made up 1% or more of the annual diet of *Cacajao calvus ucayalii* at Lago Preto (Table 5.2). *Mauritia flexuosa* was the most eaten species during the study, making up 20.0% of the diet. The uakaris ate the ripe pulp of this species, but rarely consumed the young seeds. *Licania heteromorpha* (unripe seeds) was the second most consumed species followed by *Couma macrocarpa* (unripe seeds and ripe pulp), *Chrysophyllum sanguinolentum* (unripe seeds) and *Hevea* cf. *guianensis* (unripe seeds) (Table 5.2).

Table 5.1 Species eaten by *Cacajao calvus ucayalii* at Lago Preto.

Family	Species	FEEDING RECORDS													Habit	Parts eaten	Hardness
		TOTAL	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec			
ANACARDIACEAE	*Anacardium* cf. *Gigantium*	**3**											3		t	us	2
ANNONACEAE	*Diclinanona tessmannii*	**1**		1											t	us	5
ANNONACEAE	*Guatteria* sp.1	**6**											2	4	t	rp	2
ANNONACEAE	*Guatteria* sp.2	**1**											1		t	rp	2
ANNONACEAE	*Tetrameranthus laomae*	**3**		1			1	1							t	rp, us	2
ANNONACEAE	Unidentified *Xylopia*	**2**		2											t	us, rp	2
ANNONACEAE	*Xylopia* sp.1	**3**										1		2	t	us	2
APOCYNACEAE	*Couma macrocarpa*	**86**	7	30	16	6	1		23	1		2			t	us, rp	4
APOCYNACEAE	*Paranchornia peruviana*	**19**				1	4							14	t	rp, up, us	5
APOCYNACEAE	*Rhigospira quadrangularis*	**10**					1		2	1	4	1	1		t	us, rp	3
ARECACEAE	*Astrocaryum chambira*	**1**											1		p	us	5
ARECACEAE	*Mauritia flexuosa*	**572**				11	82	164	151	149	10	3	2		p	rp, us	2
ARECACEAE	*Oenocarpus bataua*	**67**								1	43	19	2	2	p	rp	2
BOMBACACEAE	*Eriotheca globosa*	**20**				7	13								t	us	3
CECROPIACEAE	*Pourouma bicolor*	**28**										3	25		t	us	2
CECROPIACEAE	*Pourouma* cf. *tomentosa*	**10**	2	4							2		1	1	t	us	2
CECROPIACEAE	*Pourouma* sp.1	**28**											6	22	t	us	2
CECROPIACEAE	*Pourouma* sp.2	**17**											17		t	us	2
CELASTRACEAE	Unidentified Celastraceae spp.	**4**	4												v	us	n/a
CELASTRACEAE	Unidentified Celastraceae 1	**8**	1	1		2			4						v	rp, us	4

Family	Species	FEEDING RECORDS															
		TOTAL	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Habit	Parts eaten	Hardness
CELASTRACEAE	Unidentified Celastraceae 2	**10**	1						1			4	4		v	up, rp, us	5
CELASTRACEAE	*Salacia impressifolia*	**42**				14		25		2				1	v	us, rp	2
CHRYSOBALANACEAE	Unidentified Chrysobalanaceae 1	**1**										1			t	us	n/a
CHRYSOBALANACEAE	*Couepia paraensis*	**1**											1		t	us	3
CHRYSOBALANACEAE	*Couepia* sp.1	**1**						1							t	us	3
CHRYSOBALANACEAE	Unidentified *Licania*	**2**											1	1	t	us	n/a
CHRYSOBALANACEAE	*Licania heteromorpha*	**153**		2					22	29	31	36	24	9	t	us	4
CHRYSOBALANACEAE	*Licania hypoleuca*	**10**	5	5											t	us	5
CHRYSOBALANACEAE	*Licania micranthra*	**11**											11		t	us	4
CHRYSOBALANACEAE	*Licania octandra*	**2**			2										t	us	3
CHRYSOBALANACEAE	*Licania* sp.1	**2**	1		1										t	us	4
CLUSIACEAE	*Moronobea coccinea*	**5**	2	1								1	1		t	fl, us	4
CLUSIACEAE	*Rheedia* sp1.	**1**										1			t	us	3
CLUSIACEAE	*Symphonia globulifera*	**19**				1	13	1	1	3					t	ne, us	1
CLUSIACEAE	*Tovomita* sp.1	**3**											1	2	t	us	3
CLUSIACEAE	*Tovomita* sp.2	**23**	17	6											v	us, rp	3
CLUSIACEAE	Unidentified Clusiaceae 1	**5**									5				t	us	3
COMBRETACEAE	Unidentified *Combretum* spp.	**2**						1		1					v	us	3
COMBRETACEAE	*Combretum* sp.1	**1**												1	v	us	3
COMBRETACEAE	*Combretum* sp.2	**2**											2		v	us	3
CONNARACEAE	*Rourea camptoneura*	**6**					2	4							v	rp, us	2
CONVOLVULACEAE	*Maripa* sp.1	**13**				3		5	5						v	us, rp	2
CONVOLVULACEAE	*Maripa* sp.2	**1**							1						v	us, rp	2
EBENACEAE	*Diospyros poeppiguiana*	**9**				8	1								t	us	3
ELAEOCARPACEAE	*Sloanea* sp.1	**5**					5								t	us	3
ELAEOCARPACEAE	*Sloanea* sp.2	**7**			7										t	us	3
ELAEOCARPACEAE	*Sloanea* sp.3	**5**			5										t	ar	3
ELAEOCARPACEAE	*Sloanea tuerckheimii*	**1**		1											t	us	3
EUPHORBIACEAE	Unidentified Euphorbiaceae sp.1	**2**		1										1	t	us	3
EUPHORBIACEAE	Unidentified Euphorbiaceae sp.2	**2**	1	1											t	us	4
EUPHORBIACEAE	*Alchornea triplinervia*	**20**									4	16			t	us	2
EUPHORBIACEAE	*Conceveiba rhytidocarpa*	**2**		1									1		t	us	2
EUPHORBIACEAE	*Glycydendron amazonicum*	**4**												4	t	us	2
EUPHORBIACEAE	*Hevea* cf. *guianensis*	**79**	4	1	6	5	5	24	4				18	12	t	us, le, fl	5
FABACEAE	Unidentified Fabaceae sp.1	**3**		1			2								t	us	n/a
FABACEAE	*Albizia* sp.1	**2**				2									t	us	2
FABACEAE	*Dussia* spp.	**8**			3	3		2							t	us	3
FABACEAE	*Enterolobium barnebianum*	**11**				1	2		5	3					t	us, ms	3
FABACEAE	*Hymenaea* sp.1	**3**							3						t	rp	4
FABACEAE	*Inga* spp.	**44**	3	10	1				1		2	1	22	4	t	us, ar	n/a
FABACEAE	*Inga capitata*	**2**	2												t	us	2
FABACEAE	*Inga* cf. *semialata*	**7**	6	1											t	us	2
FABACEAE	*Inga gracilifolia*	**12**	1	7	4										t	us, ar	2
FABACEAE	*Inga* sp.1	**1**												1	t	us	2
FABACEAE	*Inga* sp.2	**3**			2							1			t	us, ar	2
FABACEAE	*Inga* sp.3	**1**										1			t	us	2
FABACEAE	*Inga* sp.4	**1**									1				t	us	2
FABACEAE	*Macrolobium angustifolium*	**1**			1										t	us	2

Family	Species	FEEDING RECORDS													Habit	Parts eaten	Hardness
		TOTAL	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec			
FABACEAE	*Parkia* spp.	**18**					3	2	2		6	5			t	us, gu	n/a
FABACEAE	*Parkia igneiflora*	**45**						7	14	9	9	6			t	us, ms	3
FABACEAE	*Parkia nitida*	**2**					1							1	t	gu, fl	3
FABACEAE	*Parkia* sp.1	**2**				1			1						t	gu, ms	3
FABACEAE	*Pterocarpus* sp.1	**1**										1			t	us	3
FABACEAE	*Zygia* sp.1	**20**												20	t	us	2
HERNANDIACEAE	Unidentified *Sparattanthelium* spp.	**3**				3									v	us	n/a
HERNANDIACEAE	*Sparattanthelium* sp.1	**1**			1										v	us	2
HUMIRIACEAE	Unidentified Humiriaceae 1	**9**	1	2							3			3	t	us, up	5
HUMIRIACEAE	Unidentified Humiriaceae 2	**1**									1				t	us	4
ICACINACEAE	*Dendrobangia multinervia*	**3**							3						t	rp	2
LECYTHIDACEAE	*Couroupita guianensis*	**5**						5							t	us	4
LECYTHIDACEAE	*Eschweilera* spp.	**24**	5				1			1		1	16		t	us	4
LECYTHIDACEAE	*Eschweilera coriacea*	**24**	8	6	3					3		2		2	t	us	4
LECYTHIDACEAE	*Eschweilera* sp.1	**70**										20	50		t	fl	4
LECYTHIDACEAE	*Eschweilera* sp.2	**12**											12		t	us	4
LECYTHIDACEAE	*Eschweilera tessmannii*	**8**			5						3				t	us	4
LECYTHIDACEAE	*Eschweilera* sp.3	**1**	1												t	us	4
LECYTHIDACEAE	*Eschwielera albiflora* or *parvifolia*	**49**	5								2	15	11	16	t	us	4
LECYTHIDACEAE	*Gustavia hexapetala*	**6**				1		1			1	2	1		t	us	4
LECYTHIDACEAE	*Gustavia* sp.1	**1**								1					t	fl	4
MALPIGHIACEAE	*Byrsonima* sp.1	**4**			4										?	rp	2
MARCGRAVIACEAE	*Souroubea* sp.1	**4**			3								1		v	us	2
MELASTOMATACEAE	*Miconia* sp.1	**2**										2			t	rp	2
MELIACEAE	*Guarea* sp.1	**4**									1	3			t	us	4
MENISPERMACEAE	Unidentified Menispermaceae	**2**										2			v	rp	n/a
MENISPERMACEAE	*Anomospermum reticulatum*	**8**									3	4		1	v	us, rp	2
MENISPERMACEAE	*Odontocarya* spp.	**2**							2						v	rp	2
MENISPERMACEAE	*Odontocarya floribunda*	**12**		1					4			3	1	3	v	rp	2
MORACEAE	*Brosimum* spp.	**2**											2		t	us	2
MORACEAE	*Brosimum lactescens*	**6**										5	1		t	us	2
MORACEAE	*Brosimum rubescens*	**2**										2			t	us	2
MORACEAE	*Brosimum* sp.1	**4**										1	3		t	us	2
MORACEAE	*Brosimum* sp.2 (but cf. *utile*)	**9**	6	1	1								1		t	us	2
MORACEAE	*Brosimum utile*	**10**											10		t	us	2
MORACEAE	*Ficus* spp.	**8**			4	1	1	1				1			t	rp	n/a
MORACEAE	*Ficus* cf. *guianensis*	**13**							2		6		5		t	wf	1
MORACEAE	*Ficus mathewsii*	**3**												3	t	rp	2
MORACEAE	*Ficus* sp.1	**1**								1					t	rp	2
MORACEAE	*Ficus* sp.2	**2**	2												t	rp	2
MORACEAE	*Helicostylis scabra*	**12**	5										2	5	t	us	3
MORACEAE	*Helicostylis tomentosa*	**9**		9											t	us, rp	3
MORACEAE	*Maquira* spp.	**1**				1									t	us	n/a
MORACEAE	*Maquira* cf. *guianensis*	**21**		2							12	7			t	us, rp	2
MORACEAE	*Naucleopsis mello-barretoi*	**6**										1	5		t	rp, us	2
MORACEAE	*Perebea* sp.1	**4**											4		t	us	2
MORACEAE	*Pseudolmedia laevigata*	**1**	1												t	rp	1
MORACEAE	Unidentified Moraceae 1	**11**									1	10			t	us	3

Family	Species	FEEDING RECORDS													Habit	Parts eaten	Hardness
		TOTAL	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec			
MORACEAE	Unidentified Moraceae 2	**6**												6	t	up	2
MORACEAE	Unidentified Moraceae 3 (cf. *Brosimum)*	**4**										4			t	us	2
MYRISTICACEAE	*Unidentified Myristicaceae*	**2**						1					1		t	us	n/a
MYRISTICACEAE	*Iryanthera* spp.	**3**							2				1		t	us	n/a
MYRISTICACEAE	*Iryanthera elliptica*	**34**		2	4						14	9	5		t	us	5
MYRISTICACEAE	*Iryanthera tricornis*	**40**	8	5	3				1		3	1	17	2	t	us	3
MYRISTICACEAE	*Osteophloeum platyspermum*	**11**			3	6					2				t	us, ar	4
MYRISTICACEAE	*Virola pavonis (but cf. surinamensis)*	**11**	4								1			6	t	us, ar	3
MYRISTICACEAE	*Virola* sp.1	**1**			1										t	us	n/a
MYRISTICACEAE	*Virola* sp.2	**2**	1	1											t	ar	1
MYRISTICACEAE	Unidentified Myristicaceae 1	**2**	1	1											t	us	4
MYRISTICACEAE	Unidentified Myristicaceae 2	**1**									1				t	us	4
MYRISTICACEAE	Unidentified Myristicaceae 3	**1**											1		t	us	4
MYRTACEAE	*Eugenia* sp.1	**2**			2										t	rp	1
MYRTACEAE	*Eugenia* sp.2	**7**				7									t	rp, us	1
PASSIFLORACEAE	*Passiflora ligularis*	**3**			1	2									v	rp	1
POLYGALACEAE	*Moutabea* sp.1	**7**	2	3			1			1					v	rp, us	2
POLYGALACEAE	*Moutabea* sp.2	**1**					1								v	rp	2
POLYGONACEAE	*Coccoloba* sp.1	**6**							6						v	rp	2
RUBIACEAE	*Duroia triflora*	**5**			2	3									t	rp	2
SAPINDACEAE	*Paullinia faginia*	**32**				9	23								v	rp	2
SAPINDACEAE	*Paullinia pachycarpa* or *grandifolia*	**29**									2	14	13		v	us	3
SAPINDACEAE	*Paullinia* sp.1	**2**	2												v	rp	2
SAPINDACEAE	*Paullinia* sp.2	**1**				1									v	rp	2
SAPINDACEAE	Unidentified Sapindaceae spp.	**2**							1	1					v	rp, us	n/a
SAPOTACEAE	*Chrysophyllum sanguinolentum*	**68**	10	19	20				1		6	2	10		t	us	4
SAPOTACEAE	*Ecclinusa lanceolata*	**1**		1											t	us	3
SAPOTACEAE	*Manilkara* sp.1	**13**	8		1			1		2	1				t	us	3
SAPOTACEAE	*Micropholis venulosa*	**13**									6	3	4		t	us	3
SAPOTACEAE	*Micropholis guyanensis*	**8**									4		4		t	us	4
SAPOTACEAE	Unidentified *Pouteria* sp.	**1**			1										t	us	3
SAPOTACEAE	*Pouteria cuspidata*	**14**	1	3	2				1		5		1	1	t	us	3
SAPOTACEAE	*Pouteria gomphiifolia*	**11**	5			3							1	2	t	us	3
SAPOTACEAE	*Pouteria guianensis*	**42**	28	11		3									t	us	3
SAPOTACEAE	*Pouteria oblanceolata*	**2**											2		t	us	3
SAPOTACEAE	*Pouteria* sp.2	**5**			2	3									t	us	3
SAPOTACEAE	*Pouteria* sp.3	**2**				2									t	us	3
SAPOTACEAE	*Pouteria* sp.4	**2**				2									t	us	3
SAPOTACEAE	*Pouteria* sp.5	**1**				1									t	us	3
SAPOTACEAE	*Pradosia grisebachii*	**11**	1		1	9									t	us	3
SAPOTACEAE	Unidentified Sapotaceae 1	**4**	2	1									1		t	us	3
SAPOTACEAE	Unidentified Sapotaceae 2	**6**			3	3									t	us	2
SAPOTACEAE	Unidentified Sapotaceae spp.	**18**	1		2	2		5		4	1		2	1	t	rp	n/a
unidentified family 1 vine	Unidentified family 1 (cf. *Spondias* in Anacardiaceae)	**49**			4						9	36			v	rp,us, up	2
unidentified family 2	Unidentified family 2	**5**							2	1	1		1		?	us	5
unidentified family 3	Unidentified family 3	**11**							1		8	1	1		?	us	4
unidentified family 4	Unidentified family 4	**4**										4			?	us	4

Family	Species	FEEDING RECORDS															
		TOTAL	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Habit	Parts eaten	Hardness
unidentified family 5	Unidentified family 5	**5**	2										3		t	us	4
Invertebrate	Invertebrate	**37**		2		5	3	4	2	3	4	13	1		inv	in	n/a
Invertebrate	Commensal ants and sweet sap in *Couroupita guianensis*	**5**								5					inv	in	n/a
ITEM NOT IDENTIFIED	ITEM NOT IDENTIFIED	**122**	3	2	28	13	5	12	14	12	14	9	7	3	n/a	n/a	n/a
	Totals	**2583**	**170**	**149**	**149**	**145**	**171**	**267**	**282**	**234**	**232**	**280**	**348**	**156**			

Abbreviations: rp, ripe pulp; up, unripe pulp; us, unripe seeds; ms, mature seeds; fl, flowers/nectar; ar, aril; wf, whole fruit; gu, gums; le, leaves; in, invertebrates; v, vine; p, palm; t, tree

Hardness: 1 = very soft, 2= soft, 3= medium, 4= hard, 5=very hard

Table 5.2 Plant species or other items making up 1% or more of the diet of *Cacajao calvus ucayalii.*

Rank	Species	% diet (weighted per month)
1	*Mauritia flexuosa*	20.01
2	*Licania heteromorpha*	5.04
3	*Couma macrocarpa*	4.08
4	*Chrysophyllum sanguinolentum*	3.22
5	*Hevea* cf. *guianensis*	3.06
6	*Oenocarpus bataua*	2.30
7	*Pouteria guianensis*	2.16
8	*Eschweilera* cf. *albiflora* or *parvifolia*	1.88
9	*Eschweilera* sp.1	1.79
10	*Salacia impressifolia*	1.71
11	*Paullinia faginia*	1.64
12	Species from unidentified family 1 (cf. *Spondias*)	1.62
13	*Iryanthera tricornis*	1.52
14	*Parkia igneiflora*	1.45
15	Invertebrates	1.39
16	*Pourouma* sp.1	1.32
17	*Iryanthera elliptica*	1.23
18	*Tovomita* sp.2	1.17
19	*Eschweilera coriacea*	1.17
20	*Zygia* sp.1	1.07
21	*Eriotheca globosa*	1.04
22	*Paranchornia peruviana*	1.00

5.3.3 Plant genera in the diet

Uakaris at Lago Preto fed on plant genera in different proportions (ANOVA $F_{91,1012}$=4.097 p<0.0001). The most eaten genus was *Mauritia*, of which only *Mauritia flexuosa* occurs in the region. The genera of the highest-ranked species are also ranked highly, but some specious genera are ranked higher in the diet than the species of which they are constituted (e.g. *Eschweilera*, *Pouteria* and *Inga*) (Table 5.3). The second most eaten genus was *Eschweilera*, of which both flowers and unripe seeds were eaten. *Licania*, *Couma* and *Pouteria* were the third, fourth and fifth most eaten genera. Unripe seeds of all these genera were eaten.

Table 5.3 Plant genera making up 1% or more of the diet of *Cacajao calvus ucayalii*.

Rank	Genus	% diet (weighted by month)
1	*Mauritia*	20.0
2	*Eschweilera*	6.3
3	*Licania*	6.1
4	*Couma*	4.1
5	*Pouteria*	4.0
6	*Chrysophyllum*	3.2
7	*Hevea*	3.1
8	*Inga*	3.0
9	*Pourouma*	2.9
10	*Iryanthera*	2.8
11	*Paullinia*	2.6
12	*Oenocarpus*	2.3
13	*Parkia*	2.3
14	*Salacia*	1.7
15	*Ficus*	1.4
16	Genus from unidentified family 1 (cf. *Spondias*)	1.4
17	*Brosimum*	1.3
18	*Tovomita*	1.2
19	*Zygia*	1.1
20	*Helicostylis*	1.1
21	*Eriotheca*	1.0
22	*Paranchornia*	1.0
23	*Sloanea*	1.0

5.3.4 Plant families in the diet

Uakaris at Lago Preto fed on different plant families in different proportions (ANOVA $F_{38,429}=10.923$ $p<0.0001$). 16 families individually made up more than 1% of the diet (Figure 3.4). The commonest family in the diet was Arecaceae, and most of the feeding records on this family were on *Mauritia flexuosa*. The second most eaten family was Sapotaceae, with the records spread between several important genera, notably *Pouteria* and *Chrysophyllum*. Similarly records of the third most eaten family, Fabaceae, are spread between the seeds and arils of the important genera *Inga* and

Parkia. The fourth most eaten family, Lecythidaceae, contains the second most important genus in the diet, *Eschweilera*. Chrysobalanaceae, Apocynaceae, Moraceae, Myristicaceae and Euphorbiaceae are also important families in the diet (Table 5.4).

Table 5.4 Plant families making up 1% or more of the diet of *Cacajao calvus ucayalii*

Rank	Family	% diet (weighted by month)
1	ARECACEAE	22.3
2	SAPOTACEAE	10.4
3	FABACEAE	7.6
4	LECYTHIDACEAE	7.0
5	CHRYSOBALANACEAE	6.2
6	APOCYNACEAE	5.4
7	MORACEAE	5.1
8	MYRISTICACEAE	4.2
9	EUPHORBIACEAE	4.2
10	CELASTRACEAE	3.8
11	CECROPIACEAE	2.8
12	SAPINDACEAE	2.6
13	Unidentified family 1 (cf. ANACARDIACEAE)	1.6
14	CLUSIACEAE	1.4
15	BOMBACACEAE	1.0
16	ELAEOCARPACEAE	1.0

5.3.5 Vine species in the diet

Vines made up 10.2% of the diet of *Cacajao calvus ucayalii* at Lago Preto. Vines of the genus *Paullinia* (Sapindaceae) were particularly important during April (6.9%) and May (13.5%), while the vine species *Salacia impressifolia* (Celastraceae), of which unripe seeds and ripe pulp were both eaten, was important in April (9.7%) and June (9.4%). Pulp and seeds of several other species of Celastraceae were eaten throughout the year.

5.3.6 Selectivity ratios of genera in the diet

According to Ivlev's index of selectivity (Ivlev 1961) uakaris selected a number of tree genera positively in relation to their availability. Other genera in the diet were negatively selected in relation to their availability (Figure 5.2). *Parkia*, *Pourouma*, *Hevea*, *Tovomita* and *Brosimum* were the genera most positively selected in the diet. The most eaten genus in the diet, *Mauritia*, was positively selected, but not as strongly as several other genera. *Mauritia* is very common in the environment, and produces large amounts of fruit (Chapter 4). Similarly, other commonly-eaten genera such as *Pouteria*, *Licania* and *Eschweilera* are very common in the environment and, while they were positively selected, selection was not as strong as for other genera.

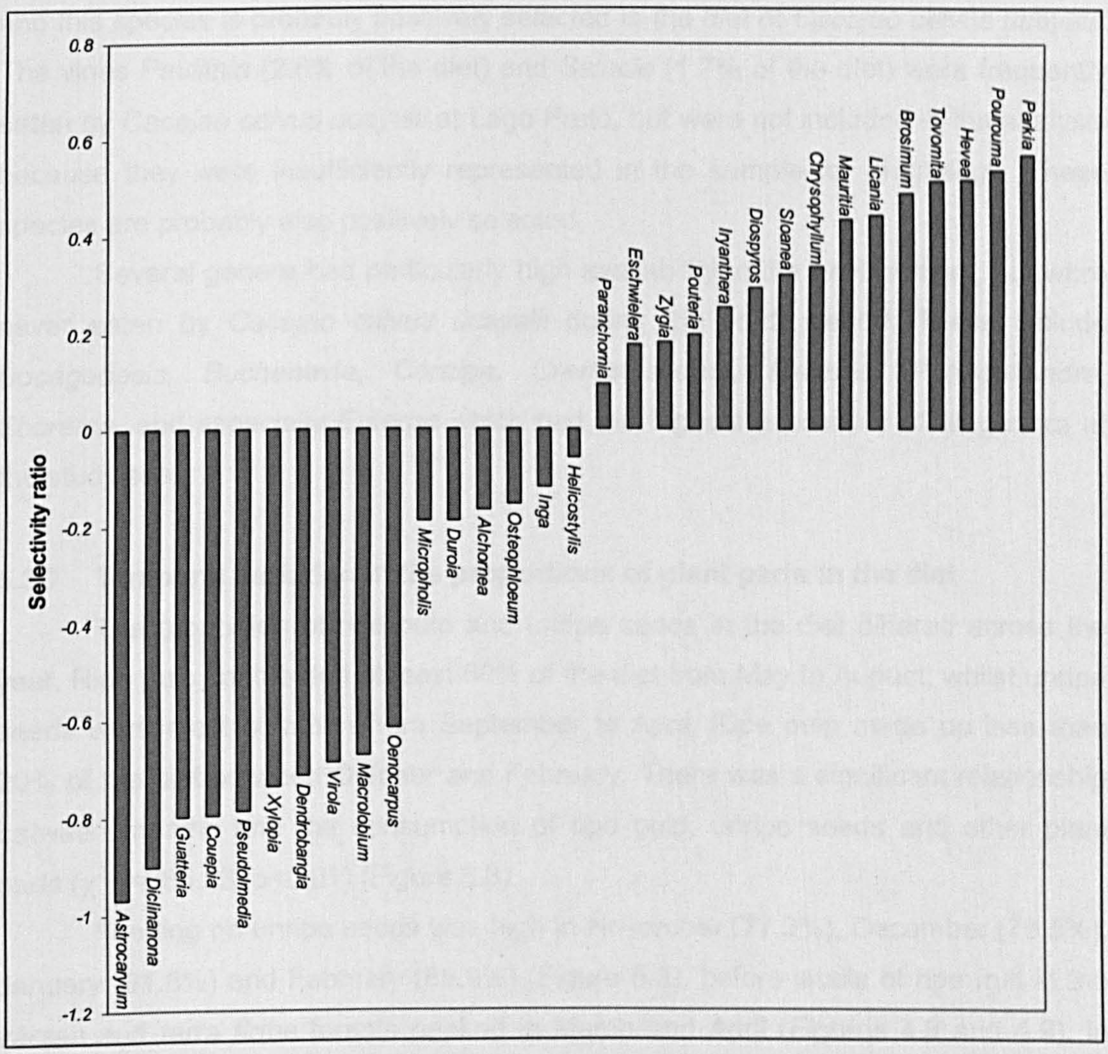

Figure 5.2 Preferences for tree genera in the diet of *Cacajao calvus ucayalii* measured with Ivlev's index of selectivity. Values between 0 and 1 indicate increasing positive selection for tree genera, whereas values between 0 and -1 indicate increasing negative selection, use of the genus being at proportions lower than availability.

Licania was in the top three most important genera for five months from July through to November, and the seeds were eaten when the fruits were very young, through almost to maturity in December. *Licania* is not fed on in intensive feeding events, where large groups will feed on a fruiting tree until few fruits remain, as in *Eschweilera* and many of the genera in Sapotaceae, but the genus is common and available for a long fruiting period. It is eaten regularly by uakaris, but in shorter, less conspicuous sessions. Uakaris would often move through fruiting *Licania* trees without feeding on the fruits, and would often eat only part of the seed discarding the rest.

Couma made up 4.1% of the diet, but no fruiting trees of this genus occurred on the phenology transects. Feeding events on this species were long and intense and this species is probably positively selected in the diet of *Cacajao calvus ucayalii.* The vines *Paullinia* (2.6% of the diet) and *Salacia* (1.7% of the diet) were frequently eaten by *Cacajao calvus ucayalii* at Lago Preto, but were not included in the analysis because they were insufficiently represented in the sample for phenology. These species are probably also positively selected.

Several genera had particularly high availability in the environment, but were never eaten by *Cacajao calvus ucayalii* during the study period. These include *Bocageopsis, Buchenavia, Caraipa, Crematospema, Malmea, Pseudoxandra, Socratea,* and especially *Euterpe* which had the highest availability of all genera at the study site.

5.3.7 Temporal variation in the proportions of plant parts in the diet

The proportion of ripe pulp and unripe seeds in the diet differed across the year. Ripe pulp contributed at least 60% of the diet from May to August, whilst unripe seeds were most common from September to April. Ripe pulp made up less than 20% of the diet between October and February. There was a significant relationship between months and the consumption of ripe pulp, unripe seeds and other plant parts (χ^2_{22}=285.23, $p<0.01$) (Figure 5.3).

Feeding on unripe seeds was high in November (77.3%), December (79.5%), January (91.8%) and February (85.9%) (Figure 5.3), before levels of ripe fruit in the *várzea* and *terra firme* forests peaked in March and April (Figures 4.8 and 4.9). In March there is an increase in the amount of pulp eaten before the ripening of *Mauritia flexuosa*, after which ripe pulp dominated the diet for the duration of the *Mauritia flexuosa* fruiting season. The proportion of ripe pulp in the diet of *Cacajao calvus ucayalii* is inversely correlated with the proportion of unripe seeds in the diet (Pearson correlation, n=12, r = -0.978, $p<0.0001$) (Figure 5.4). The proportion of ripe pulp in the diet is negatively correlated with the availability of all fruits in the home range of *Cacajao calvus ucayalii* at Lago Preto (Pearson correlation, n=12, r = -0.670, $p<0.05$) (Figure 5.5). This indicates that *Cacajao calvus ucayalii* switches from feeding on unripe seeds to ripe pulps during times of lower fruit availability. These periods coincide with a high availability of ripe pulps of *Mauritia flexuosa* and

Oenocarpus bataua (Chapter 4), which are important in the diet of *Cacajao calvus ucayalii* at these times.

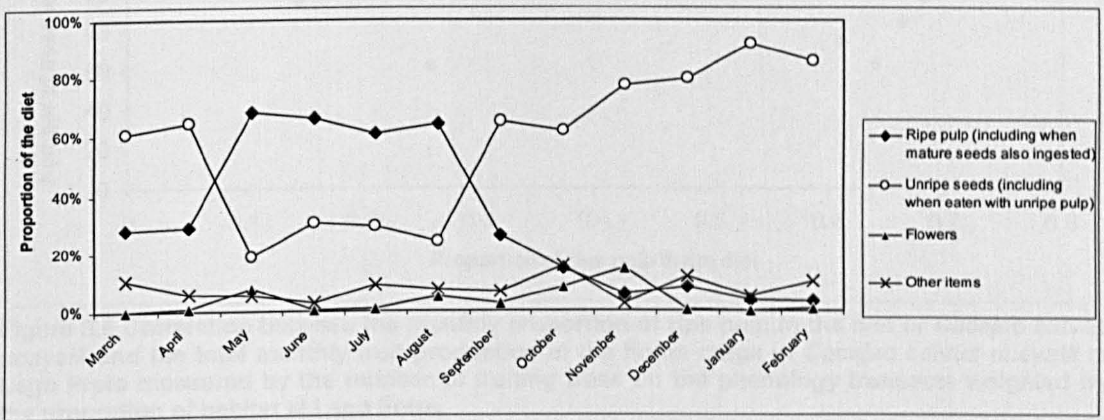

Figure 5.3 Seasonal variation in the proportions of seeds, pulp and nectar in the diet of *Cacajao calvus ucayalii*.

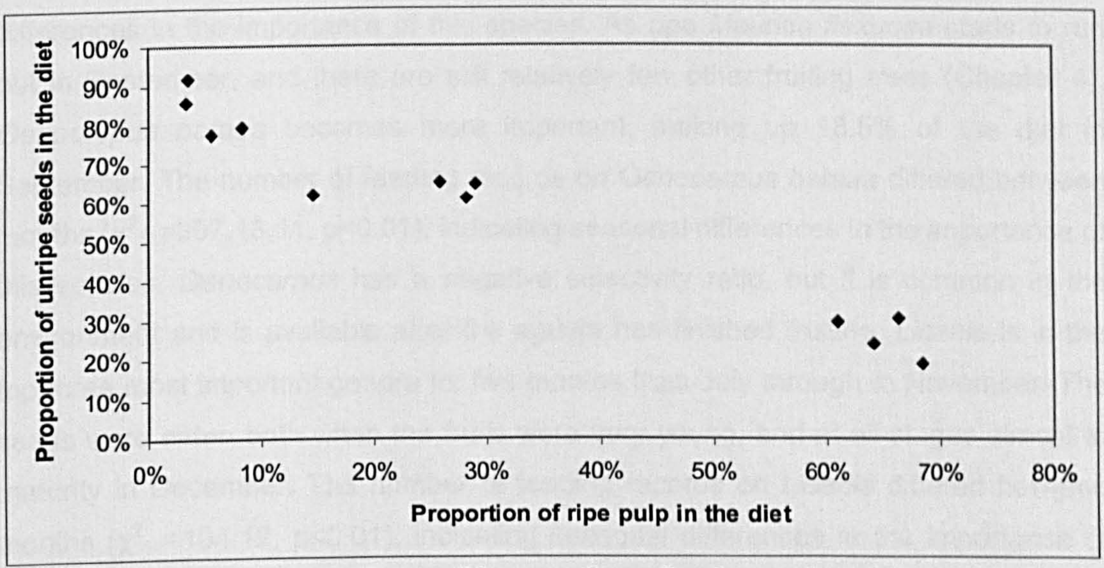

Figure 5.4 Correlation between the monthly proportions of unripe seeds and ripe pulp in the diet of *Cacajao calvus ucayalii*.

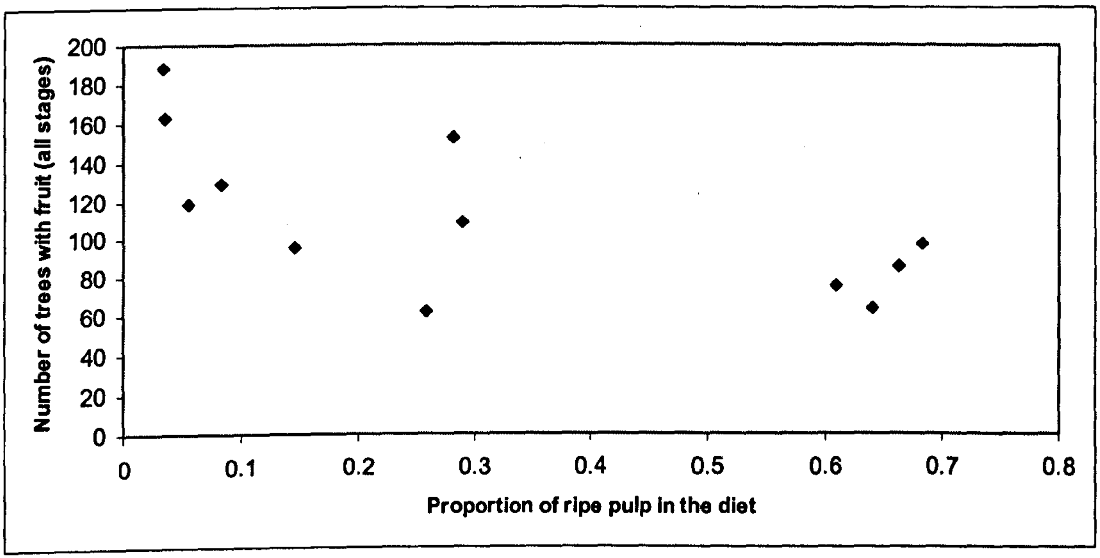

Figure 5.5 Correlation between the monthly proportion of ripe pulp in the diet of *Cacajao calvus ucayalii* and the total monthly fruit production in the home range of *Cacajao calvus ucayalii* at Lago Preto measured by the number of fruiting trees on the phenology transects weighted by the proportion of habitat at Lago Preto.

5.3.8 Temporal variation in the proportion of species in the diet.

Mauritia flexuosa was the most eaten item in May (48.0% of all records), June (61.4%), July (53.5%) and August (63.7%). The number of feeding records on *Mauritia flexuosa* differed between months (χ^2_{11}=889.11, p<0.01), indicating seasonal differences in the importance of this species. As ripe *Mauritia flexuosa* starts to run out in September, and there are still relatively few other fruiting trees (Chapter 4), *Oenocarpus bataua* becomes more important, making up 18.5% of the diet in September. The number of feeding records on *Oenocarpus bataua* differed between months (χ^2_{11}=307.13.11, p<0.01), indicating seasonal differences in the importance of this species. *Oenocarpus* has a negative selectivity ratio, but it is common in the environment and is available after the aguaje has finished fruiting. *Licania* is in the top three most important genera for five months from July through to November. The seeds were eaten both when the fruits were very young, and at all stages almost to maturity in December. The number of feeding records on *Licania* differed between months (χ^2_{11}=104.12, p<0.01), indicating seasonal differences in the importance of this genus. In October uakaris frequently fed on a fruiting vine of an unidentified species (unidentified family 1 cf. *Spondias*), eating the unripe seeds initially, but then the pulp. This species made up 12.9% of the diet in October, and the number of feeding records on it differed between months (χ^2_{11}=207.65, p<0.01), indicating seasonal differences in the importance of this species. In November the flowers of *Eschweilera* were the most used resource at Lago Preto, making up 14.4% of the feeding records. The number of feeding records on *Eschweilera* flowers differed

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between months (χ^2_{11}=244.43, $p<0.01$), indicating seasonal differences in the importance of flowers of this genus. The developing seeds of various species of *Eschweilera* are available for a long fruiting period, and featured in the top ten ranked food items in seven months of the year. The number of feeding records on *Eschweilera* seeds differed between months (χ^2_{11}=117.57, $p<0.01$), indicating seasonal differences in the importance of seeds of this genus. Various *Inga* species together made up 3.0% of the diet, and were eaten largely between November and March. The number of feeding records on *Inga* differed between months (χ^2_{11}=116.34, $p<0.01$), indicating seasonal differences in the importance of this genus. The unripe seeds of *Pourouma* and *Zygia* featured prominently in the diet in December, when they were the two highest-ranked food items. The number of feeding records on *Pourouma* differed between months (χ^2_{11}=243.42, $p<0.01$), as did the number of feeding records on *Zygia* (χ^2_{11}=303.56, $p<0.01$), indicating seasonal differences in the importance of these genera. The unripe seeds of the large latex-filled fruits of *Paranchornia* were also important in December (9% of the diet), and the number of feeding records differed between months (χ^2_{11}=160.28, $p<0.01$), also indicating seasonal differences in the importance of this genus. Between January and April, unripe seeds from the specious family Sapotaceae were particularly important. This family was ranked 2nd most eaten (10.4% of the diet). The number of feeding records on Sapotaceae differed between months (χ^2_{11}=282.38, $p<0.01$), indicating seasonal differences in the importance of this family. Unripe seeds of *Hevea* cf. *guianensis*, the fifth most eaten species in the study, were eaten in all months except August, September and October. *Hevea* was ranked in the top ten genera in the diet in March (4.0%), May (2.9%), June (9.0%), July (1.4%), November (5.2%), and December (7.7%). The number of feeding records on *Hevea* differed between months (χ^2_{11}=69.80, $p<0.01$), indicating seasonal differences in the importance of this genus. *Hevea* cf. *guianensis* was present in all habitats at Lago Preto.

5.3.9 Fruit protection and hardness and the use of specialised dentition

Fruits of many of the species consumed were protected by copious sticky white latex, particularly species in the families Apocynaceae and Sapotaceae. Some other species (e.g. *Iryanthera elliptica*) were protected by a bitter-tasting fluid that oozed out of the thick husk when punctured. The uakaris did not appear bothered by either of these kinds of protection, and their faces were sometimes covered in black (oxidised) latex after feeding on certain species.

Six of the top 10 species in the diet of *Cacajao calvus ucayalii* at Lago Preto were classified as 'hard' or 'very hard', two of the exceptions being the palms *Mauritia flexuosa* and *Oenocarpus bataua*. Uakaris at Lago Preto fed on fruit of different hardness categories in different proportions (ANOVA $F_{4,55}=23.587$ $p<0.0001$). In 2307 feeding records on fruits in which the hardness was recorded, 2% were on 'soft' fruits, 47% on 'medium' fruits (of which over half were *Mauritia flexuosa*), 18% were 'medium hard', 25% were 'hard' and 7% were 'very hard'.

'Medium hard' to 'very hard' fruits were opened using the enlarged canines. Seeds or seed fragments were often firmly embedded within the pieces of opened fruits. The uakaris used their procumbent incisors to remove these seeds, and incisor tooth-marks were often clearly visible on discarded seeds inside the husk. Seeds were then masticated with the molars, often tipping the head back when consuming large seeds, presumably to move the seed into position.

5.3.10 Animals in the diet

Invertebrates eaten included ants, caterpillars, termites, mantids, and katydids, but the majority where not identified beyond family level. 1.7% of feeding records were made up of animal material. Uakaris also spent 3.5% of their time searching living or dead leaves, presumably for invertebrates (see Chapter 6.3.1). Uakaris would often appear to pick items off branches or foliage and transfer them to the mouth, but it was rarely possible to confirm that invertebrates were being consumed. For these reasons it is hard to quantify the actual proportion of insects in the diet, and 1.7% is probably an underestimate. Twice, subgroups of uakaris (on both occasions mainly females and juveniles) fed for extended periods on a tree of unidentified species that was infested with caterpillars. Once, uakaris were observed catching termites on the wing with their hands. A male uakari was also observed holding a small, possibly partially-eaten lizard.

Once, a group of uakaris fed for almost an hour in an emergent *Couroupita guianensis* tree, splitting open the ends of the branches behind the leaves, revealing chambers containing small black commensal ants. The walls of these chambers were sweet, and the monkeys may have been consuming both the ants and the sap. When a group of uakaris visited the same tree 10 months later, they fed on the seeds of the immature fruits, and no individuals were observed feeding on the ants.

5.3.11 Diet differences between the age-sex classes

In the scan samples, the majority of feeding observations on fruits classified as 'very hard' (requiring considerable pressure with a knife to open), were by adult uakaris. Young uakaris (under 12 months old) were never recorded successfully opening and feeding on these species. Items with a hardness ratings of 'hard', and especially 'very hard', such *Paranchornia peruviana*, *Hevea* cf. *guianensis*, *Iryanthera elliptica*, and the unidentified 'Celastraceae sp2', were often dropped intact, with tooth-marks indicating that attempts had been made to open them. Adult male uakaris fed on harder fruits more than adult female uakaris (U=21590.0; P<0.001, two-tailed Mann-Whitney U-test).

5.3.12 Associations with other primates

During the study, uakaris at Lago Preto spent 224 hours 20 minutes (23.7% of contact time) in the vicinity of one or more other primate species. All primate species present at Lago Preto were observed in the vicinity of *Cacajao calvus ucayalii* on at least one occasion with the exception of *Cebuella pygmaea* which is difficult to detect. *Aotus nancymae* was only recorded in the vicinity of *Cacajao calvus ucayalii* on one occasion, and is nocturnal, so is excluded from the analysis. *Ateles chamek* was recorded with *Cacajao calvus ucayalii* on two occasions when a single individual travelled with a mixed group of *Cacajao calvus ucayalii* and *Lagothrix lagotricha* for 5 hours 30 minutes and 1 hour 40 minutes. Because of the low abundance of *Ateles chamek* at Lago Preto, this individual was considered aberrant and was excluded from the analysis.

Presence of other primate species in the vicinity of *Cacajao calvus ucayalii* does not necessarily constitute an association. Even occasional longer periods spent in the vicinity can be the result of chance, rather than association. The duration of periods spent in the vicinity of *Cacajao calvus ucayalii* differed between species (ANOVA $F_{7,300}$=15.843 p<0.0001). A pairwise multiple comparison (Tukey test) showed that *Saimiri sciureus* and *Lagothrix lagotricha* spent more time in the vicinity of *Cacajao calvus ucayalii* than other species (p<0.05). Associations can therefore be said to occur between *Cacajao calvus ucayalii* and *Saimiri sciureus* and between *Cacajao calvus ucayalii* and *Lagothrix lagotricha*. Occasionally, on hearing the calls of woolly monkeys, uakaris rushed towards the woolly monkey group until they were travelling or feeding together.

Differences in the time spent with *Cacajao calvus ucayalii* between *Cebus apella* and both *Pithecia monachus* and *Saguinus* spp. were close to significant (p=0.064 and p=0.082 respectively). Both *Cebus* species are wary of humans at Lago Preto, and many apparent associations may have been ended when the capuchin monkeys detected the researcher. Although the pairwise multiple comparison (Tukey test) did not show significant differences between the time either of the *Cebus* species spent with *Cacajao calvus ucayalii* and the time *Pithecia* and *Saguinus* spent with *Cacajao calvus ucayalii*, both *Cebus* species appeared to associate with *Cacajao calvus ucayalii*.

Cacajao calvus ucayalii spent 201 hours (21.3% of contact time) in association with *Lagothrix lagotricha, Saimiri sciureus, Cebus apella* or *Cebus albifrons*. In a total of 171 associations, 134 were of 2 species including *Cacajao calvus ucayalii*, 32 were of 3 species including *Cacajao calvus ucayalii*, and 5 were of 4 species including *Cacajao calvus ucayalii*.

In 945 hours 10 minutes of contact time there were 89 associations involving *Saimiri sciureus*, ranging from 10 minutes to 5 hours 40 minutes in duration (mean 82.2 minutes). There were 41 Associations involving *Lagothrix lagotricha* ranging from 10 minutes to 5 hours 10 minutes in duration (mean 98.5 minutes). There were 58 associations involving *Cebus apella*, ranging from 10 minutes to 5 hours 20 minutes in duration (mean 41.2 minutes). There were 25 associations involving *Cebus albifrons*, ranging from 10 to 80 minutes in duration (mean 28.4 minutes). Many associations did not end during the contact time, and in some cases mixed groups slept together and were found again in the morning. In these cases the association was not recorded as continuous.

5.3.13 Overlap in the diet and competition with other species

The diets of other primate species have not been studied at Lago Preto, but many of them certainly feed on some of the same plant species as *Cacajao calvus ucayalii*, particularly those species where ripe pulps are consumed. All species that associate with *Cacajao calvus ucayalii* at Lago Preto have been seen feeding on some of the same ripe pulps, including *Mauritia flexuosa*. The only other primate observed feeding on unripe seeds during the study period at Lago Preto was *Pithecia monachus*.

Non-primate seed-eaters at Lago Preto include the cavid rodents *Dasyprocta fuliginosa*, *Myoprocta pratti* and the squirrels *Sciurus* spp. *Dasyprocta* spp. feed on large-seeded species in the families Fabaceae, Arecaceae, Lecythidaceae, Chrysobalanaceae, Myristicaceae and Meliaceae (Silvius and Fragoso 2003) many of which are also eaten by *Cacajao*. Since *Dasyprocta* and *Myoprocta* live entirely on the forest floor and feed on mature seeds, they do not compete with uakaris for seeds in the canopy. *Cacajao calvus* at Lago Preto were not observed feeding on the forest floor, but it is probable that *Cacajao* reduces seed availability for terrestrial rodents by reducing the number of seeds that reach maturity. There have been few studies on Amazonian squirrels, but *Sciurus* spp. at other sites feed on a variety of seeds (Emmons and Feer 1997), and there is likely to be dietary overlap with *Cacajao*.

Uakari monkeys are particularly abundant at Lago Preto and it is possible that they impact on the abundances of other animals with similar diets. Using data from 4 sites on the Yavarí and Yavarí-Mirín Rivers (Table 5.6), there is no correlation between the abundances of *Cacajao calvus ucayalii* and *Lagothrix lagotricha* (Pearson Correlation, n=4, r = -0.521, p>0.05) (Figure 5.6). There is no correlation between the abundances of *Cacajao calvus ucayalii* and *Pithecia monachus* (Pearson Correlation, n=4, r = -0.006, p>0.05) (Figure 5.7). Despite the small number of sites considered, there is a negative correlation between the abundances of *Dasyprocta fuliginosa* and *Cacajao calvus ucayalii* (Pearson Correlation, n=4, r = -0.996, p<0.01) (Figure 5.8). There is also a negative correlation between the abundances of *Sciurus* spp. and *Cacajao calvus ucayalii* (Pearson Correlation, n=4, r = -0.979, p<0.05) (Figure 5.9). At Lago Preto the abundance of *Cacajao calvus ucayalii* is extremely high and the abundances of *Dasyprocta fuliginosa* and *Sciurus* spp. are particularly low.

Table 5.5 Abundance of fruit pulp and seed-eating species at sites on the Yavarí and Yavarí-Mirín. Abundance data at Lago Preto from Puertas *et al.* (2006). Density and abundance data from Yavarí and Yavarí-Mirín from Salovaara *et al.* (2003).

Species	Abundance (ind./100 km)			
	Yavarí	Lower Yavarí-Mirín	Upper Yavarí-Mirín	Lago Preto
Red uakari monkey *Cacajao calvus*	14.79	47.33	6.07	308.97
Woolly Monkey *Lagothrix lagotricha*	181.78	114.26	28.31	24.83
Monk saki monkey *Pithecia monachus*	23.86	23.76	33.12	27.59
Black agouti *Dasyprocta fuliginosa*	5.12	4.60	5.95	3.45
Amazonian squirrel *Sciurus* spp.	8.08	6.64	10.44	2.71

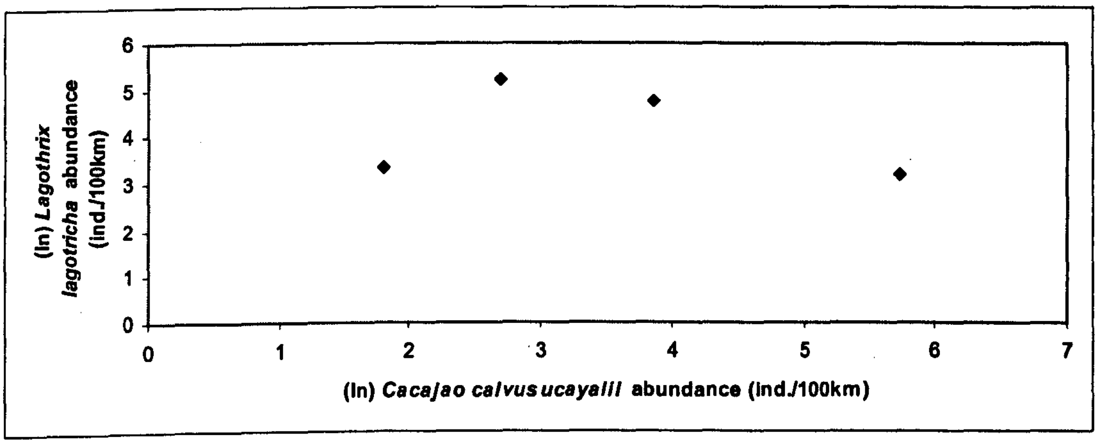

Figure 5.6 Abundances of *Cacajao calvus ucayalii* at various sites on the Yavarí and Yavarí-Mirín plotted against abundances of *Lagothrix lagotricha*.

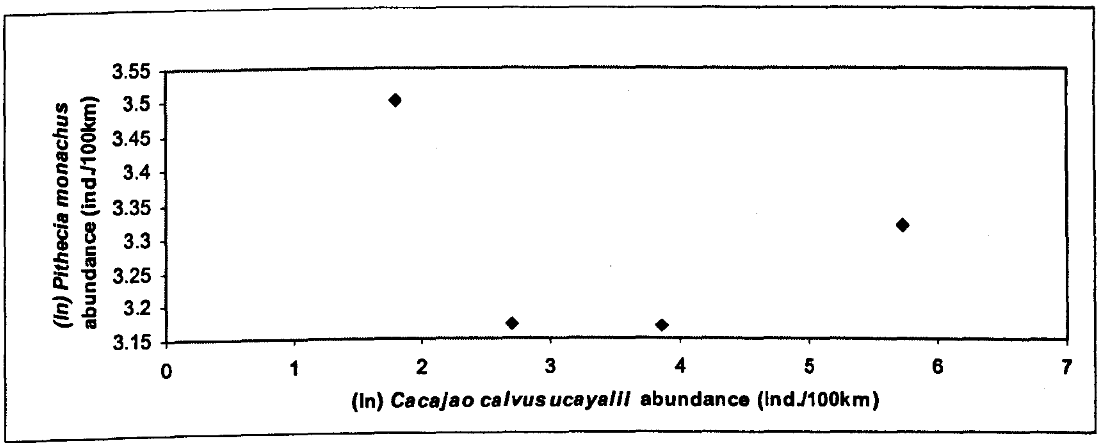

Figure 5.7 Abundances of *Cacajao calvus ucayalii* at various sites on the Yavarí and Yavarí-Mirín plotted against abundances of *Pithecia monachus*.

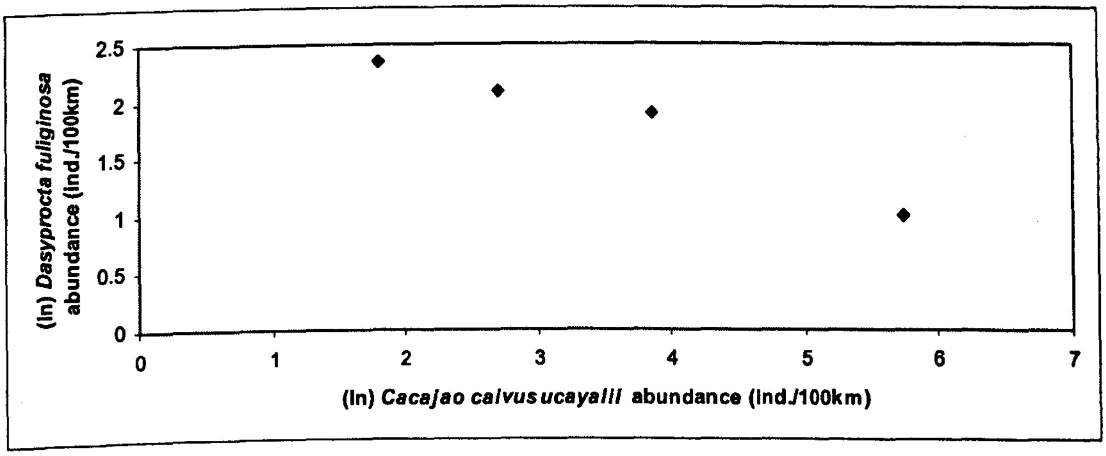

Figure 5.8 Abundances of *Cacajao calvus ucayalii* at various sites on the Yavarí and Yavarí-Mirín plotted against abundances of *Dasyprocta fuliginosa*.

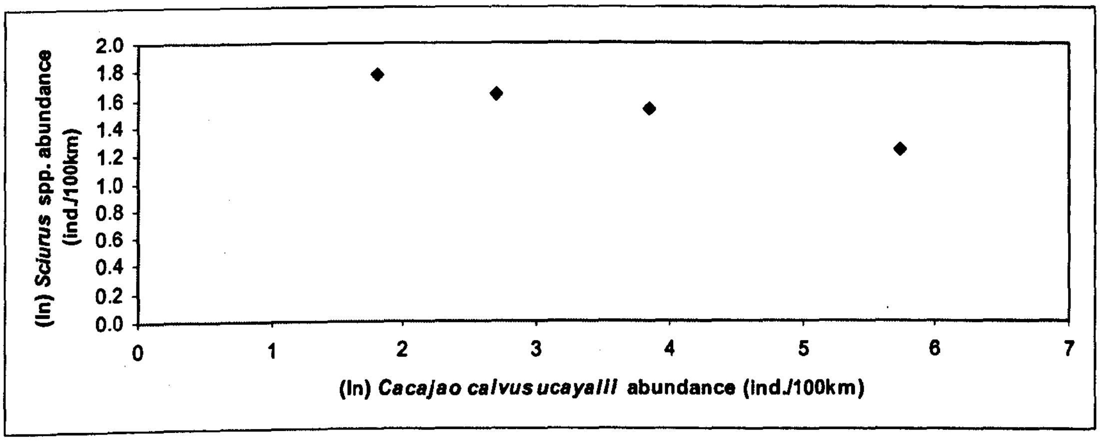

Figure 5.9 **Abundances of *Cacajao calvus ucayalii* at various sites on the Yavarí and Yavarí-Mirín plotted against abundances of *Sciurus* spp.**

5.4 Discussion

While the ripe pulp of *Mauritia flexuosa* was clearly the most frequently eaten item at Lago Preto between May and August, the main resources for *Cacajao calvus ucayalii* for most of the year are immature and unripe seeds. Seeds featured in 58.3% of feeding records at Lago Preto. This is similar to *Cacajao calvus calvus* at Lake Teiú (66.9%) (Ayres 1986), but less than *Cacajao melanocephalus melanocephalus* at Pico da Neblina (81%) (Boubli 1999). The large proportion of ripe pulp eaten at Lago Preto compared to other sites is due largely to the dominance of *Mauritia flexuosa* in the diet. *Mauritia flexuosa* does not occur at Lake Teiú, and only made up 4.5% of the diet at Pico da Neblina (Boubli 1999). *Cacajao calvus calvus* at Lake Teiú fed mainly on immature seeds during the low water season when few ripe fruits were available, eating more ripe pulp in the high water season (Ayres 1986). This was seen to some extent in *Cacajao calvus ucayalii* at Lago Preto during high water in March when ripe pulp consumption was quite high, but when there was a relative seasonal shortage of fruit across all habitats at Lago Preto, the ripe pulps of *Mauritia flexuosa* and *Oenocarpus bataua* dominated the diet. *Mauritia flexuosa* palms are nutritious, the pulps consisting of 53% fat, 43% carbohydrate and 4% protein (Lopes *et al.* 1980), and it cannot be said that there is a food shortage for the uakaris when this species is available. Many other primate species also feed extensively on *Mauritia flexuosa* at Lago Preto (*pers. obs.*), and the species is also very important in the diets of many terrestrial animals (Bodmer 1989). It is considered a key species in western Amazonian forests (Bodmer *et al.* 1990, 1999).

Through the rest of the year, the diet of *Cacajao calvus ucayalii* is dominated by large-seeded, hard-shelled species, largely from the families Lecythidaceae, Sapotaceae and Chrysobalanaceae. In 95.2 hours of observation, Aquino (1995) recorded *Cacajao calvus ucayalii* feeding on around 50 tree species, of which the most important were *Couma macrocarpa, Schistostemon* spp., *Eschweilera* spp., *Mauritia flexuosa, Pouteria* spp., *Rhigospira quadrangularis* and *Parahancornea peruviana.* The fruits of most of these species are hard shelled. These species were all important at Lago Preto; with the exception of *Schistostemon* spp. *Licania* was also very important both at Lago Preto, and to *Cacajao calvus calvus* at Lake Teiú (Ayres 1986). Immature *Licania* seeds were still available long after ripe *Mauritia flexuosa* had run out and may be a particularly important resource between October and December before fruiting begins to peak in the *terra firme* and *várzea* forests. Immature and unripe fruit has been found to be available for 3 or 4 times longer than ripe pulps (Leighton and Leighton 1982; Norconk 1996), so predators on unripe seeds are likely to be less subject to seasonal food shortages than species dependent on ripe pulp (Norconk 1998). There is perhaps a brief period of scarcity of food for uakaris when the aguaje finishes towards the end of September and in October and November. During this period, flowers of *Eschweilera* are eaten, as they are in the same months at Lake Teiú by *Cacajao calvus calvus* (Ayres 1986). Flowers and nectar made up 3.4% of the diet at Lago Preto; less than at Lake Teiú, but still making up an important part of the diet during some months.

Ayres (1986) recorded close to 83 plant species in the diet of *Cacajao calvus calvus* during one year (and nearly 100 over two years). Of these, five made up close to 50% of the diet. At Lago Preto, over 164 species were identified in the diet of *Cacajao calvus ucayalii*, and the top 10 species eaten made up 45.4% of the diet. Ayres (1986) recorded 176 tree species in 996 sampled trees across all habitats at Lake Teiú, compared to 368 species in 1464 sampled trees across all habitats at Lago Preto. The higher diversity in the diet at Lago Preto must be largely due to the larger number of tree species present at Lago Preto. Only two of the five commonest species eaten at Lake Teiú were from genera making up more than 2% of the diet of *Cacajao calvus ucayalii* at Lago Preto; *Eschweilera* and *Chrysophyllum*. The most important species for *Cacajao calvus calvus* at Lake Teiú was *Eschweilera turbinata* (synonymous with *Eschweilera albiflora*), its hard-shelled fruit and flowers making up 15% of the diet. This species was also common at Lago Preto, and occurred in the diet of *Cacajao calvus ucayalii*; it was originally identified as a morphospecies during the study, which was eventually found to include *Eschweilera albiflora* and *Eschweilera parvifolia.* Together these similar species made up 1.9% of the diet, and were ranked 8th most frequently eaten. *Eschweilera* appears to be important to most populations of *Cacajao. Cacajao melanocephalus ouakary* at Jaú fed on several *Eschweilera* species (Barnett *et al.* 2005), but it was of lesser importance to *Cacajao melanocephalus melanocephalus* at Pico da Neblina (Boubli 1999). These were both relatively-short studies and *Eschweilera* may have been important during months where no data were collected.

Ayres (1986) examined stomach contents of 5 *Cacajao calvus calvus* and 3 *Cacajao melanocephalus.* All these animals had large numbers of insects or other arthropods in their stomachs. *Cacajao calvus calvus* (mean 106.4 insects) had more insects than *Cacajao melanocephalus* (mean 21.0 insects) but the sample sizes are too small to infer anything, except to confirm that *Cacajao calvus calvus* feeds on seasonal infestations of Lepidoptera larvae. These results, and the observation that uakaris at Lago Preto spent 3% of their time searching foliage, suggest that insect eating is probably more important to the genus than suggested by the Figure of 1.7% in this study.

The preference for hard-shelled fruits in the Pitheciinae is well documented (see Kinzey 1992). At other sites, *Cebus apella*, *Cebus albifrons* and *Lagothrix lagotricha* are also known to feed on seeds (Peres 1991), but seeds are almost certainly far less important to these species. These species have less specialised dentition than *Cacajao*, which does not enable them to open very hard fruits. *Cebus apella* opens some hard fruits such as *Cariniana* (Peres 1991) and *Couroupita* (*pers. obs.*) by bashing them against large branches. *Pithecia* have been studied at other sites and unripe seeds make up a large proportion of the diet (Norconk and Conklin-Brittain 2004; Cunningham and Janson 2006). Kinzey and Norconk (1990) attempted to quantify the hardness of fruits preferred by three primate species, comparing the hardness of fruits in the diet of *Chiropotes satanas*, *Pithecia pithecia* and *Ateles paniscus.* Kinzey and Norconk found that *Chiropotes* can open harder-shelled fruits than either *Pithecia* or *Ateles.* No studies have compared the hardness of fruits in the diets of *Cacajao* with other species, but *Cacajao* has similar dentition and diet to *Chiropotes* (Ayres 1989). From the size of the dentition it can be assumed that *Cacajao* will be able to open harder-shelled fruits than sympatric *Pithecia sp.* A semi-free-ranging subadult *Cacajao calvus ucayalii* at the Pilpintuwasi Amazon Animal Orphanage in Iquitos was able to open very quickly all unopened seeds of *Bertholletia excelsa* presented, while a subadult *Pithecia* cf. *monachus* at the same site was apparently unable to open most examples of the seed (*pers. obs.*).

Quantitative data could not be collected due to interference from other tame monkeys at the site. It appears likely that *Cacajao* is able to exploit several 'very hard' shelled species that the sympatric *Pithecia* is not. Similarly, larger individuals of *Cacajao calvus ucayalii* are able to open harder fruits than smaller individuals. Boubli (1999) observed that juvenile *Cacajao melanocephalus melanocephalus* could not open many of the harder top-ranking species eaten by adults at Pico da Neblina, and obtained part of their food intake by taking opened fruits from adults. Boubli suggested that this may be the reason for his observation that juveniles were often seen in close proximity to adult females.

Male *Cacajao calvus ucayalii* at Lago Preto feed on harder fruits than adult females and younger animals. Sexual dimorphism is pronounced in the dentition of *Cacajao calvus*, perhaps more so than in *Chiropotes* (Kay *et al.* 1988) or even *Cacajao melanocephalus* (Hershkovitz 1987a). The canines and the jaw are proportionally larger in adult males, and are accompanied by well developed temporal 'jaw closure' muscle masses overlying the frontal and parietal bones of the skull. These attach to a sagital crest in mature individuals (Hershkovitz 1987a). Thorén *et al.* (2006) showed that sexual selection has a stronger effect on canine size than body size in haplorhine primates, and the sexual dimorphism in *Cacajao* has prompted some to predict that there might be some display function to the teeth (R. Kay pers. com.), and they could also be used in fighting. Fontaine (1981) recorded some 'open-mouth' behaviour patterns in captive *Cacajao calvus ucayalii* at Monkey Jungle in Florida, but these were not obvious at Lago Preto. While the large canines appear to be functional in enabling males to open harder fruits than females and young, it seems likely that the muscle masses and larger teeth have more than a purely fruit-opening function.

Twelve other primates occur sympatrically with *Cacajao calvus ucayalii* on the Yavarí River, one of the highest primate diversities in South America. This may be due to the particularly high floral diversity of the forests between the Amazon and the Yavarí rivers (Puertas and Bodmer 1993). The high number of sympatric primate species living in Yavarí Valley inevitably raises questions about how the various species compete with each other for resources, and how this competition may have affected the composition of the primate community. Ayres (1986) was apparently unaware of the occurrence of *Cacajao calvus ucayalii* in extensive *terra firme*, which was previously not well documented. Ayres proposed that non-occurrence *of Cacajao calvus calvus* in the *terra firme* was likely to be a consequence of competition with other arboreal frugivores. *Cacajao* and *Chiropotes* have similar diets and occupy similar niches in their respective ranges, though *Chiropotes* lives exclusively in *terra firme* forests (Ayres 1989). Ayres (1989) suggested that *Chiropotes* could live in *terra firme* forests because primate diversity is lower in eastern Amazonia in the range of *Chiropotes*, and competition was lower in *terra firme* for this reason. It may be more likely that the diet of *Chiropotes* enables it to compete in the *terra firme* forests of eastern Amazonia in the same way as the diet of *Cacajao calvus calvus* enables it to live *várzea* forests. *Terra firme* forests in eastern Amazonia have more seasonal rainfall than those in western Amazonia, leading to more seasonal peaks in fruit production, similar to those seen in the highly-seasonal flooded forest habitats in western Amazonia. *Chiropotes* and *Cacajao* are both able to switch to immature seeds during periods of scarcity of ripe pulps. The finding that *Cacajao calvus ucayalii* uses *terra firme* more than any other habitat, may explain why the ranges of *Cacajao* and *Chiropotes* do not overlap, for they are ecologically similar.

Primate diversity in north-eastern Peru is extremely high, and there are several areas where sympatric species number 13 or more (Terborgh 1983; Janson and Emmons 1990; Puertas and Bodmer 1993). Although data have not been collected on the diets of other species at Lago Preto, observations suggest that there is considerable dietary overlap between the primate species on the Yavarí. This is particularly evident from April to July when *Mauritia flexuosa* palms are in fruit and mixed groups of primates feeding on them are common. Terborgh (1983) provides evidence that, in seasons when resources are limited, five species of sympatric primates (*Cebus apella, Cebus albifrons, Saimiri sciureus, Saguinus fuscicollis* and *Saguinus imperator)* in Manu National Park, Peru show a striking decrease in dietary overlap. Similarly one would expect species at Lago Preto to feed on different resources during seasonal shortages. Because *Mauritia flexuosa* fruits at a time when there is a relative shortage of fruit in other habitats, however, the levels of seasonality seen at some other sites, including Manu and Lake Teiú are not seen on the Yavarí, and there is no obvious period of overall low fruit availability. There are very strong seasonal patterns of fruit availability in some of the individual habitats at Lago Preto. This leads to seasonal variation in the use of habitat. A community member from Nueva Esperanza on the Yavarí-Mirín River, a community which occasionally hunts red uakari monkeys, commented during an informal interview that uakaris eaten in the community were fatter (and therefore better to eat) in April, coinciding with a perceived abundance of food, particularly 'lechecaspi' (*Couma* spp.) and 'Sapote' (Sapotaceae).

Cacajao calvus ucayalii at Lago Preto regularly form mixed parties with *Lagothrix lagotricha, Cebus apella, Cebus albifrons* and *Saimiri sciureus*. Because

Cacajao calvus feed largely on unripe seeds, they are perhaps less likely to be affected by increased scramble competition for food when travelling with species which prefer ripe fruits, especially since they travel in large groups anyway. Because uakaris also eat ripe fruit, they may also benefit from travelling with other primates who locate fruiting trees, as observed in *Saimiri sciureus* and *Cebus apella* in Manu National Park by Podolsky (1990). *Lagothrix lagotricha* may be able to reduce the effects of this competition by physically monopolising smaller food patches, as it did against other species at Tinigua National Park (Stevenson *et al.* 2000). *Lagothrix* was occasionally observed directing aggression towards *Cacajao* when in very close proximity at Lago Preto. Squirrel monkeys have a higher component of insects in their diet, and tend to forage lower in the canopy (Terborgh 1983), and may benefit by feeding on insects disturbed by uakaris, as well as from increased vigilance from aerial predators.

Although sometimes observed in the vicinity of them, *Pithecia* did not associate with *Cacajao calvus ucayalii* at Lago Preto, and in fact appeared to be disturbed by the presence of the uakaris. Aquino (1998) also recorded mixed groups of *Cacajao calvus ucayalii* with *Lagothrix lagotricha, Cebus apella, Cebus albifrons* and *Saimiri sciureus*, and not *Pithecia*. The diet of *Pithecia* is much closer to that of *Cacajao* than the diets of other primates at Lago Preto, and it is possible that they do not associate with uakaris there because there is intense scramble competition for seeds in large uakari groups. Uakaris also have a much longer day range than *Pithecia* (Setz 2006), and might simply leave the *Pithecia* behind, or leave their territory too quickly. *Pithecia* were recorded 'associating' with *Cacajao* by Leonard and Bennett (1996), and this is also reported by locals in single individuals or pairs of uakaris on the Yanayacu River (unconfirmed reports, see Chapter 8). This may be due to smaller group sizes, where the benefits to one or both of the species in locating fruiting trees might outweigh the costs of increased scramble competition. This may occur where populations have been reduced by hunting. It is also possible that they are not travelling together, but just feeding in the same trees, which would not constitute an association by the definition used in this study. Leonard and Bennett (1996) did not mention how they defined 'associations'.

Norconk *et al.* (1997) highlighted striking similarities between the diets of macaws (*Ara* spp.) and *Chiropotes satanas*, and there can be little doubt that a similar situation exists for *Cacajao* (Barnett *et al.* 2005). The degree to which these species compete has not been measured. Similarly, several rodents feed on the seeds of hard-shelled fruits, although at later stages of seed development. At Lake Teiú there are no cavid rodents, because the site is inundated for much of the year, and uakaris seem to exploit this vacant niche by foraging on fallen, especially germinating, seeds on the ground during the low-water season (Ayres 1986). On the Yavarí, where there is *terra firme*, terrestrial mammals are likely to find these resources first. This may be why uakaris were never seen foraging on the ground at Lago Preto, although there is probably also a higher risk of predation from big cats on the Yavarí. The negative correlation between the abundances of *Cacajao* and other seed-eating mammals suggests that *Cacajao calvus ucayalii* might be restricting the abundances of these seed-eating rodents through competition. Negative correlations between uakari populations and populations of seed-eating rodents, particularly the arboreal squirrels, and not with pulp-eating monkeys, suggest that *Cacajao calvus ucayalii* populations might be limited by the availability of large seeds rather than the fruit pulps, but cause and effect has not been established, and there may be other ecological reasons for these patterns.

5.5 Summary

1. 50.6% of the diet of *Cacajao calvus ucayalii* at Lago Preto was made up of unripe seeds, 37.4% was ripe pulp, 3.7% was flowers and nectar, and the remaining 8.3% was made up of other animal material and plant parts, including mature seeds, unripe pulps, arils, leaves and gums.

2. One-hundred and sixty-four plant species were identified in the diet of *Cacajao calvus ucayalii* from feeding records. *Mauritia flexuosa* (ripe pulp) was the most eaten species during the study, making up 20.0% of the diet. *Licania heteromorpha* (unripe seeds) was the second most consumed species followed by *Couma macrocarpa* (unripe seeds and ripe pulp), *Chrysophyllum sanguinolentum* (unripe seeds) and *Hevea* cf. *guianensis* (unripe seeds).

3. The most eaten genera were *Mauritia* (principally ripe pulp, but also seeds), *Eschweilera* (unripe seeds and flowers), *Licania* (unripe seeds), *Couma* (unripe seeds and pulp) and *Pouteria* (principally unripe seeds, but also pulp).

4. The commonest family in the diet was Arecaceae, followed by Sapotaceae, Fabaceae and Lecythidaceae. Chrysobalanaceae, Apocynaceae, Moraceae, Myristicaceae and Euphorbiaceae are also important families in the diet.

5. According to Ivlev's index of selectivity (Ivlev 1961), *Parkia*, *Pourouma*, *Hevea*, *Tovomita* and *Brosimum* were the genera most positively selected in the diet. The most eaten genus in the diet, *Mauritia*, was positively selected, but not as strongly as several other genera. *Mauritia* is very common in the environment, and produces large amounts of fruit. Similarly, other commonly-eaten genera such as *Pouteria*, *Licania* and *Eschweilera* are very common in the environment and, while they were positively selected, selection was not as strong as for other genera.

6. Ripe pulp contributed 60% of the diet from May to August, whilst unripe seeds were most common from September to April. The proportion of ripe pulp in the diet is negatively correlated with the availability of all fruits in the home range of *Cacajao calvus ucayalii* at Lago Preto. This indicates that *Cacajao calvus ucayalii* switches from feeding on unripe seeds to ripe pulps during times of lower fruit availability. These periods coincide with a high availability of ripe pulps of *Mauritia flexuosa* and *Oenocarpus bataua*, which are important in the diet of *Cacajao calvus ucayalii* at these times.

7. Uakaris fed largely on the seeds of hard-shelled fruits, including some very hard species. Young uakaris under 12 months old were never recorded successfully opening and feeding on these species, and Adult male uakaris fed on harder fruits more than adult female uakaris.

8. Animal material made up 1.7% of feeding records, but this is probably an underestimate, because uakaris spent 3.5% of their time searching foliage.

9. *Cacajao calvus ucayalii* at Lago Preto spent 21.3% their time in association with *Lagothrix lagotricha*, *Saimiri sciureus*, *Cebus apella* or *Cebus albifrons*. Both *Cebus* species are wary of humans at Lago Preto, and many apparent associations may have been ended when the capuchin monkeys detected the researcher.

10. The diets of other primate species have not been studied at Lago Preto, but many of them certainly feed on some of the same plant species as *Cacajao calvus ucayalii*, particularly those species where ripe pulps are consumed. The only other primate observed feeding on unripe seeds during the study period at Lago Preto was *Pithecia monachus*. There was no correlation

between the abundances of *Cacajao calvus ucayalii* and *Lagothrix lagotricha* or *Pithecia monachus* at sites on the Yavarí, but there was a negative correlation between the abundances of both *Sciurus* spp. and *Dasyprocta fuliginosa* with *Cacajao calvus ucayalii*. This may be due to competition for large seeds.

Chapter 6

Habitat Use in *Cacajao calvus ucayalii* and the Ecological Determinants of its Fission-Fusion Grouping Pattern

6.1 Introduction

6.1.1 Ranging and habitat use in *Cacajao*

Cacajao is generally considered a habitat specialist on seasonally-flooded forests (e.g. Ayres 1986; Barnett and Brandon Jones 1997; Chapter 1). *Cacajao melanocephalus* occurs in black-water *igapó* flooded forests, and *Cacajao calvus* occurs in white-water *várzea* forests, but many populations of *Cacajao* show evidence of seasonal migration between other forest types. Defler (1989) noted that *Cacajao melanocephalus ouakary* in Colombia foraged in *terra firme* away from *igapó* flooded forest for much of the year, but during the early stages of the wet season spent almost all of their time in the *igapó*. Barnett *et al.* (2005) also found that when the waters were at their highest, *Cacajao melanocephalus ouakary* occurred only in *igapó* forest, but used other forest types during the low-water season. Aquino (1998) suggested that *Cacajao calvus ucayalii* migrated from *terra firme* to *aguajal* swamp forests between March and July, largely to feed on *Mauritia flexuosa* palms. *Cacajao calvus calvus* appears to be something of an exception, in being restricted to extensive *várzea* (Ayres 1986).

Ayres (1986, 1989) compared the feeding ecology of *Cacajao* with that of *Chiropotes*, which occurs exclusively in *terra firme* forests. Ayres proposed that the non-occurrence of *Cacajao* in the *terra firme* was likely to be a consequence of competition with other arboreal frugivores. *Cacajao* is distributed through western Amazonia, and is generally sympatric with more primate species than *Chiropotes* is in eastern Amazonia. Ayres was assuming that *Cacajao* only occurred in seasonally-inundated habitats, but Heymann (1992) and Aquino (1999) found *Cacajao calvus ucayalii* in *terra firme*, near the Quebrada Blanco in the Yavarí-Ucayali interfluvium, many kilometres from *várzea* forest. Preliminary studies on the Yavarí (Bowler 2003) also recorded *Cacajao calvus ucayalii* ranging largely through *terra firme* and *aguajal* habitats. *Cacajao calvus ucayalii* is sympatric with twelve other primates in these areas, one of the highest primate diversities in South America. Since *Cacajao calvus ucayalii* does not appear to avoid competition in the Yavarí-Ucayali interfluvium by using *várzea* forests exclusively, it must avoid competition in other ways.

6.1.2 Determinants of group size in primate populations

Male and female primates adopt different strategies to maximise their genetic contribution to the next generation. Female reproductive success depends on the number of healthy offspring raised, which in turn depends on food, and safety from predators. On the other hand, male reproductive success depends largely on the number of females fertilised, and is more variable than female reproductive success (Dunbar 1996). Access to females is the most important factor determining a male primate's reproductive strategy. Several authors have shown that males 'go where the females are' and that male group size depends on female group size (e.g. Altmann 1990; Mitani 1996). Because male group size is determined largely by female group size, the strategies adopted by female primates ultimately determine primate grouping patterns.

In deciding whether to forage alone or in groups, female primates must look to maximise access to food and protection from predators. Access to food may be reduced in groups because of competition from co-foragers, while some benefit may be gained in groups from increased ability to locate fruiting trees, or from increased ability to monopolise resources (Wrangham 1989). Larger groups confer advantages in predator avoidance, and in reducing the cost of vigilance (Clutton-Brock and Harvey 1977; Terborgh 1983). Group sizes are therefore largely a trade-off between predation risk and within-group competition (Dunbar 1996). There are additional factors which may determine group sizes. Females may receive some protection from other group members from the infanticide of their offspring by extra-group males (Dunbar 1996). There may also be cognitive constraints on group sizes, related to the number of individuals with which an individual can maintain a relationship (Joffe and Dunbar 1997). The concern in this Chapter is primarily with the ecological determinants of group size, and in particular the effects of the distribution of resources on group sizes in *Cacajao calvus ucayalii*.

6.1.3 Group fragmentation and fission-fusion societies

Many primate species travel in groups that do not change in size in the short term. The size of these groups is often determined by long-term demographic effects. Some primate species appear more flexible in the size of the groups they travel in. Ayres (1986, 1989) described *Cacajao calvus calvus* as 'foraging in groups of variable sizes', but did not use the term 'fission-fusion' to describe the grouping system. More recently the term has been used to describe the grouping systems of the Pitheciinae, including *Cacajao* (e.g. Kinzey and Cunningham 1994; Defler 1999; Veiga *et al.* 2006). The term fission-fusion is generally used for any social organisation that is flexible in the size and composition of the groups within a community (Chapman *et al.* 1993). Common chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles* spp.) show a particular kind of fission-fusion sociality in which all-male groups patrol territory borders, and females are frequently solitary

(Nishida 1968; Wrangham 1977; Goodall 1986; McFarland 1986). McFarland (1986) posited that these similar social organisations have evolved in response to similar selection pressures. Symington (1988, 1990) showed that group size in *Ateles chamek* was correlated with food crop size. Predation pressure is low in *Ateles* and *Pan* (McFarland 1986; McFarland-Symington 1990), and McFarland-Symington (1990) concluded that it probably did not restrict the lower limit of group sizes. Rather, spatial and temporal patchiness of food resources resulted in a high-level of feeding competition between females within groups, leading to the evolution of fission-fusion social organisations in these genera. Chapman *et al.* (1995) suggested that social strategies probably influence the relationships between food resource variables and subgroup size in both *Ateles geoffroyi* and *Pan troglodytes.*

The grouping patterns seen in *Ateles* and *Pan* are clear examples of fission-fusion systems. Most Neotropical primates have previously been thought to forage, feed and rest in cohesive groups (Robinson and Janson 1987). Strier (1989) observed that these definitions obscured intermediate grouping patterns, where some degree of group fragmentation occurred. Kinzey and Cunningham (1994) and Defler (1999) noted that in several Neotropical primates, group fragmentation has been recorded to various degrees, often with some variability between populations of the same species. *Cebus olivaceus* spread out very widely to travel (Robinson 1988), and some groups of *Lagothrix lagotricha* foraged in separate subgroups during the day (Soini 1986; Defler 1996). Defler's groups of *Lagothrix lagotricha* were often in vocal contact and usually came together in the evening to sleep, or when large fruit crops were available. Some groups of *Saimiri* fissioned into smaller groups (Baldwin and Baldwin 1972), as did *Alouatta palliata* (Glander 1987), and *Saguinus* spp. (Castro and Soini 1977). More extreme examples of group fragmentation occurred in *Cacajao calvus* (Ayres 1986) and *Cacajao melanocephalus* (Defler 1999), and very similar grouping systems have been observed in *Chiropotes satanas* and *Chiropotes albinasus* (Veiga *et al.* 2006). Subgroups were also observed in *Chiropotes satanas* by van Roosmalen (1981), but other populations of *Chiropotes* do not appear to fission (Ayres 1989). It is clear that there is a continuum between primate groups that spread out and partially fission, and extreme cases where subgroups may be out of contact. There is also flexibility within species in the degree of cohesiveness of groups. It is the extreme cases of group fragmentation, such as those that occur in *Cacajao,* that are generally referred to as fission-fusion (e.g. Kinzey and Cunningham 1994).

6.1.4 Group sizes in *Cacajao*

Large group sizes are typical for the genus *Cacajao*. *Cacajao melanocephalus* occurs in groups of 100 or more individuals (Boubli 1994, 1999; Defler 1999; Barnett *et al.* 2005), and *Cacajao calvus calvus* in groups of 45 to 50 (Ayres 1986, 1989). *Cacajao calvus ucayalii* has been observed in groups of 200 or more individuals (Aquino 1988, 1998; Bowler 2003). Most groups of *Cacajao* that have been studied have fissioned into smaller groups (Ayres 1986; Heymann 1992; Aquino 1998; Defler 1999; Bowler 2003; Barnett *et al.* 2005), but Boubli (1994, 1997, 1998, 1999) studied a group of 70 *Cacajao melanocephalus melanocephalus* in *caatinga* forests that did not fission, although the group spread out widely during travel. Heymann (1992) suggested that the type of organisation observed in *Cacajao calvus* could be linked with seasonal migrations.

Long-term studies of some species (e.g. Altmann and Altmann 1979; Goodall 1986; Dunbar 1984) have shown that changes in group size are not determined by short-term ecological variation, but by long-term demographic and social relationships. While this may also be true in *Cacajao calvus ucayalii* for the overall size of the group, foraging group sizes often change on a daily or hourly basis at Lago Preto. Foraging group sizes are therefore probably determined by ecological factors, especially outside of the uakaris' short breeding season (Chapter 7). *Cacajao calvus ucayalii* at Lago Preto forage in flexible groups of various sizes, ranging from a few individuals to several hundred. *Cacajao calvus ucayalii* ranged through three different habitats at Lago Preto. The effects of different patterns of food availability in these three habitats on the ranging activity and grouping patterns observed in *Cacajao calvus ucayalii* are examined in this Chapter. These analyses give an insight into how the uakaris use the environment, and the resources within, and are invaluable in answering questions on why the uakaris have a patchy range, or how changes in the environment might impact uakari groups and populations.

6.2 Methods

Data were collected at the Lago Preto study site in the Lago Preto Conservation Concession using scan sampling at ten-minute intervals (Altmann 1974). On each scan, the location, habitat and size of the uakari group being followed were recorded. The behaviour and age-sex class of each individual uakari visible during the scan was recorded. Any interactions observed between uakaris and their potential predators were recorded in detail *ad libitum.* A full account of the methods used is given in Chapter 3.

Overall activity budgets were calculated from the sum of the number of records of each behaviour each month, multiplied by the average number of individuals scanned each month, divided by the number of individuals scanned in the month.

The boundaries of the home range were determined using locations recorded in the scans. Because uakaris left the study area on occasion, and either could not be found or could not be followed, the resulting home range is a minimum estimate. Because individuals and groups were not identifiable, it is not clear if all the subgroups used the entire home range, or just overlapping parts of it. Because of these uncertainties in estimating the home range, the home range was determined using the simple 'minimum-convex polygon method' (Stickel 1954), modified with some assumptions based on habitat topography and the location of barriers to ranging, such as lakes.

Habitat preferences were calculated by Ivlev's index of Selectivity, which compares availability (A) with use (U) by (U-A)/(U+A) (Ivlev 1961). Availability for each habitat was calculated as a proportion of the home range estimated from a satellite image overlaid with a grid. Habitat use was calculated from the proportion of scans recorded in each habitat. Ivlev's index produces an index for each habitat, of between 1 (total selection) and -1 (total avoidance).

Within the continuum of group fragmentation, it is often difficult to determine whether the group is widely spread, or has divided into two. Kinzey and Cunningham (1994) raised the questions 'how do you define group cohesion?' and 'how far apart must animals be to refer to the group as fragmented?', but did not suggest any definitions. *Cacajao calvus ucayalii* at Lago Preto were often widely spread with no easily distinguishable subgroups. At other times the group was divided into two or more subgroups travelling apart, but in vocal contact. Very commonly the group was continuous, but with one or more 'core areas' where there were higher densities of uakaris. Because *Cacajao calvus ucayalii* at Lago Preto often fissioned completely into groups that were apparently not in contact with each other, counts of all monkeys in vocal contact, were used to measure the fissioning of uakaris. In practice all monkeys 'within earshot' were counted to give the group size.

Group sizes were estimated at ten-minute intervals from repeat counts taken whenever the opportunity arose. Estimating group size was often extremely difficult, because uakaris travelled in very large, widely-spaced groups, which could be spread over several hectares. When an entire group or large part of a group passed through the same part of the canopy it was sometimes possible to obtain an exact count, but it was not practical to get ahead of a foraging group repeatedly to count the uakaris. To avoid underestimating the size of groups, and overestimating the frequency of group fissions, estimates of group sizes were taken from repeat counts and calls heard throughout the 10-minute period preceding the scan. If necessary, estimates were taken from scans and exact counts taken earlier in the observation period (if the group was known not to have split or fused with other groups). These methods approximate the recommendations made by Chapman *et al.* (1993), who highlight the difficulties of determining primate subgroup sizes in fission-fusion societies. It was often possible to estimate group sizes from the frequent contact calling of large groups of uakaris in response to falling branches, food-calls, long contact calls or intragroup aggression (see Chapter 7). Because not all 'subgroups' always reacted to the stimulus, it often took several bouts of calling from various subgroups to estimate the size of very large groups.

To reduce further the likelihood of underestimating group sizes, the highest counts from each hour were used to give hourly group sizes during the day. In hours where no full counts were made, the highest estimate was used, ignoring any particularly high outlying estimates. The maximum group size observed during each contact was taken as the overall size of the group travelling together.

Group fragmentation into subgroups that remained in vocal contact was treated as different to complete group fission where contact between the subgroups was lost. The diameter of the group at its widest point was recorded every ten minutes. Good estimates could not be obtained in the majority of scans, since individuals were often several hundred meters from the observer, and the diameter could only be estimated from contact calls. On many occasions the diameter of large groups of uakaris was on or past the limit of hearing on either side of the researcher, and only a minimum estimate could be given. The limit of hearing varied widely depending on wind, rain, habitat and on which calls were being given by the monkeys. On occasion, 'bark' calls (see Chapter 7) could be heard from distances in excess of 150m, but when bark or other loud calls were not being given, range was more limited.

6.3 Results

6.3.1 Activity budget

Cacajao calvus ucayalii at Lago Preto spent 38.2% of their time moving, 28.2% feeding, 3.5% searching foliage, 24.4% resting and 5.8% engaged in other behaviours (Figure 6.1). There was seasonal variation in the proportion of time spent engaged in different activities. There is a significant negative relationship between the time spent feeding each month and the time spent resting (Pearson Correlation, n=12, r=-0.588, p<0.05), but not between time spent feeding and time spent moving (Pearson Correlation, n=12, r=-0.383, p>0.05) or time spent moving and time spent resting (Pearson Correlation, n=12, r=-0.425, p>0.05), meaning that when uakaris are spending less time feeding they are spending the extra time resting rather than moving through the forest looking for food.

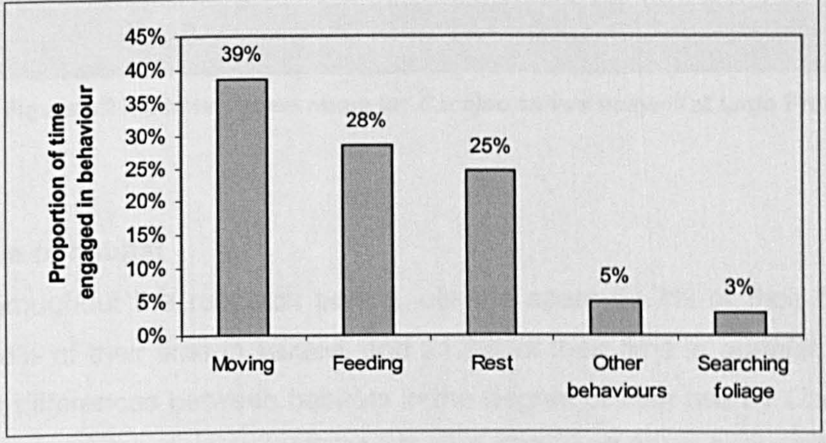

Figure 6.1 Activity budget for *Cacajao calvus ucayalii* at Lago Preto (n=3750).

6.3.2 Home range and daily ranging

Determining the daily ranging distances for *Cacajao calvus ucayalii* at Lago Preto was not usually possible because the fission-fusion behaviour of the groups meant that one could not always be sure that the same group of uakaris was followed throughout the day. Contacts with uakari groups lasting complete or almost complete days, however, suggest that the daily range of *Cacajao calvus ucayalii* at Lago Preto regularly exceeds 6000m. Similarly, it was not clear if all the groups had the same home range, or if they came together in overlapping parts of their home ranges. Uakari groups regularly left the study area and the Conservation Concession for several days, and could not be located until they re-entered the area. Occasionally all groups left the area. The minimum-convex polygon method (Stickel 1954) gave a conservative estimate for a minimum home range of 1200ha for at least one of the groups at Lago Preto in all seasons throughout the study period (Figure 6.2). A much larger home range is probable.

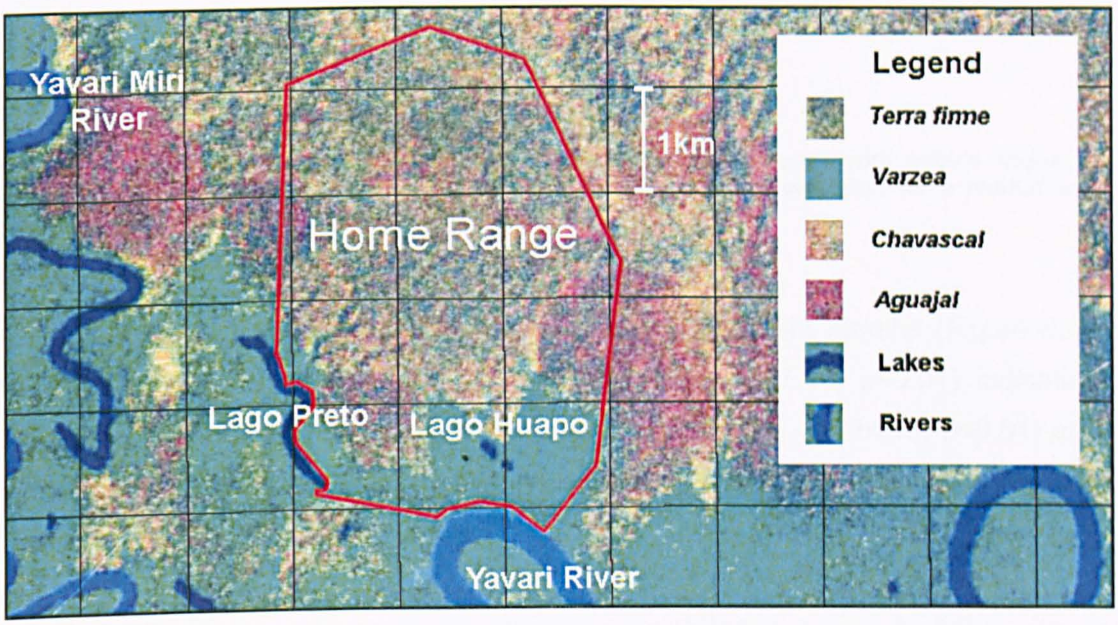

Figure 6.2 Minimum home range for *Cacajao calvus ucayalii* at Lago Preto.

6.3.3 Use of habitat

Throughout the research period, uakaris spent 54.7% of their time in *terra firme*, 24.0% of their time in *várzea*, and 21.3% of their time in *aguajal*. There were significant differences between habitats in the degree of their use by *Cacajao calvus ucayalii* across the year (ANOVA $F_{2,33}=5.509$ $p<0.01$). A pairwise multiple comparison (Tukey test) showed that *terra firme* was used to a different degree to *várzea* and *aguajal* habitats ($p<0.05$), but that *várzea* and *aguajal* did not differ in the degree to which they were used during the research period.

Ivlev's selectivity indices suggest that throughout the research period, there was no strong positive or negative selection for any habitat (Figure 6.3), but use of the *terra firme* habitat throughout the research period was slightly less than would be expected if use was proportional to the relative amount of habitat available in the home range of the monkeys ($\chi^2_{11}=652.49$, $p<0.01$). Use of the *aguajal* ($\chi^2_{11}=2260.80$, $p<0.01$) and *várzea* ($\chi^2_{11}=1210.48$, $p<0.01$) habitats was slightly greater than what would be expected if use was proportional to the relative amount of habitat available in the home range of the monkeys.

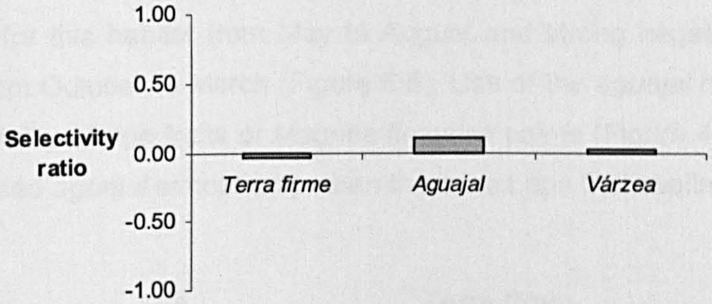

Figure 6.3 Habitat preferences of *Cacajao calvus ucayalii* measured with Ivlev's index of selectivity. Values between 0 and 1.0 indicate increasing positive selection for a habitat and values between 0 and -1.0 negative selection.

Habitats were used in different proportions in different months (Figure 6.4). The use of *terra firme* differed between months (χ^2_{11}=737.46, p<0.01) indicating seasonality in the use of this habitat. The use of *aguajal* (χ^2_{11}=2224.16, p<0.01) and *várzea* (χ^2_{11}=1229.47, p<0.01) habitats also differed between months, indicating seasonality in the use of these habitats.

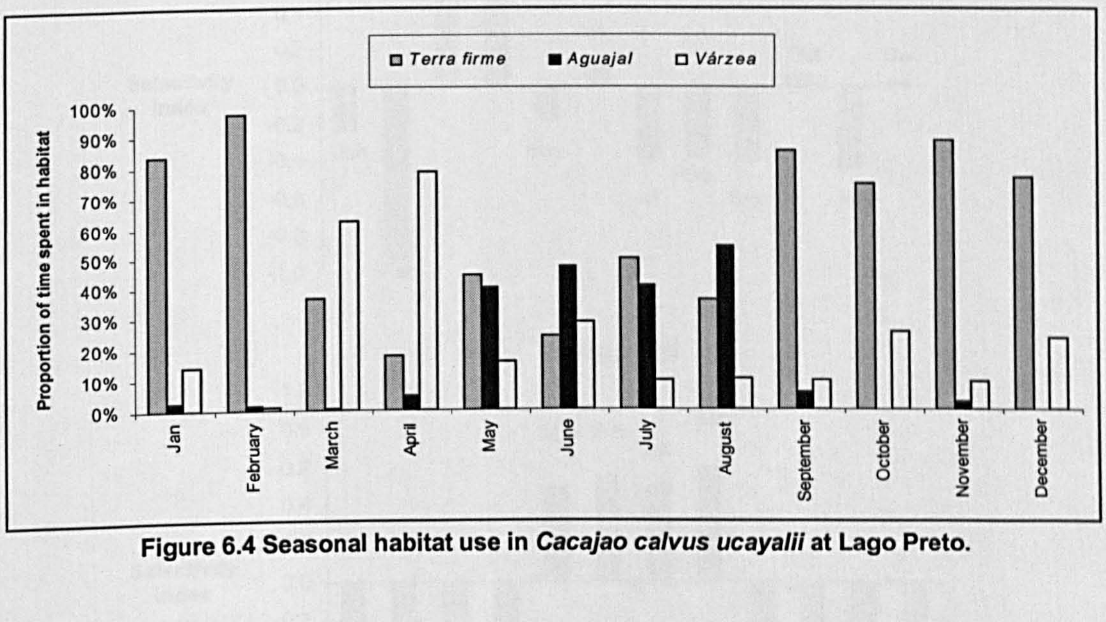

Figure 6.4 Seasonal habitat use in *Cacajao calvus ucayalii* at Lago Preto.

Ivlev's selectivity indices show weak positive selection for *terra firme* between September and February. Selection is negative for this habitat the rest of the year, with fairly strong negative selectivity in April and June. Selectivity for *várzea* forests is high in March and April, when the habitat is inundated, and declines in May as *Mauritia flexuosa* in the *aguajal* starts to ripen. Use of the *várzea* was low from June through to February, when the *várzea* was either dry or only partially flooded.

Selectivity for the *aguajal* habitat was very seasonal, with very strong positive selection for this habitat from May to August and strong negative selection for this habitat from October to March (Figure 6.5). Use of the *aguajal* habitat coincides with the availability of ripe fruits of *Mauritia flexuosa* palms (Figure 4.12). *Cacajao calvus ucayalii* used *aguajal* almost only when there was ripe fruit available.

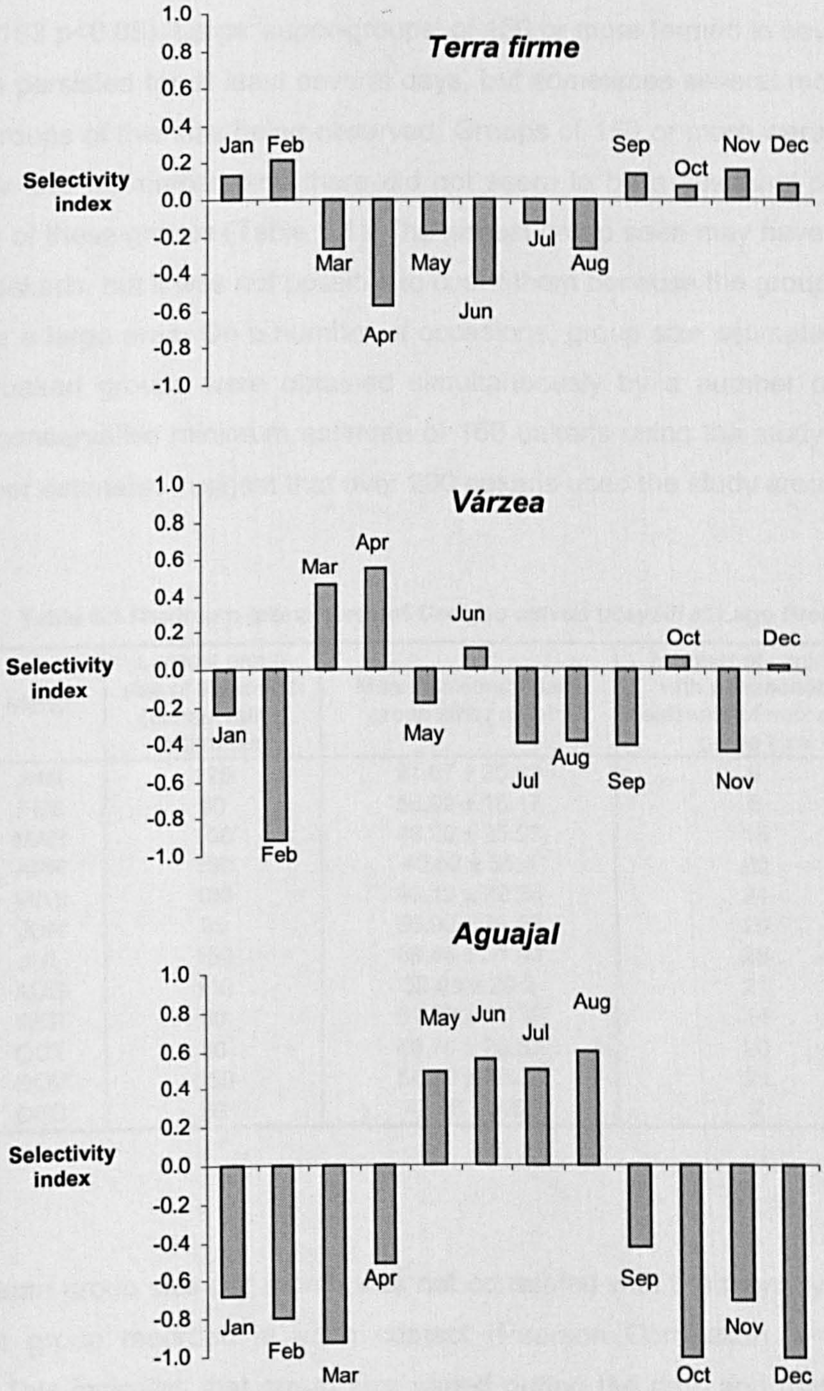

Figure 6.5 Monthly selection for habitats measured with Ivlev's index of selectivity. Values between 0 and 1 indicate increasing positive selection for a habitat, use of the habitat being higher than availability. Values between 0 and -1 indicate increasing negative selection, use of the habitat being at proportions lower than availability.

6.3.4 Group size

Group sizes ranged from 1 to 150+ individuals, and both large and small groups often persisted for several days. Groups sometimes foraged as a single unit, but at other times would fission during the day coming together on occasion, especially at night to sleep. The mean maximum group size observed per contact was 51.3. Maximum group size per contact varied between months (ANOVA $F_{11,195}=2.183$ $p<0.05$). Large 'super-groups' of 150 or more formed in several months, and often persisted for at least several days, but sometimes several months passed without groups of this size being observed. Groups of 150 or more were observed in April, July and November, and there did not seem to be a seasonal pattern in the formation of these groups (Table 6.1). The largest group seen may have been of 200 or more uakaris, but it was not possible to count them because the group was spread over such a large area. On a number of occasions, group size estimates for several different uakari groups were obtained simultaneously by a number of observers, giving a conservative minimum estimate of 160 uakaris using the study area at one time. Upper estimates suggest that over 200 uakaris used the study area at one time.

Table 6.1 Maximum group sizes of *Cacajao calvus ucayalii* at Lago Preto.

Month	Largest group size of the month (conservative estimates)	Mean maximum daily group size / month	Number of contacts with a reasonable estimate of max daily group size
JAN	125	91.67 ± 25.82	6
FEB	80	56.00 ± 18.17	5
MAR	100	43.20 ± 25.97	15
APR	150	40.62 ± 35.4	29
MAY	100	46.19 ± 22.36	21
JUN	85	50.90 ± 21.68	20
JUL	150	58.46 ± 31.90	28
AUG	110	59.05 ± 20.2	21
SEP	80	51.79 ± 17.39	14
OCT	80	46.70 ± 23.53	20
NOV	150	54.29 ± 39.85	21
DEC	50	42.86 ± 9.51	7

Mean group size per month was not correlated with the monthly mean of the maximum group recorded in each contact (Pearson Correlation, n=12, r=0.347, p>0.05). This indicates that group size varied during the day, and that group sizes recorded during a contact were not related to the size of the largest aggregations of uakaris during that contact.

Mean group size was 43.5. Mean group size varied between months (ANOVA $F_{11,748}=5.700$ $p<0.0001$), but since habitat use was also seasonal, the effects of habitat on group size may have influenced this. Mean group size within the *terra firme* habitat varied between months (ANOVA $F_{11,395}=4.399$ $p<0.0001$). Uakari groups did not forage in the *aguajal* and *várzea* habitats frequently enough during each month of the year to enable a similar analysis for these habitats.

Mean group size of *Cacajao calvus ucayalii* varied between habitats (ANOVA $F_{2,756}=15.571$ $p<0.0001$). A pairwise multiple comparison (Tukey test) showed that group size was different between *várzea* and other habitats ($p<0.05$), but that group sizes did not differ between *terra firme* and *aguajal* habitats (Table 6.2). Group size in *terra firme* was similar between months with less rainfall (May to October, mean 43.4) and months with higher rainfall (November to April, mean 49.3) (ANOVA $F_{1,405}=3.6133$ $p=0.0548$).

Table 6.2 Mean group sizes in habitats at Lago Preto from hourly estimates.

Mean group size N=759	**Group size in *aguajal*** Mean (s.d.)	**Group size in *terra firme*** Mean (s.d.)	**Group size in *várzea*** Mean (s.d.)
43.5	47.0 ± 23.02	45.6 ± 24.9	35.3 ± 21.5

Group sizes varied from 1 to 101+ in all habitats. The variable group sizes are consistent with the frequent observations of groups splitting and fusing, and smaller group sizes represent subgroups that have split from larger groups. Two peaks in frequency of group sizes of 21 to 30 and 41 to 50 may indicate that subgroups were consistently of around 21 to 30 individuals while groups of 41 or more may have been made up of two or more groups of 21 to 30 (Figure 6.6). Group sizes in *várzea*, where a significantly smaller mean group size was observed, were commonly in the range 21 to 30 individuals.

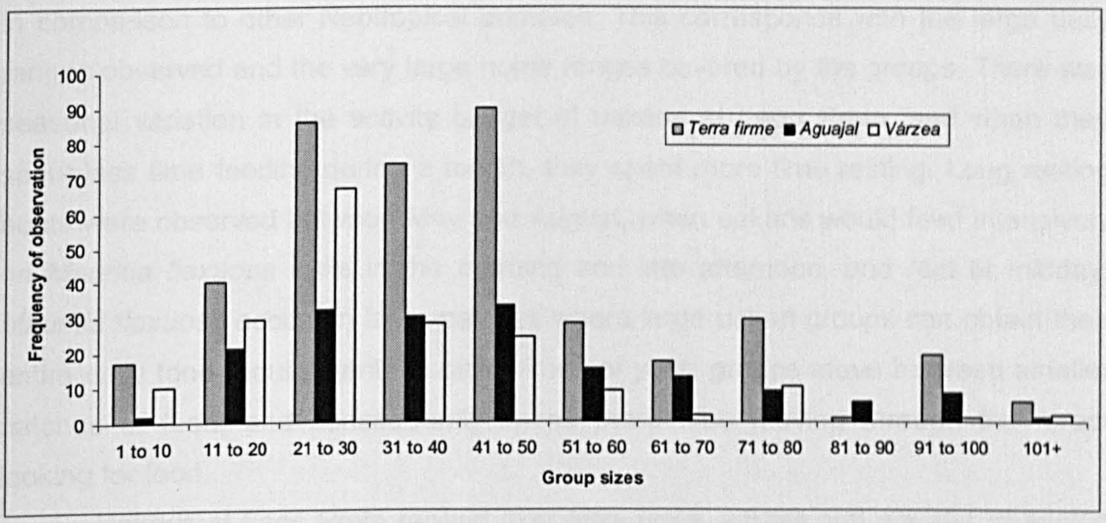

Figure 6.6 Frequencies of group size categories in habitats at Lago Preto from hourly estimates

6.3.5 Group spread

The perceived maximum diameter of uakari groups depended largely on the calls of the uakaris and on the wind and rain. Distances were often very large, especially with big groups, and it was often impossible to see how far back a group extended, but it was clear that the spread of the groups varied greatly, and often quite rapidly. Resting groups were often densely packed. Once a group of 45 animals was counted leaving a single tree after a resting bout, while a further 2 to 5 animals rested elsewhere. Groups also came together for intensive feeding bouts on fruiting trees, often giving 'hic' calls on locating the tree (see Chapter 7). During travel, the uakari groups regularly moved in procession with a narrow front, but also frequently spread out and foraged with a wide front. Although difficult to measure, the spread of uakari groups was clearly very variable.

6.4 Discussion

The activity budget for *Cacajao calvus ucayalii* at Lago Preto was similar to that of *Cacajao calvus calvus* at Lake Teiú (Ayres 1986), although Ayres included social behaviours under 'rest'. Aquino (1998) recorded considerably more time spent moving in *Cacajao calvus ucayalii* (57.4%). This may reflect more patchily distributed resources with longer inter-patch distances, but probably has more to do with small sample sizes, and the unhabituated, often hunted, groups with which he was working. Nonetheless *Cacajao calvus* spends a large proportion of its time travelling in comparison to other Neotropical primates. This corresponds with the large daily ranges observed and the very large home ranges covered by the groups. There was seasonal variation in the activity budget of uakaris at Lago Preto, and when they spent less time feeding during a month, they spent more time resting. Long resting bouts were observed between May and August, when uakaris would feed intensively on *Mauritia flexuosa* fruits in the morning and late afternoon, and rest at midday. *Mauritia flexuosa* occurs in large patches where large uakari groups can obtain their entire daily food requirement. At other times of year, groups move between smaller patches of food, and consequently spend more time moving through the forest looking for food.

Uakaris at Lago Preto ranged over *terra firme*, *várzea* and *aguajal*, changing their habitat preferences seasonally. The most used habitat at the site was *terra firme*. *Cacajao calvus ucayalii* observed by Bodmer *et al.* (2003) on the upper Yavarí-Mirín do not live near large areas of *várzea* forest, although the upper Yavarí-Mirín is bordered by periodically-flooded forest, in which the flooding cycles are dependent on local rainfall. Heymann (1990), Aquino (1998) and Leonard and Bennett (1995) recorded *Cacajao calvus ucayalii* only in *terra firme* forests and *aguajal* palm-swamps. E. Heymann (Pers. com.) suspects that *Cacajao calvus ucayalii* observed at his study site on the Quebrada Blanco are probably not migrating seasonally to relatively distant *várzea* forest types and, therefore, may be living exclusively in upland forests. Thus *Cacajao calvus ucayalii* appears more flexible in its habitat requirements than previously thought.

Ayres' (1986) study group of *Cacajao calvus calvus* lived entirely in seasonally-inundated *várzea* forests at Lake Teiú, in what is now the Mamirauá Sustainable Reserve. One of the major differences between the *várzea* forest at Ayres' site and at Lago Preto is in the extent of this habitat. *Várzea* covers the entire geographical range of *Cacajao calvus calvus* at Mamirauá, but extensive *várzea* on the Yavarí occurs only near the mouth. Much of the *várzea* on the Yavarí occurs in relatively narrow strips along the river. Ayres (1986) divided the *várzea* at Mamirauá into 'chavascal' and '*restingas*', which he subdivided into 'higher' and 'lower' *restingas*. Ayres' *chavascal* flooded for 6 to 8 months of the year to a depth of 6 to 7m. Higher *restingas* at Ayres' study site flooded for 2 to 4 months to a depth of 1 to 2.5m, and lower *restingas* flooded for 4 to 6 months of the year to a depth of 5m. Ayres' 'lower *restinga*' may be similar to what we refer to in this study as 'lower forested *várzea*'. *Chavascal* was the commonest of the three vegetation types at Mamirauá, perhaps also due to more extreme annual flooding than occurs on the Yavarí. The core area of Mamirauá does not contain *aguajal* palm-swamps, possibly because of this extreme flooding. Extreme seasonality of the *várzea* forest is probably why *Cacajao calvus calvus* at Lake Teiú is one of only 4 species living at the site (Ayres 1986), but *várzea* forests have high productivity because of the annual influx of nutrients. *Cacajao calvus calvus* is able to take advantage of these resources at Lake Teiú by feeding on unripe seeds, a resource that is less seasonal than the ripe fruit many other primates depend on (Ayres 1986; Ayres 1989). At Lago Preto, *Cacajao calvus ucayalii* benefits from the high seasonal productivity of *várzea* and can avoid seasonal shortages by using other habitats. This may in part explain why *Cacajao calvus ucayalii* occurs at such high densities at the site.

Like *Cacajao calvus ucayalii* at Lago Preto, other populations of *Cacajao* migrate seasonally between habitats, and often include *terra firme* in their home ranges (Defler 1989; Barnett *et al.* 2005; Aquino 1998; Boubli 1998, 1999). Far from *terra firme* being a 'real barrier' to *Cacajao*, as Ayres (1986; 1989) proposed, preventing the genus from spreading to the forests of the lower Amazon, for much of the year, *terra firme* forests are the preferred habitat for *Cacajao calvus ucayalii*. Thus it could be competition with *Chiropotes* that prevents *Cacajao* from spreading east, rather than a lack of flooded-forest habitat. The use of adjoining areas of *terra firme* by many populations of *Cacajao* during periods of low fruit availability, and the occurrence of *Cacajao calvus ucayalii* away from *várzea* forests, suggest that Ayres' (1986) population of *Cacajao calvus calvus* are actually relatively unusual in using exclusively *várzea* forests. A pattern of seasonal use of seasonally-inundated and *terra firme* forests might be more normal for *Cacajao calvus*, but confirmation of reports of *Cacajao calvus ucayalii* in the Pacaya-Samiria National Reserve would provide another example of *Cacajao calvus ucayalii* in extensive *várzea*, and this one would be sympatric with 12 other primates (see Chapter 9).

In deciding whether to forage alone or in groups, primates try to maximise access to food and protection from predators, and these must be considered the greatest ecological determinants of foraging group size in *Cacajao calvus ucayalii*. It is difficult to measure predation on primate populations (Cheney and Wrangham 1987), and there is no way of estimating levels of predation at Lago Preto. One possible response to predation is crypsis. *Cacajao calvus* does not appear to use this strategy, which is best employed by small groups (Cheney and Wrangham 1987). *Pithecia* cf. *monachus* appears to use this strategy to some extent, moving around more quietly than *Cacajao calvus* and often hiding in the canopy on seeing researchers (personal observation). *Cacajao calvus* in contrast is noisy. Even at larger distances *Cacajao calvus* groups can be heard moving through the canopy with noisy crashes, and contact calls are very common (see Chapter 7). Groups at

Lago Preto alarm call frequently, but only react strongly (moving rapidly down in the canopy) to very loud, high-pitched 'strong' alarm calls that are occasionally given. Most of these appear to be false alarms, sometimes given in response to vultures (*Cathartes* spp. or *Coragyps atratus*). Vultures are generally ignored or even chased from their perches (Personal observation).

In 945 hours of observation, only once was the cause of a true strong alarm seen. Multiple strong alarm calls were given during three bouts of alarm calling within the space of about one minute. For all three bouts, there was a very strong, sustained response from the entire group of 50 animals, which fled through the canopy and responded with 'chick' and 'hic' calls (see Chapter 7). During the third bout a very large raptor, almost certainly a harpy eagle (*Harpia harpyja)* or crested eagle (*Morphnus guianensis*), was seen stalling close to the centre of the group. The attack took place in *aguajal*, which has an open canopy, and did not appear to be successful. No other bouts of alarm calling observed during the study period were of similar intensity to any of the three bouts observed during this attack. *Cacajao calvus ucayalii* at Lago Preto were also observed twice alarm calling at tayra (*Eira barbara*), and they probably have other terrestrial and arboreal predators. The response to tayra was more similar to the occasional mobbing of researchers, with 'chick' calls and some display behaviours, although with higher intensity. While ground predators may be of limited importance, they may also explain why uakari monkeys frequently go quiet as they reach their sleeping site in the evening, and possibly why they sleep in such large groups. Terrestrial predators are usually considered less important to arboreal primates than aerial predators and the main threat to the uakaris is probably large eagles. Predation rates are unlikely to vary much temporally, so it is likely that temporal differences in group size are due to the availability and distribution of food, but predation rates may differ between habitats. Grieser Johns (1997) found that harpy eagles appeared commonest in logged forest with a more open canopy, and captured more prey in those habitats. Large eagles have been observed in all habitats at Lago Preto, but uakaris might be more vulnerable to attack from eagles in *aguajal*, because of its open canopy. It seems unlikely that the smaller group sizes observed in the *várzea* habitat are due to reduced predation pressure in this habitat, and the availability and distribution of food resources probably creates the grouping patterns observed.

Ayres (1989) compared the ecology of the closely-related *Cacajao calvus calvus*, *Chiropotes albinasus* and *Chiropotes satanas*. These species have similar diets, but *Cacajao calvus calvus* lives in white-water *várzea* forests, while *Chiropotes* species live in *terra firme* forests. Ayres reported that large groups of *Chiropotes* *albinasus* (Ayres 1981) and *Chiropotes satanas* (Roosmalen *et al.* 1981) foraged as single units. These groups often spread out or split, but separation was never more than a few hundred metres. Groups of *Chiropotes* travel rapidly between food trees which are often widely spaced, stopping at fruiting trees for intense feeding bouts. This pattern was also observed in *Chiropotes satanas* by Norconk and Kinzey (1994). *Cacajao calvus calvus* did not forage as a single unit, often splitting into smaller groups that disperse throughout the home range (Ayres 1989). Larger feeding groups were commonest when there was an abundance of mature fruits, while more scattered parties were commonest during the dry season. Ayres (1989) related these differences between *Cacajao* and *Chiropotes* directly to the contrasting habitat preferences of the genera. Both genera specialise in feeding on large, hard, immature fruits, which are distributed in larger patches than the ripe, softer fruits eaten by other primates. This enables *Cacajao* and *Chiropotes* to form large groups (Ayres 1989). In *várzea*, while the patches of immature fruit are still larger than those of ripe fruit, the patches are smaller than in *terra firme* (Ayres 1989), which Ayres (1989) argues has led *Cacajao* to adopt a foraging strategy in many ways similar to that of *Ateles*.

At Lago Preto *Cacajao calvus ucayalii* lives in a combination of three habitats including both white-water *várzea* forests and *terra firme* forest. Thus we can test Ayres' (1989) theory on the foraging strategies adopted by *Chiropotes* and *Cacajao*. When foraging in *várzea* forests *Cacajao calvus ucayalii* should behave like *Cacajao calvus calvus,* and when foraging in *terra firme* forest we might expect *Cacajao calvus ucayalii* to show similarities to *Chiropotes*. In terms of mean foraging group size, this prediction is borne out, with *Cacajao calvus ucayalii* fissioning into smaller groups in *várzea* than in *terra firme*. When *Cacajao calvus ucayalii* forages in the *aguajal* habitat, group sizes are of a similar size to those in *terra firme*. *Aguajal* consists of large stands of *Mauritia flexuosa* palms that can be considered extremely large food patches able to accommodate the entire troop. The groups do not need to fission when foraging in this habitat. This is consistent with Ayres' (1989) explanation of the grouping system of *Cacajao*. Recently, regular fissioning has been observed in *Chiropotes albinasus* and *Chiropotes satanas* by Veiga *et al.* (2006); they observed no clear relationship between these grouping patterns and the distribution of resources, but in *Chiropotes satanas,* group fusion was commonest in the wet season. Veiga *et al.* (2006) suggest that this may be due to the fruiting patterns of key resources, such as *Simarouba amara*, which has a clumped distribution.

Similar observations have been made for other species. Defler (1999) reported that smaller group sizes in *Cacajao melanocephalus* were observed during the season when fewest fruits were available. Boubli (1999) recorded large groups of *Cacajao melanocephalus* that did not fission, noting that the preferred food during the study period occurred in large clumps that could accommodate the entire feeding group. Peres (1996) demonstrated that groups of *Lagothrix* dispersed more when ripe fruit was less abundant, and groups were more cohesive when ripe fruit availability was higher. At Lago Preto the situation was complicated by the seasonal movement of *Cacajao calvus ucayalii* between habitats during times of low fruit availability, so no significant difference is seen between group sizes in *terra firme* between months with less rainfall (and lower fruit availability) and months with higher rainfall (and higher fruit availability). Instead *Cacajao calvus ucayalii* changes its habitat preferences and its grouping patterns within those habitats. Observations at Lago Preto are consistent with the theory that foraging group sizes are determined by the patch sizes of the resources being utilized.

Leighton and Leighton (1982) considered three possible mechanisms where patch size could determine foraging-group size. Firstly they proposed that the number of feeding spaces could be limited by accessibility of food. This is of particular importance when monkeys are feeding on fruits that occur in dense clusters like palms. When feeding on palms, *Cacajao calvus ucayalii* at Lago Preto would queue for access to the racemes and retreat with fruits having selected them. Even large groups were able to feed on palms simultaneously, especially since the palm species fed on by uakaris (largely *Mauritia flexuosa* and *Oenocarpus bataua*) tend to grow in clumps. Secondly, Leighton and Leighton (1982) suggested that interference competition could limit the number of feeding spaces, either as a direct result of agonistic encounters, or by passive avoidance. Aggression during feeding bouts of *Cacajao calvus ucayalii* was rare, although it did occur. The third mechanism suggested by Leighton and Leighton (1982) was that feeding spaces could be limited by the density and abundance of items. At times large groups of *Cacajao calvus ucayalii* fed in intensive bouts, on fruits that were clearly numerous and densely packed in the crown of a fruiting tree. For example, many feeding bouts on Sapotaceae and Lecythidaceae species were long and intense, characterised by a 'heavy rain' of fruit husks. In these situations, feeding spaces were apparently not limited. Thus in the case of red uakaris, it appears most likely that Leighton and Leighton's (1982) first theory applies, and that group sizes are controlled by patch size. Larger groups than those seen in other primates are able to form because of the large patch size of the uakaris' favoured foods.

A tendency to form large 'supergroups' of several hundred animals may be reinforced by selection pressure to minimise visitation rates on feeding trees.

Immature seeds do not 'renew' in the same way as some ripening pulps, and a wide front of uakaris feeding in intense bouts might not leave much food in its wake. Uakari groups could therefore be under more pressure than other predominantly pulp-eating primates not to forage where another group has been. This might explain why uakaris might require the large home ranges they use, and could result in large uakari supergroups travelling in the same direction.

Heymann (1992) hypothesised that the social organisation of red uakaris comprises three levels: the foraging unit (up to 10 individuals), the group (25-50 individuals) and the troop (50 to more than 100 individuals). This hypothesis may be supported by the results of this study. Group sizes in the ranges 21 to 30 and 41 to 50 were more common than other ranges. This could indicate that groups may frequently be of around 21 to 30 individuals while groups of 41 or more may contain two or more 'subgroups' of this size. Heymann (1992) suggested that this type of organisation could be linked with seasonal migrations, and this hypothesis is certainly supported by observed differences in mean group sizes in different habitats at Lago Preto. The existence and composition of Heymann's 'foraging units' are considered in Chapter 7.

There is no evidence for strong predation on either *Ateles* or *Pan,* which feed primarily on ripe fruits and experience strong intraspecific competition for food (McFarland 1986). In the absence of strong ecological advantages for foraging in groups, very small foraging parties are common, and it appears that the large size of the 'troop', or 'community' as it is known by chimpanzee researchers, may be maintained largely for social rather than ecological reasons; ultimately to obtain access to mates. Norconk and Kinzey (1994) compared the travel patterns of *Ateles* and *Chiropotes,* highlighting differences between the grouping patterns observed in the two genera. Norconk and Kinzey attributed the relatively cohesive groups of *Chiropotes* to more clumped resources than those of *Ateles*, between which the troop fragments while remaining in visual or vocal contact. Despite the similarities between *Ateles* and *Cacajao* pointed out by Ayres (1989), including frequent complete fission of subgroups, the fission-fusion grouping pattern shown by *Cacajao calvus* appears to have more in common with *Chiropotes* than *Ateles. Cacajao calvus ucayalii* at Lago Preto forage in a similar pattern to *Chiropotes* when in *terra firme* forest. They forage in larger parties than when in *várzea* and partially fragment when several feeding trees are found. Additionally, complete fissioning similar to that seen in *Cacajao calvus* has been observed in *Chiropotes* by Veiga *et al.* (2006). The frequent complete fissioning of *Cacajao calvus ucayalii* appears to be a more extreme case of the same type of group fragmentation typically seen in *Chiropotes.*

The fission-fusion grouping pattern shown by *Cacajao calvus* enables the groups to react to short term ecological pressures while maintaining large social groups. Large groups can occur year round, even when the distribution of resources demands that foraging groups are smaller, with groups often meeting up at the end of each day. These large troops and the complex grouping system have consequences for the evolution in communication and social behaviour in *Cacajao calvus*. These behaviours are discussed in Chapter 7.

6.5 Summary

1. *Cacajao calvus ucayalii* at Lago Preto spent 38.2% of their time moving, 28.2% feeding, 3.5% searching foliage, 24.4% resting and 5.8% engaged in other behaviours. There is a negative relationship between the time spent feeding each month and the time spent resting, but not between time spent feeding and time spent moving, or between time spent moving and time spent resting. Thus, when uakaris are spending less time feeding they are spending the extra time resting.

2. The daily range of *Cacajao calvus ucayalii* at Lago Preto regularly exceeds 6000m. The home range of at least one of the groups at Lago Preto was at least 1200ha. A much larger home range is probable.

3. Ivlev's selectivity indices show weak varying selection for habitats through the year. Selectivity for *várzea* forests is high in March and April, when the habitat is inundated, and low from June through to February, when the *várzea* was either dry or only partially flooded. Selectivity for the *aguajal* habitat was very seasonal, with very strong positive selection for this habitat when there was ripe *Mauritia flexuosa* fruit available, and strong negative selection when it was not.

4. Uakari group sizes ranged from 1 to 150+ individuals, and the largest group seen may have exceeded 200. Mean group size was 43.5, and the mean maximum group size observed per contact was 51.3. Group sizes often varied throughout the day, and groups sizes during the day were not related to the largest group sizes observed during the contact.

5. Mean group size was lower in *várzea* than in other habitats. Fission-fusion grouping patterns in *Cacajao calvus ucayalii* resembled the grouping patterns of *Cacajao calvus calvus* in *várzea* and *Chiropotes* in *terra firme*.

Chapter 7

Social Organisation and Communication in *Cacajao calvus ucayalii*

7.1 Introduction

The ecological pressures that led to the fission-fusion grouping patterns observed in *Cacajao calvus ucayalii* were considered in Chapter 6, but nothing was inferred about the composition of these groups, or the social organisation within the grouping patterns. Because *Cacajao calvus ucayalii* forages in groups of varying sizes, the social organisation of the troop must have the flexibility to allow the groups to fission and fuse. The overall composition and distribution of age-sex classes within the group, however, is likely to be driven by reproductive strategies rather than the distribution or availability of food.

Most of what was known about the social behaviour of *Cacajao calvus* before this study came from Fontaine's (1981) work on a group of semi free-ranging *Cacajao calvus ucayalii*. Ayres (1986) did not collect data on the social behaviour of *Cacajao calvus calvus*, but made some observations on the subject. Ayres (1986) recorded a socionomic sex ratio in a troop of 45-48 animals of 1:1. This is similar to that observed in *Chiropotes* (Ayres 1989; Veiga *et al.* 2006). Ayres (1986) recorded the formation of temporary pairs during the mating season, and the formation of bachelor groups of up to 8 or 9 adult males. Ayres (1986) also plotted the testis and body weight of *Cacajao calvus calvus* against data for other primates from Harcourt *et al.* (1981). *Cacajao calvus* has a relatively small testis weight in relation to its body size, which suggests low levels of sperm competition, but these data include just 5 other cebids for comparison. Ayres (1986) observed that the testis weight was similar to that of *Colobus polykomos* or *Theropithecus gelada*, which have single-male breeding systems, but did not mention that the ratio was the same as that in *Ateles geoffroyi* and not much lower than in *Lagothrix lagotricha*. Ayres (1986) posited that pair formation and observations of bachelor groups were evidence for a single-male breeding system in *Cacajao calvus ucayalii*.

Zinner *et al.* (2001) noted that, in species that have large aggregations of hundreds of individuals, there is a tendency for 'one-male units' to form. Zinner *et al.* (2001) proposed that large group sizes are incompatible with a typical multimale-multifemale group structure, because females cannot maintain social relationships with most other group members. Thus, they would be at risk from unknown and infanticidal males. Zinner *et al.* (2001) suggest that females have stable relationships with single males to protect them from unknown males. Applying this theory to *Cacajao calvus ucayalii*, Knogge *et al.* (2006) presented the results of a small pilot study conducted at Lago Preto on the nearest neighbours, spatial configuration and composition of foraging groups. Knogge *et al.* (2006) suggest that within the large troops, *Cacajao calvus ucayalii* are organised into small units composed of 'around 2 adult females and offspring, 2 sub adults and always 1 guarding adult male'.

Chiropotes is very closely related to *Cacajao*, and recent studies by Veiga *et al.* (2006) have demonstrated that they also form large fission-fusion groups of up to 50 individuals or more, although troop sizes are generally smaller than in *Cacajao* (Ayres 1989). Veiga and Silva (2005) noted that male *Chiropotes satanas* were affiliative, and spent most of their time closest to other adult males. Veiga and Silva (2005) did not note the formation of bachelor groups or the formation of one-male units. Garber and Kowalewski (in press) highlight high levels of male within-group intra-sexual tolerance observed in several of the Atelinae, which are closely related to the Pitheciidae (Schneider and Rosenberger 1996). In *Brachyteles* and *Ateles* males associate with each other more than with females, are tolerant of each other's sexual activity and work together to repel other males (Strier *et al.* 2002; Symington 1990). Since dispersal is female biased in these species, Garber and Kowalewski (in press) suggest that kinship might play an important role in this male-male tolerance, but they also point out that male tolerance of within-group copulations by other males was observed by Peres (1996) in *Lagothrix*, in which dispersal may be bisexual (Garber and Kowelewski in press; Di Fiore and Campbell 2007; but see Nishimura 1992, 1994).

Groups containing multiple males may offer females the advantage of increased infant survivorship (Altmann 1990; Garber 1997). Garber and Kowalewski (in press) suggest that female promiscuity and sexual receptivity during non-fertile periods would reduce the likelihood of infanticide by maintaining male-female bonds. The cost of tolerance of another male's sexual activity must be offset by the benefit of cooperation. In the Atelinae the benefit appears to be in the cooperative defence of the group from extragroup males. Extra-group males are potential competitors for receptive females, and may also be infanticidal (Symington 1990). The costs of male-male tolerance are lower when males are kin, and for this reason Garber and Kowalewski (in press) predicted that dispersal in *Chiropotes* and *Cacajao* would be female biased. This is supported in *Chiropotes* by observations of lone females by Peetz (2001) and Veiga and Silva (2005).

Cacajao calvus ucayalii exhibits conspicuous sexual dimorphism in its dentition, the jaw and the associated musculature. Male uakaris have a proportionately larger jaw and canines than females, and fully-adult males have large 'jaw-closure' muscle masses on the top of the head. While the males are able to open larger hard fruits than females and young (see Chapter 5), it seems unlikely that the muscle masses have a purely fruit-opening function. R. Kay (*pers. comm.*) suggested that the striking dental dimorphism might predict some kind of display based around the teeth in this primate, and it is also possible the teeth are used in fighting between males. Fontaine (1981) described some 'open-mouth' visual communication patterns in captivity. In captivity, the development of the jaw-closure muscle masses was sudden, and associated with a rapid increase in size at the onset of the mating season (Fontaine, 1981). Dental sexual dimorphism is likely to be the result of sexual selection. Kay *et al.* (1988) correlated dental dimorphism with social behaviour. Species with monogamous or polyandrous social structures have low canine dimorphism, species with dominance rank social structures have the highest canine dimorphism, and species with fission-fusion social structures and transitory inter-male breeding-season competition fall between these two extremes. Kay *et al.* (1988) concluded that inter-male competition is the most important factor in explaining variation in canine dimorphism. Thus, we might predict high levels of male competition in *Cacajao calvus.* In *Cacajao melanocephalus*, low levels of aggression were noted by Boubli (1999) and high levels of male-male tolerance were observed by Cunha and Barnett (1989).

Ayres (1986, 1989) did not comment on levels of male tolerance or aggression, except to note that he observed bachelor formations harassing male-female pairs during the breeding season. Beyond this, and the recent pilot study by Knogge *et al.* (2006), little is known about levels of aggression or affiliation in *Cacajao.* Inter-male aggression and tolerance in *Cacajao calvus ucayalii* and the spatial distribution of age-sex classes within groups are examined in this Chapter to determine the social system. The findings are discussed to determine whether *Cacajao calvus ucayalii* has a single-male breeding system as predicted by Ayres (1986), Zinner *et al.* (2001) and Knogge *et al.* (2006), or a multi-male breeding system as predicted by Garber and Kowalewski (in press), and found in the related *Chiropotes satanas* (Veiga and Silva 2005) and Atelinae (e.g. Strier *et al.* 2002; Symington 1990). Predictions are made as to whether dispersal might be male or female biased. These factors could affect the demography of *Cacajao calvus ucayalii* populations. Seasonality in breeding behaviour is also likely to be important in the demography of populations and the mating behaviour and distribution of births is also considered in this Chapter.

The large troops and complex fission-fusion grouping pattern described in Chapter 6 will have influenced the evolution of communication and social behaviour in *Cacajao calvus.* Ayres (1989) noted the rich repertoire of visual and vocal communication in *Cacajao*, but did not put these calls into context except to note that the commonest '*Ca-Ca-Ca-Ca*' call (referred to as the '*hic*' call in this thesis, following Fontaine 1981) was probably important in locating nearby group members. Ayres suggested that signalling in *Cacajao* and *Chiropotes* was likely to differ considerably, because of differences in their patterns of spatial dispersion. Fontaine (1981) described calls and visual signals in captive *Cacajao calvus ucayalii* in some detail, recording in particular a large number of facial expressions. Some anecdotal comments have been made on uakari communication in the field (Ayres 1986; Heymann 1990; Swanson Ward and Chism 2003), but communication in wild populations of the species has not been studied in any detail. The communication of *Cacajao calvus ucayalii* in the context of its natural environment is described in this Chapter, recording several behavioural patterns and calls not recorded by Fontaine (1981). These behaviours are important in the context of the social behaviour described in this Chapter, and the significance of these active signals is discussed. In addition, *Cacajao calvus ucayalii* has a very obvious passive signal in the form of its bright red face. The function and evolutionary significance of this signal is also discussed.

7.2 Methods

7.2.1 Group composition

The age-sex classes of group members were recorded as *infant one* (1-3 months), *infant two* (3-12 months), *juvenile* (12 to 36 months), *subadult*, *subadult male*, *adult male*, and *adult female*. Additionally, females carrying young were recorded as *adult female carrying dependent young*. Definitions of each category are given in Chapter 3. Where females were recorded carrying young (either *infant one* or *infant two* age classes), the size of the young was recorded as a percentage of the size of the female. The colour of the face and the position in which the young was carried were also recorded. This helps to age the infant (Fontaine 1981). Babies carried on bellies or with grey-brown or partially grey-brown faces were assumed to be *infant one* and under 3 months old. By recording the presence of these infants an idea of the seasonality of births was gained. Between April 2003 and March 2005 data were collected in every month except February 2004. Counts of infants were also made during an additional field season in April 2006.

When an entire group, or large part of a group, passed through the same part of the canopy, it was sometimes possible to obtain a good count, and record the age-sex class of individuals in the order they passed. Because of the continuous effort required to collect data on feeding ecology, it was not possible to move ahead of the group frequently to record the composition of the groups.

7.2.2 Nearest neighbour distances

During scan sampling, one 'focal individual' was randomly selected for each scan. The age-sex class of this individual was recorded, along with the age-sex classes of the nearest neighbour if the nearest neighbour could be seen clearly. Additionally, if the age-sex class of other nearest neighbours within 10m of the focal individual could easily be determined, these were also recorded in the order of closeness to the focal individual. When it was clear that the focal individual had no neighbours closer than 30m, this was also recorded.

Because visibility was generally poor in the canopy, the age-sex of nearest neighbours was not always determined. Only a short period was available to identify nearest neighbours. The number of nearest neighbours recorded does not represent *all* nearest neighbours within 10m of the focal individual, only those closest to the focal individual for whom the age-sex class could be determined. These data were used to determine the number of males occurring within 10m of adult females at any one time.

7.2.3 Social behaviours

Behavioural categories were recorded during scan sampling (Altmann 1974). In addition to the categories 'feed', 'search', 'rest' and 'move', social behaviours were recorded. Social grooming was subcategorized into 'give' groom (the age-sex class of the recipient was also recorded) and 'receive' groom (the age-sex class of the giver was also recorded). Grooming was recorded during scan sampling throughout the research period, but between 14th May 2003 and 30th November 2003, all instances of grooming were recorded in which the age-sex classes of both animals was determined. Aggressive acts, such as chasing or fighting were subcategorised into 'Give' aggression (the age-sex class of the recipient was also recorded) and 'Receive' aggression (the age-sex class of the giver was also recorded).

Extended sequences of social behaviour, such as fighting or sexual behaviour were recorded *ad libitum* (Altmann 1974) whenever they occurred. All observations of mating were recorded and described in as much detail as possible. Other rare behaviours with a social function, such as ano-genital rubbing, were also described *ad libitum*.

When display behaviours were recorded in scan samples, the specific behaviour was always recorded. Display behaviours included several described by Fontaine (1981), including *arm raising*, *branch slapping*, *branch shaking*, *urine washing*, *straight-legged strut*, *branch swaying*, *vertical hanging* and *hindquarters bounce*. When new display behaviours were observed they were described in detail. Display behaviours aimed at researchers were recorded as 'observing researcher'. An exhaustive ethogram of visual signals was not produced. Many signals described by Fontaine (1981) are subtle and were only occasionally observed at Lago Preto. Facial expressions are not discussed, because observer-subject distances were generally too great for detailed observation.

7.2.4 Vocal communication

In addition to the scan sampling described in Chapter 3, in which display behaviours were recorded, observations on communication in red uakaris were recorded *ad libitum* (Altmann 1974). When individual monkeys were seen giving a vocal, tactile or visual signal, the signal, the behaviour and the age-sex classes of the givers and receivers of the signal were recorded, along with any other stimuli considered relevant. When rarer calls were heard, but the giver was not seen, the context and behaviour of the group was noted.

Between 31st July and 29th August 2003 a second observer counted all calls of all types given by the uakari group during a one minute period starting on the point at which the scan sample data was collected. Calls were recorded using a digital recorder and directional microphone to verify counts and to assist in the classification of calls. Samples were not taken if the group was reacting to the presence of the researchers. Samples where the centre of the group was more than 60m from researchers were discarded because in these cases the majority of the group was out of earshot for the quieter calls.

7.3 Results

7.3.1 Group composition

The age-sex classes were not evenly distributed through the groups, with males forming bachelor groups on the periphery of large groups. Partial group composition counts frequently recorded all-male parties of 1 to 10 *adult* and *subadult males*. Sometimes these groups also contained juvenile animals. Occasionally bachelor groups were observed apparently out of contact with other uakari groups, but normally they appeared to follow behind large uakari groups. This is shown by the significant negative correlation between the number of uakaris sampled in partial or complete counts of the composition of a group and the ratio of *adult* and *subadult males* to other age-sex classes (Pearson Correlation, n=50, r = -0.382, p<0.01). More males are recorded in smaller group counts. For this reason only full or nearly full counts of group composition could be used to determine the average composition and age/sex ratios. It was never possible to get a complete composition for groups of 50 or more animals, because they were too dispersed. Groups of 18 to 31 uakaris, for which near complete composition was recorded, all contained minimum counts of 4 to 6 *adult males*. Observations of single uakaris were rare, and were all of *adult males*.

7.3.2 Nearest neighbours

The frequencies that different age-sex classes were the nearest neighbours of *adult males* were unequal (χ^2_7=549.660, p<0.01). *Adult males* were nearest neighbours of *adult males* in 68.6% of observations (Figure 7.1). The frequencies that different age-sex classes were the nearest neighbours of *adult females* were unequal (χ^2_7=64.257, p<0.01). Excluding carried infants, *infant twos* were the commonest nearest neighbours of adult females. Excluding infants, *adult females* were the next commonest neighbours for *adult females* (26.7%, compared to *adult males* 18.1%). *Subadult males* were not recorded as the nearest neighbours of focal *adult females* in scan samples (Figure 7.2), although *adult females* were recorded as the closest animals to *subadult males* on occasion (Figure 7.3), and one record of mating was between an *adult female* and a *subadult male* (see Chapter 7.3.5). The frequencies that different age-sex classes were the nearest neighbours of *subadult males* were unequal (χ^2_7=59.600, p<0.01). *Subadult males* were most often closest to *adult males* (56.7%) or *subadult males* (20.0%) (Figure 7.3). The frequencies that different age-sex classes were the nearest neighbours of *juveniles* were unequal (χ^2_7=33.333, p<0.01). The nearest neighbours of *juveniles* were most often other *juveniles* (38.9%), followed by *adult males* (22.2%) and then *adult females* (16.7%) (Figure 7.4). The frequencies that different age-sex classes were the nearest neighbours of *infant twos* were unequal (χ^2_7=68.704, p<0.01). *Infant twos* where most often nearest neighbours to *adult females*, even though infants being carried were not recorded as nearest neighbours (Figure 7.5).

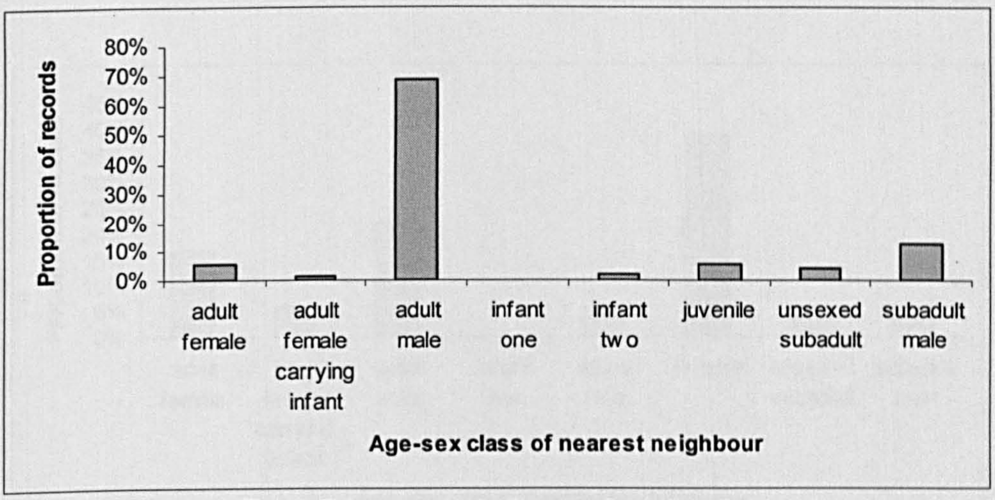

Figure 7.1 nearest neighbours of *adult males.*

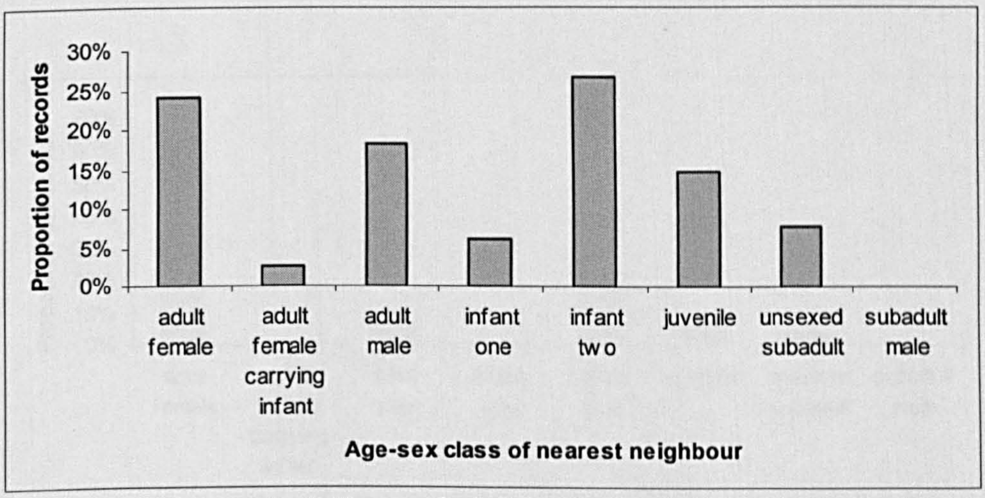

Figure 7.2 nearest neighbours of *adult females* (excluding carried infants).

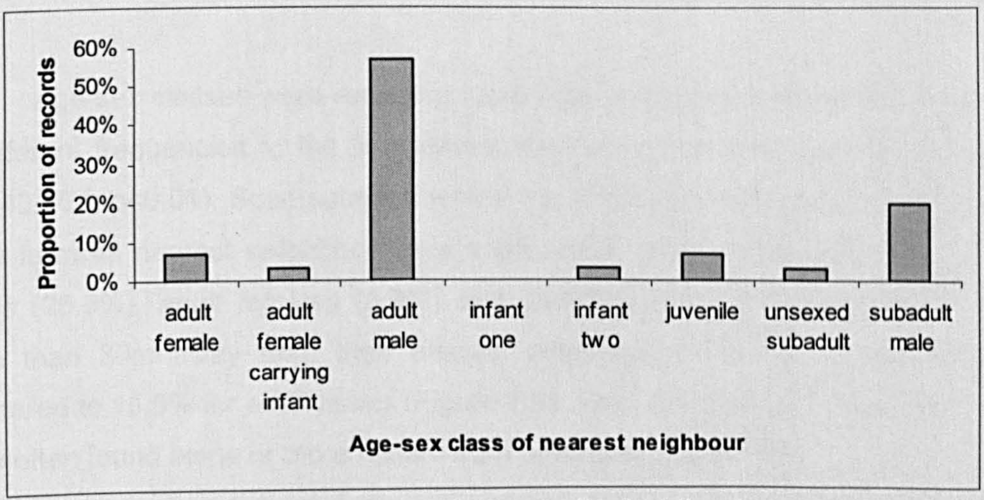

Figure 7.3 nearest neighbours of *subadult males.*

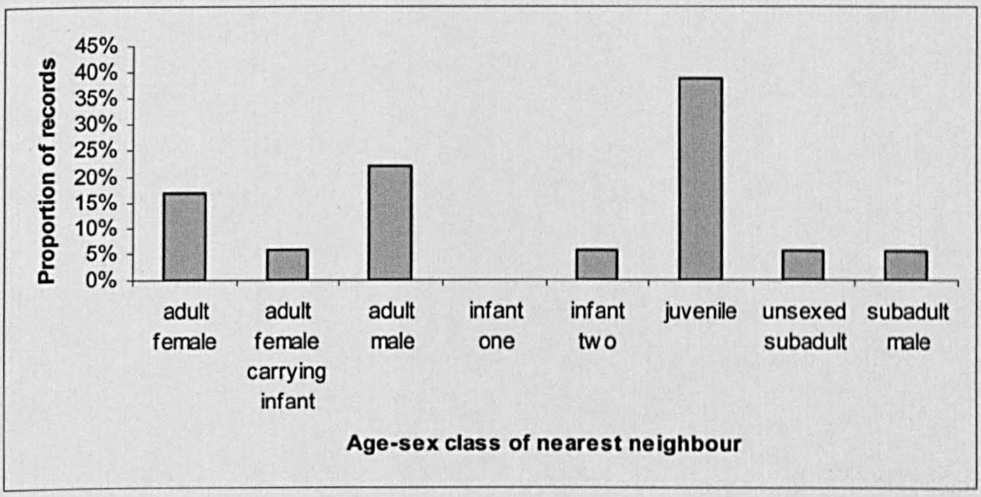

Figure 7.4 nearest neighbours of *juveniles*.

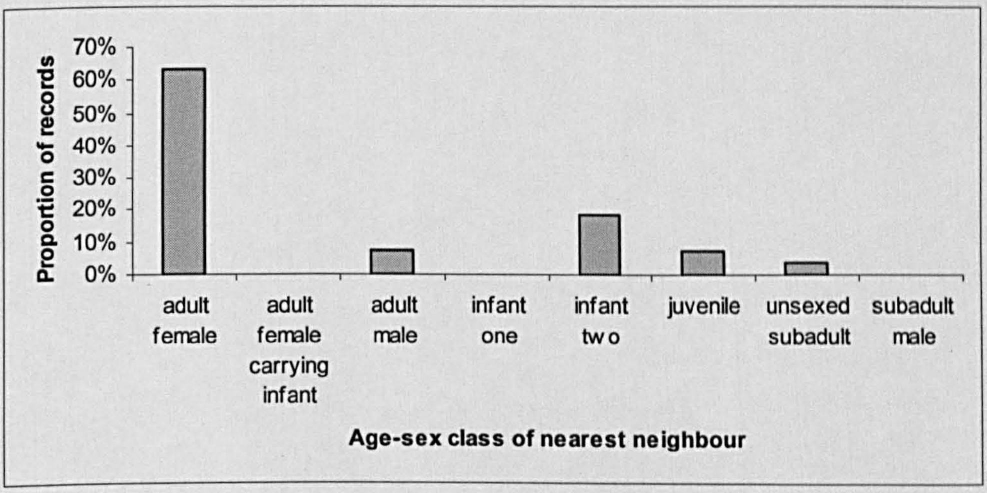

Figure 7.5 nearest neighbours of *infant twos*.

Age-sex classes were recorded more than 30m from their nearest neighbour at different frequencies to the frequencies they were recorded as focal individuals (X^2_7=40.767, p<0.01). Scan samples where the focal individual was more than 30m away from its nearest neighbour were made up by *adult males* (67.3%), *subadult males* (26.9%), *adult females* (3.8%) and *juveniles* (1.9%). *Subadult males* were more than 30m away from their nearest neighbour in 31.8% of scan samples compared to 15.9% for *adult males* (Figure 7.6). Thus *adult* and *subadult males* were more often found alone or more distant from other group members.

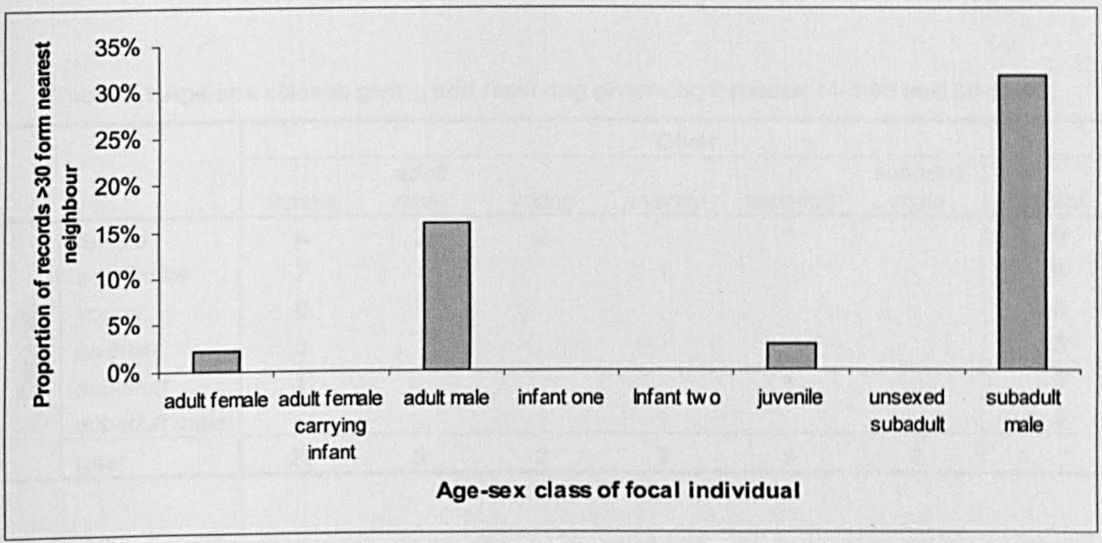

Figure 7.6 Observations in which the focal individual was >30m from its nearest neighbour.

7.3.3 *Adult males* within 10m of *adult females*

In 39 scans, where *adult females* were the focal individuals and it was possible to determine the age-sex classes of more than one neighbour within 10m, 20 observations contained no *adult males*, 12 observations contained one *adult male* and 7 contained two *adult males*. Since only the closest *visible* neighbours within 10m were recorded, more males could have been within 10m at each scan. This shows that adult females are often close to more than one adult male.

7.3.4 Grooming

Grooming made up 1.8% of the activity budget. Grooming was conducted during bouts of resting, often in dense cover. All age-sex classes were involved in grooming between 14th May 2003 and 30th November 2003 (Table 7.1). Females were 'givers' in 21 out of 30 observations, and were 'receivers' in 9. *Adult females* were observed giving and receiving grooming from all age-sex classes except *subadult males*, and *adult males* were observed grooming both *adult females* and other *adult males*, but not *subadult males*.

Table 7.1 Age-sex classes giving and receiving grooming between 14-5-03 and 30-11-03.

		Giver						
		female	*adult male*	*young*	*juvenile*	*subadult*	*subadult male*	**total**
Receiver	*female*	4	2	2		1		**9**
	adult male	7	1		1			**9**
	young	6						**6**
	juvenile	3						**3**
	subadult	1				1		**2**
	subadult male				1			**1**
	total	**21**	**3**	**2**	**2**	**2**	**0**	

7.3.5 Mating

Mating was observed on six occasions between late April and mid June, and made up less than 0.1% of the activity budget.

- On 11th June 2003 three matings occurred within the span of 47 minutes and involved at least two different males. The number of females involved was unclear. At 15:47 an *adult female* presented to an *adult male*, and copulation lasted 57 seconds. There were no other uakaris particularly close, but the pair was not far from the rest of the group. At 16:03 a small *adult male* or *subadult male* was seen copulating with an *adult female* some distance from the rest of the group. This lasted 30 seconds after which the male mounted again for a further 30 seconds. The pair moved off together after mating. At 16:34 an *adult male* was observed mating with an *adult female* some distance from the rest of the group.

- On 12th June 2003 at 08:50 an *adult male* was observed mating with an *adult female.*

- On 30th April 2004 at 13:58 a mature *adult male* was observed mating with an *adult female* in the lower canopy at least 15m away from the next nearest neighbour. Mating lasted a minimum of 40 seconds, after which the male spent 10 to 20 seconds rubbing his ano-genital region on a branch before leaving in the opposite direction to the female.

- On 16th May 2004 at 8:56 an *adult male* was observed mating with an *adult female* 25m away from rest of group. Copulation lasted 30 seconds, after which the male spent about 10 seconds rubbing his ano-genital region on a branch. 10 minutes later the same male was seen following the same female.

7.3.6 Agonistic and display behaviour

Agonistic and display behaviours made up 41.8% of all social behaviour. Actual fighting with physical contact was rarely observed, and did not appear in the scan sample data. Most agonistic behaviour, not including display behaviour, consisted of chasing accompanied by *rhä* and *chick* calls. Aggressive chasing was highly conspicuous and *give chase* made up 0.48% of scan samples. In all records of aggression it was *adult males* giving the aggression (n=18). Aggression was aimed at different age-sex classes at different frequencies ($\chi^2_7=29.600$, $p<0.01$). Aggression was most often aimed at other *adult males* (40%) or *subadult males* (35%), but was also seen directed at *juveniles* and unsexed subadults. There was a single observation of an *adult male* chasing an *adult female* carrying an infant.

On several occasions, groups of *adult* and *subadult males* were chased away from the main group by other adult males, who appeared to wait for support from other *adult males* before giving chase. Aggressive chasing was often preceded or followed by display behaviours such as *hindquarters bounce*, *lateral* or *vertical hang*, *branch shake*, *straight-leg strut* or *branch sway*. Penes were often displayed during chases or associated display behaviours. These sequences of behaviour often lasted several minutes and included up to 8 males.

Display behaviours were highly visible and made up 0.77% of the activity budget. While this does not include display behaviours clearly aimed at researchers, it was sometimes difficult to separate out display behaviours induced by researchers from those occurring naturally. Display behaviours recorded in scan samples included *urine wash* (0.03%), *branch bounce* (0.08%), *lateral swing* (0.08%), *branch shake* (0.11%), *straight-legged strut* (0.11%), *branch sway* (0.18%) and *vertical swing* (0.18%) (Table 7.2). Other display behaviours were recorded outside the scan samples. Only *adult males* were recorded performing display behaviours in the scan samples, although some display behaviours were observed being performed by other age-sex classes outside the scan samples.

Table 7.2 Display behaviours in *Cacajao calvus ucayalii* recorded at Lago Preto

Behaviour	Description	Context at Lago Preto
Arm raising (Fontaine 1981)	Raising a straight forelimb, out in front of the body.	Often observed in response to researchers.
Branch slapping (Fontaine 1981)	An arm raise that is brought down sharply onto the substrate.	Often observed in response to researchers. Only recorded in adult males.
Tattoo	Both arms are slapped on the substrate alternately in a short rapid sequence.	Rarely observed. Not recorded in other studies.
Piloerection (Fontaine 1981)	Piloerection of the dorsal pelage.	Observed when uakaris reacted to researchers, and in combination with other display behaviours.
Arched back (Fontaine 1981)	Arching of the back, usually in combination with piloerection.	Often observed in response to researchers.
Branch shaking (Fontaine 1981)	Brief, vigorous shaking of branches.	Often observed in response to researchers. Often accompanied by hic and chick calls from other group members.
Branch breaking and dropping (Fontaine 1981)	Breaking and dropping of branches.	Often observed in response to researchers. Often accompanied by hic and chick calls from other group members.
Branch rocking or swaying (Fontaine 1981)	Rocking rhythmically back and forth on branches.	Only recorded in *adult males*. Usually performed in the tops of canopies in very conspicuous locations and was sometimes done in pairs, apparently not towards each other with both animals often looking towards other uakaris.
Hindquarters bounce (Fontaine 1981)	Bilateral, abrupt leg extension and flexion resulting in a rapid bobbing motion.	Often observed in response to researchers.
Strut (Fontaine 1981)	Running or bounding across supports with locked knees and elbows. Often with piloerection, and a raised tail.	Only recorded in *adult males*, usually during chase behaviours.
Vertical swing	Suspended by the hind legs below a branch, swinging backwards and forwards and with his arms hanging outstretched beyond the head. Usually with piloerection, and often for several seconds.	Only observed in *adult* and *subadult males*. Often during male-male aggression. Sometimes done in pairs in the tops of trees during male-male conflicts. Often before or after bouts of branch rocking, hindquarters bounce or branch shaking behaviours. Not recorded in other studies.
Lateral swing	Similar to the vertical swing, but suspended below a branch by one hind leg and one arm.	Often observed in response to researchers. Often before or after bouts of branch rocking, hindquarters bounce or branch shaking behaviours. Not recorded in other studies.
Penis display	Erect penis exposed. The penis is pink in colour.	*Adult male* uakaris often revealed their penises during other display behaviours.
Urine washing (visual component) (Fontaine 1981)	Vigorous movements with the forearm from the groin forwards, whist urinating onto the fur of the stomach and chest. Rear limbs also occasionally used.	Urine washing was only observed in *adult males*.

7.3.7 Vocal Communication

The *hic* call (Table 7.3) was the commonest call at Lago Preto. *Hic* calls were given at a mean rate of 0.24 calls/individual/minute (1.09 notes/individual/minute), but calling rates varied from 0 to 0.75 calls/individual/minute (5.95 notes/individual/minute). No significant difference was recorded between the rate *hic* calls were given during different behaviours (ANOVA F2,172=0.593 p>0.05), but when fruiting trees were discovered, *hic* calls appeared to be given at high rates. All age-sex categories were observed giving *hic* calls, but *adult males* appeared to use this call only rarely, and usually as a single note. *Hic* calls were recorded with all other call categories, and were often elicited by *chick*, *bark*, *rhork* or *scream* calls, or by loud noises such as falling branches, and monkeys landing on palm fronds. *Hic* calls were given during all modes of behaviour.

Chick calls (Table 7.3) were given at a mean rate of 0.03 calls/individual/minute. They have a range of variations that are not easily defined. Quieter *chick* calls were given in response to falling branches, *scream* calls, or when less habituated groups reacted to researchers. Louder 'strong' *chick* calls were given in response to threats such as birds of prey. On hearing a strong *chick* alarm call, individuals became alert and looked up. Very loud strong *chick* calls were occasionally heard, and were followed by rapid rushing and descent by monkeys, eliciting further *chick* and *hic* calls (see Chapter 6 for descriptions of responses to predators). Quiet *chick* calls were often answered with *hic* calls or with another *chick* call, but individuals did not always look up or stop what they are doing. A different high-pitched type of *chick* call was given during fights and chases between adult males. These high-pitched *chick* calls were not described by Fontaine (1981) and were often accompanied by low-pitched *rhä* calls given by adult males.

Bark calls (Figure 7.3) were only observed being given by *adult males*, and were given at a mean rate of 0.01 calls/individual/minute. Barking individuals often barked continuously for several seconds or sometimes minutes, and were recorded calling in short bursts at a rate of up to 2.3 calls/second. *Bark* calls appeared particularly common in individuals that were alone or in very small groups far from the main group. Individuals on the extreme edges of groups often gave *bark* calls. Occasionally, *bark* calls were given at the end of a rest period. Sometimes *bark* calls were ignored, but they usually elicited *hic* calls. Occasionally *bark* calls were answered with *bark* calls from other individuals, resulting in sequences of alternating *bark* calls between two individuals.

Table 7.3 Calls in *Cacajao calvus ucayalii* recorded at Lago Preto.

Call	Description	Context at Lago Preto
Hic (Fontaine 1981) (Ca-Ca-Ca-Ca, Ayres 1986)	A short staccato 'he' or 'hic' given in series or as a single note (mean = 4.7 notes per call).	Given by all independent age-sex classes.
Chyook (Fontaine 1981)	A short quiet note, similar to a hic call, with a harder, more defined ending. It is given as a single note, and is highly variable; it may sound like "wick" or "wook", or have a whistle-like element. This call may be an intermediate call between a hic note and a chick call.	The context of this call was not determined.
Chick (Fontaine 1981)	Loud, high-pitched call with metallic ringing notes compared with the harsher bark call with which it intergrades. It is a single note, but often repeated.	Given by all independent age-sex classes. A distinct type of chick call was often heard during bouts of aggression.
Bark (Heymann 1990)	A loud, harsh dog-like bark, given in single notes which are often repeated, sometimes in long sequences. This call may intergrade into a rhork call.	Only heard given by *adult males*.
Rhork (Fontaine 1981)	Long, harsh, guttural low-pitched calls. They are usually loud, but are occasionally given as a shorter quieter call. Often several rhork calls are given in sequence by a single caller. Rhork calls may intergrade with scream calls.	Higher pitched rhork calls are given by younger animals. This is a relatively rare call, but appears to be used frequently during heavy rain, possibly by lost young animals. Lower-pitched rhork calls were given by *adult males*, sometimes within sequences of barks.
Rhä (Fontaine 1981)	Low pitched call similar to a rhork call, but slightly higher in pitch and more 'hiss-like'.	Given by males during aggressive encounters.
Scream (kreek and wa, Fontaine 1981)	Long high pitched calls, higher pitched and louder than a rhork call. Often given in sequences up to 30 seconds or more. Fontaine (1981) described two scream calls; 'kreek' and 'wa'. The difference between these calls could not be determined at Lago Preto.	Higher-pitched screams were given by *infants* and *juveniles* during periods of intense stress, such as when being chased by other individuals. Lower-pitched screams may be from older animals during chases or fights.
Wee-ook (Fontaine 1981)	High-pitched, bird-like whistles which vary considerably. Sometimes grade into quiet chick or chyook calls.	The context of this call was not determined.

7.3.8 Births

Infant one uakaris (0 to 3 months) were recorded on multiple occasions in August, September, October and November 2003. A single observation of a very small infant carried low on the belly was recorded in April 2004. In December 2004 a single observation of an *infant one* was recorded, and in February 2005 an older *infant one* (possibly in the early stages of *infant two*) was observed. In April 2006 a minimum count of 5 young uakaris in the mid to later part of the *infant two* stage were observed in a group of 50 to 80 individuals. From these observations the following approximate dates of births can be deduced:

- At least three births occurred between August and November 2003 (probably many more given the frequency of observation of infants).
- At least one birth occurred around February 2004 (probably not many more given the large number of hours of observation during the study period).
- At least one birth occurred around October or November 2004 (probably not many more given the large number of hours of observation during the study period).
- At least five births occurred between August and November 2005 (probably many more, given that less than half of the uakari population at the Lago Preto study site was sampled, and full counts of the groups sampled were not made).

From these observations it can be seen that uakaris are seasonal breeders, generally giving birth between August and November. It was also clear that far fewer births occurred at Lago Preto in 2004 than in 2003 and 2005.

7.4 Discussion

7.4.1 Social behaviour

The large group sizes and fission-fusion grouping patterns described in Chapter 6 clearly impact on the social organisation and mating systems adopted by *Cacajao*. There are two competing theories on how social groups are organised in the species. Garber and Kowalewski (in press) hypothesise that *Cacajao* has a multi-male breeding system in which males are likely to be tolerant of each other's sexual activity, and females are likely to be promiscuous. Garber and Kowalewski (in press) suggest that kinship might play an important role in this male-male tolerance. The closely-related *Chiropotes satanas* also forms large fission-fusion groups of up to 50 individuals or more (Veiga *et al.* 2006), and appears to have this kind of social organisation (Veiga and Silva 2005). Veiga and Silva (2005) noted that male *Chiropotes satanas* were affiliative, and were most often closest to other adult males. There are some obvious differences between Veiga *et al.*'s (2006) groups of *Chiropotes satanas* and *Cacajao calvus ucayalii*. Veiga *et al.* (2006) did not note the formation of bachelor groups in *Chiropotes*, or sequences of aggression between groups of males. Veiga (pers. com.) recorded very low levels of aggression in *Chiropotes satanas* (0.1%). Aggression in *Cacajao calvus ucayalii* at Lago Preto was higher, and more comparable to levels seen in *Ateles geoffroyi* (Fedigan and Baxter 1984) and *Lagothrix lagotricha* (Stevenson 1998). Bouts of aggression between groups of male *Cacajao calvus ucayalii* suggest a more competitive breeding system.

Knogge *et al.* (2006) put forward an alternative theory on the social organisation of *Cacajao calvus*, apparently based on Heymann's (1992) hypothesis on grouping patterns. Zinner *et al.* (2001) proposed that large groups are incompatible with a typical multimale-multifemale group structure. Zinner *et al.* (2001) predict that the formation of one-male units in large groups should be favoured, because females cannot maintain social relationships with all group members, and would be at risk from infanticidal males. Thus, Knogge *et al.* (2006) suggest that social organisation in *Cacajao calvus ucayalii* follows the pattern observed in other species that form very large groups, and are organised into 'one-male units'. Knogge *et al.* (2006) observed small units comprised of 'around 2 adult females and offspring, 2 subadults and 1 guarding adult male', but only during a short-term study.

The results of this Chapter show that adult and subadult males were most often closest to other males, but no distinction was made between males in bachelor groups and males associating with adult females. The overwhelming impression gained during this research at Lago Preto was that males that were travelling with adult females also appeared to associate with other males. Adult males were observed grooming each other and some display behaviours appeared to be conducted by pairs of adult males. The results show that females were regularly within 10m of more than one male, but sample size is low, and 10m is potentially a large distance in terms of social relationships.

It is possible to explain these observations within the 'one-male unit' model. Stammbach (1987) summarised a number of studies on the social behaviour of several baboon species which form one-male units within larger groups. In all of these studies, some one-male units had more than one male, who often joined as a follower. Another possibility is that the males defending the females cooperate even though they are from different one-male units. In hamadryas baboons (*Papio hamadryas*) for example, two or three one-male units are strongly associated with each other in 'clans' (Abegglen 1984).

Advantages to male primates in forming one-male units are in maximising the chances of fertilising females within the one-male unit. It is in the females' interest, however, to avoid the infanticide of their offspring by confusing the paternity of their offspring (van Schaik 2000). Observations of mating and female receptivity in wild uakaris are extremely rare. The observation of a subadult male copulating at Lago Preto does not suggest that adult *males* in one-male units control access to females, although this single observation could have been of a very rare event. Copulation in Fontaine's (1981) captive population was promiscuous.

Observations of adult male *Cacajao calvus ucayalii* engaging in aggressive chasing behaviours, apparently in cooperating groups, suggest that males leading one-male units would be under threat from bachelor groups. It is not inconceivable that a single male could defend a one-male unit from a group of bachelor males, as this occurs in other species (e.g. Stammbach 1987; Steenbeek *et al.* 2000), but the impression gained at Lago Preto was that one-male units did *not* form.

Garber and Kowalewski's (in press) model for the organisation of groups of *Cacajao* is akin to that seen in the Atelinae. In *Brachyteles* and *Ateles,* males associate with each other more than with females. They are tolerant of each other's sexual activity and work together to repel other males (Strier *et al.* 2002; Symington 1990). Since dispersal is female biased in these species, males are generally related, lowering the cost of this high degree of tolerance. Garber and Kowalewski also point out, however, that male tolerance of within-group copulations by other males was observed by Peres (1996) in *Lagothrix*, in which dispersal is bisexual. Evidence suggests that dispersal in *Chiropotes* may also be female biased, but all lone uakaris observed at Lago Preto were male, and the formation of bachelor groups of up to 8 adult males in *Cacajao calvus ucayalii* does not support the theory that dispersal is female biased. Presumably male uakaris leave the foraging groups of their mothers to join these bachelor groups. The impression gained at Lago Preto was that younger males in bachelor groups tended to stay on the periphery of these groups. It is possible that young males migrate to these groups where they form affiliative bonds with other males. Pairs or small groups of bachelor males may then attempt to usurp males that control or associate with groups of females.

At Lago Preto, aggression from adult males was usually directed at adult males, subadult males and juveniles. It is possible that young males are targeted by adult males that associate with females. Sexual crypsis has been noted in *Cacajao melanocephalus* (Defler 2003). Fontaine (1981) reported that captive juvenile male *Cacajao calvus ucayalii* entered a subadult male phase lasting 2 to 3 years, in which the uakaris displayed physical characteristics typical of adult females, including pendulous scrotal alae resembling female labia. The function of this sexual crypsis is unknown, but if young males are likely to receive aggression from other adult males, sexual crypsis could reduce attacks and delay enforced dispersal from a natal group.

Ayres (1986) observed that *Cacajao calvus* has a relatively-small testis weight in relation to its body size, and suggested that that this implied low levels of sperm competition, but did not appear to take into account the testis to body weight ratio observed in more closely-related species. Ayres (1986) observed that the testis weight was similar to that of *Colobus polykomos* or *Theropithecus gelada*, which have single-male breeding systems, but the ratio is the same as that in *Ateles geoffroyi* and not much lower than in *Lagothrix lagothricha*, which shows affiliative behaviour between males. Ayres (1986) posited that the testis to body weight ratio, and the pair formation and bachelor groups he observed supported evidence for a single-male breeding system. A single-male breeding system within the large groups seen in *Cacajao* would require an organisation similar to that suggested by Knogge *et al.* (2006). Although the organisation of foraging units in *Cacajao* may resemble that of *Theropithecus*, and be created for much the same reasons, (i.e. the inability of females to maintain social relationships with all members of a large group), the male affiliation observed in *Cacajao* at Lago Preto hints at a system more akin to that of *Ateles* and *Chiropotes*, and the testis to body weight ratio supports this when phylogeny is taken into account. *Cacajao* may differ from *Chiropotes* in that it forms smaller social units within large groups, but more convincing data are required to demonstrate whether these are one-male or, at least sometimes, include two or more affiliative males. More data on the nearest neighbours of the adult males that are associating with females are required before conclusive statements on the social organisation of *Cacajao calvus ucayalii* can be made.

7.4.1.1 A new hypothesis for the social organisation of *Cacajao calvus ucayalii*

The results and observations in this Chapter suggest that the large 'supergroups' that form in *Cacajao calvus ucayalii* are made up of much smaller units. The most important female bonds may be relationships between mothers and their older female offspring, while males may bond with other males after leaving their mothers, forming bachelor groups within the supergroup. Juvenile males may be forced away from their mothers' units by adult males during the breeding season, which may account for the sexual crypsis observed in *Cacajao*. Groups of affiliated males, who may or may not be related, may fight or display to other groups of males for access to females during the breeding season. Stronger groups of males who are able to associate with groups of females may be tolerant of each other's mating activity, and females are likely to be promiscuous. Social units may move around within and between supergroups, explaining highly variable 'maximum group sizes' observed in each contact (Chapter 6). Thus, the boundary between 'dispersal' and 'fission-fusion' may be blurred in this species.

7.4.2 Vocal communication

The calls of *Cacajao calvus ucayalii* at Lago Preto were varied and not always clearly distinct, with calls often intergrading into other types of calls. Uakaris appeared more vocal than any other primates at Lago Preto, and it can be surmised that many of the calls, particularly *hic* and *bark* calls, serve to coordinate the movements of large widely-spaced groups, or to keep track of members of a social unit within the troop. *Hic* calls are given mainly by females and juveniles and may serve to keep track of members a social unit over short distances. *Hic* calls appeared much less frequent in smaller groups, although insufficient data were collected to show this. This call appeared particularly common during the early morning when large groups of uakaris appeared to be active in the canopy, but were not feeding or travelling in one direction as a group. *Bark* calls were given mainly by adult males and may coordinate group movements. Males foraging far from the rest of the group often gave *bark* calls, but the occasional exchange of *bark* calls in sequence with other males, suggests that there may be another inter-male social function to this call. The intensity of several of the calls seemed to vary depending on the context they were given in.

7.4.3 Tail wagging and the adaptive significance of the short tail

Cacajao is the only Neotropical primate genus with a shortened, non-prehensile tail; it is around 34-36% the length of the head and body (Hershkovitz 1987a). The related *Pithecia* and *Chiropotes* both have tails which exceed their body lengths, but are not prehensile (Hershkovitz 1985, 1987b). Walker and Ayres (1996) highlighted the role of primate tails in balance and for guiding leaps, and suggested that *Cacajao* compensated for the lack of tail by using alternative positional behaviours. Walker and Ayres (1996) do not suggest a reason for the reduced tail in *Cacajao*, but suggest that the selection pressures must have been great to overcome the advantages for its use in balance, but not great enough to overcome the selection pressure to maintain it for display.

All the Pitheciinae use their tails for communication. *Pithecia* shake their tails vigorously when excited (Personal observation; Buchanan *et al.* 1981) and *Chiropotes* use their tails for a number of signals. One such signal is 'tail wagging', which authors have interpreted variously as 'signalling excitement' (Hick 1968), 'relieving tension' (Fernandes 1993), or 'acting as a contact signal' (van Roosmalen *et al.* 1981). These two genera have particularly long tails, whose size is exaggerated by thick fur. In *Pithecia* this can make the tail look almost as large as the body.

Side-to-side tail wagging was recorded in captive *Cacajao calvus* by Fontaine (1981) who interpreted it as a signal to 'communicate general arousal'. Walker and Ayres (1996) reported tail wagging concurrent with calls in Ca*cajao calvus calvus*. At Lago Preto *hic* calls were often accompanied by side-to-side tail wagging. Additionally, when individuals gave the bark call, a single, deep forward wag accompanied each bark. Front-to-back tail wagging was not recorded by Fontaine (1981), probably because it occurs with *bark* calls that were not recorded in Fontaine's captive population. The tail is also used in the *straight-leg strut* display and other aggressive displays, when it is often held erect above the body with piloerection. While it was not quantified during data collection, side-to-side tail wagging was clearly a very common, at times almost constant, behaviour in *Cacajao calvus ucayalii* at Lago Preto, particularly in young individuals. Constant tail-wagging was also observed in *Cacajao melanocephalus* by Boubli (1997), who did not offer a possible explanation for the signal. Defler (2003) suggested that the tail movements in *Cacajao melanocephalus* communicate a good state of well-being and that they stop wagging the tail in moments of stress. Tail wagging may be a contact signal for drawing the attention of other group members. If tail wagging acts chiefly as a contact signal, then tail movements would be expected to stop in moments of stress when individuals wanted to *avoid* drawing attention to themselves from aggressive conspecifics or predators. Conversely, in situations of mild stress, when individuals want to draw the attention of relatives or other group members, perhaps in young individuals signalling to their mothers, tail wagging might be expected to increase.

While it is possible that different locomotory needs to related species could have led to the shortened tail in *Cacajao*, the obvious importance of the tail in communication suggests selection pressures related to signalling effectiveness or efficiency. Fontaine (1981) observed that the short tail was not used in feeding or locomotion, and tail wagging was the only function he could determine, but he did not suggest this function as a selection pressure for a shortened tail. A short tail can be 'wagged' (the whole tail moving in the same direction at any moment in time, as opposed to 'shaken' as in *Pithecia*) at a higher rate than a long tail, giving a clear conspicuous signal, without a high energy cost. This can be demonstrated by attempting to wag sticks or lengths of thick rope of different lengths from the wrist. That *Cacajao* is highly vocal suggests an increased need for constant communication during foraging in large widely spaced groups. The shortened tail could also have evolved out of the uakaris' need to maintain contact in widely-spaced groups, and to communicate efficiently while foraging.

7.4.4 The adaptive significance of the red face in *Cacajao calvus*

Perhaps the most obvious signal in *Cacajao calvus* is not an active signal, but a passive one. The red uakaris' scarlet face is coloured, not by pigments, but by vascular specialisation in the skin that allows blood to flow near to the surface (Hill 1965). The bright colour is clearly signalling something to someone, since explanations such as thermoregulation seem untenable, but the questions have always been 'what?' and 'to whom?' Ayres (1986) suggested two theories on why *Cacajao calvus* has a bright red face. This Chapter reconsiders the problem in the light of the 20 years of research on sexual signalling published since Ayres' thesis.

Ayres' (1986) first hypothesis to explain the red face is based largely on the observation by Clutton-Brock and Harvey (1976) that sexual swellings, and brightly coloured "sexual signalling skin", occur principally in species that have large multi-male social groups that range over a large area and often split into subgroups. Ayres (1986) followed Dixson (1983) in suggesting that the red face could therefore indicate reproductive status. Dixson (1983) recognises that *Cacajao calvus* is exceptional amongst platyrrhine primates in having brightly-coloured skin, which is generally more common in catarhine primates. Dixson suggests that the red head is a male sexual signal, and might have some significance in social communication.

Ayres (1989) points out that the 'indicating reproductive status' theory fails to explain why the closely-related *Cacajao melanocephalus*, which also lives in similar large fission-fusion multi-male social groups, lacks the red face. For this reason Ayres (1986) appears to favour the second theory he described. This theory originates from a suggestion made to Ayres by W. D. Hamilton, and is based on the idea that the red face communicates good health. This colour fades in dead uakaris, and sick uakaris also turn pale. This phenomenon was described by Hill (1965), and Lasry and Sheridan (1965) reported paling of the face in a captive *Cacajao calvus* with Chagas' myocarditis (*Trypanosomiasis cruzi*), a blood parasite transmitted by the faeces of a bloodsucking reduviid bug. The BBC (CBBC 2005) shot video footage of a very sick captive male red uakari that had a very pale face (Figure 7.7). Ayres (1986) suggests that the red face is a signal by which individuals can assess the health status of potential mates, enabling them to select mates with low parasite burdens and, therefore, good resistance to parasites. This follows Hamilton and Zuk's (1982) hypothesis that parasites adversely affect male secondary sex characters and that females prefer unparasitised over parasitised males. Evidence for female selection for male traits in primates, and especially for red facial skin, has previously been lacking, but Waitt *et al.* (2003) provide evidence that female rhesus macaques prefer redder-faced males over paler ones. As yet, there is no such evidence in *Cacajao calvus.*

Figure 7.7 Sick adult male red uakari monkey (Picture from video footage, CBBC 2005)

The second theory allowed Ayres (1986) to develop a theory to answer the question 'why doesn't *Cacajao melanocephalus*, which has similar ecology and morphology, share the bald red head of *Cacajao calvus*?' Hamilton and Zuk's (1982) theory predicts that brighter signals in different species will be correlated with higher parasite burdens, and this was shown to be true in a survey of North American passerine birds. Ayres (1986) cited high rates of infection with malaria (*Plasmodium brasilianum*) in *Cacajao calvus* found by Almeida and Deane (1970), and Davies *et al.* (1991) found that *Cacajao calvus* had the highest rate of malarial infection in 17 species of Amazonian primate, whereas *Cacajao melanocephalus* had no recorded infections. However, malaria must be discounted from this discussion because, as Barnett and Ross (in preparation) point out, malaria was introduced to South America by human colonists post 1500 (see Leclerc *et al.* 2004; Lim *et al.* 2005) and therefore cannot have contributed to the evolution of the red facial skin in *Cacajao calvus.* There are other blood parasites endemic in Amazonia, such as the trypanosomes observed by Lasry and Sheridan (1965), but there is a lack of information on parasite burdens in *Cacajao.* Ayres (1986) suggests that the habitat differences between *Cacajao calvus* and *Cacajao melanocephalus* could lead to a higher parasite burden in *Cacajao calvus.* There are higher numbers of haematophagous insects, the vectors of many blood parasites, in the white-water flooded forest habitat of *Cacajao calvus* than in the black-water flooded-forest habitat associated with *Cacajao melanocephalus* Ayres (1986). Ayres proposes that this might have led to higher pressure to select mates for resistance to parasites, and could ultimately account for the red face in *Cacajao calvus*.

If Ayres is correct we might predict that red faces in other primate species might be associated with swamp or flooded forests. There are a few primate species which are strongly associated with flooded habitats. Allen's swamp monkey (*Allenopithecus nigroviridis*), and the proboscis monkey (*Nasalis larvatus*) inhabit swamp habitats in Africa and Asia respectively, and the blackish squirrel monkey (*Saimiri vanzolini*) is sympatric with *Cacajao calvus calvus* in Amazonian *várzea*. None of these have red facial skin, although adult male *Nasalis larvatus* do have bright red penes used in display. Several other platyrrhine monkey species have populations which live permanently in flooded habitats, including eleven species which live sympatrically in the extensive white-water flooded forests of the Pacaya-Samiria National Reserve in Peru. Again, none of these have red faces. Several other species of primates do have red facial skin (Table 7.4). Four of these are from the genus *Macaca*, but the others presumably evolved red facial skin independently. *Cacajao calvus* is the only one of these 'red-faced' monkeys that lives in flooded forests. These observations do not support the theory that large numbers of haematophagous insects in white-water forests are generally a key factor in the evolution of red faces, although it is possible it was a factor for *Cacajao calvus*.

What the red-faced species *do* all have in common is that all these species live in large multimale-multifemale social groups, some of which have fission-fusion grouping patterns. These species all have non-red-faced close relatives, which in most cases do not vary much in group size, social system or habitat preference from the red-faced counterparts. Of particular note are the other red-faced cebids *Chiropotes albinasus* and *Ateles paniscus*. In each of the three closely-related genera *Chiropotes, Cacajao* and *Ateles* there is one taxon that has red facial skin, and one or more closely related taxa that do not. Of the three genera, only *Cacajao* lives in flooded habitats. Thus, another explanation for the red skin seems more likely. As proposed by Dixson (1983) for *Cacajao*, the red facial skin of all primates in Table 7.4 probably evolved under multi-male breeding conditions, with large group sizes, and in some cases a fission-fusion grouping pattern. *Cacajao* also has a brief, synchronised breeding season, during which competition for mating opportunities is probably intense. The 'affiliative male' social organisation revealed in this Chapter could have led to the increased importance of mate choice based on skin colour, in place of fighting or aggressive displays between males.

The problem remains that *Cacajao melanocephalus* has a very similar social structure to *Cacajao calvus*, and does not have a red face. However, red faces are the exception in most taxonomic groups, and *all* red-faced monkeys have non-red-faced relatives. The emphasis should therefore be on why it *did* evolve in red-faced species. There are other differences between *Cacajao calvus* and *Cacajao melanocephalus*, such as body size and pelage colour. Sexual dimorphism and sexual dental dimorphism are more pronounced in *Cacajao calvus* than in *Cacajao melanocephalus*. *Cacajao melanocephalus* is also probably more similar to the ancestral form (Hershkovitz 1987a), which presumably did not have a red face.

If only females were selecting for red faced mates, then one might expect that only the males would have red facial skin, as seen in *Mandrillus sphinx*. In *Cacajao calvus,* however, the females and young are also red-faced (though the adult males are generally redder). Males do appear to form brief 'consortships' with females, or at least follow them for extended periods during the brief breeding period (Ayres 1986; Personal observation). It is possible that they do also select females with whom to create social bonds on the basis of the red facial colour.

Since young *Cacajao calvus* also have red faces, the facial colour may have a secondary importance in social signalling. *Cacajao calvus* have a wide range of facial expressions and they have pale-white eyelids, with which they communicate their resting state (Fontaine 1981), so facial colour does appear to have at least some other function in communication. Fontaine (1981) went so far as to suggest that the function of the red face might be to facilitate the detection of facial expressions. Fontaine assumed a 'visual acuity in *Cacajao* roughly comparable to that of man' in postulating this theory. In fact *Cacajao* has polymorphic colour vision, in which all males and some females are dichromatic, while some females are trichromatic (Sumner and Mollon 2003). Changizi *et al.* (2006) suggest that trichromatic colour vision could have evolved in primates specifically to detect two blood-related dimensions in skin-colour variation, facilitating better discrimination between emotional states, socio-sexual signals and threat displays in conspecifics. If the red face had a function in facilitating the detection of facial expressions, as Fontaine suggests, one might also expect *Cacajao* to have evolved trichromatic vision to detect subtleties in facial hues, although dichromatic individuals can still detect one of the two blood-related dimensions in skin colour variation (Changizi *et al.* 2006).

Table 7.4 The habitat preferences, group and social systems of red-faced primates.

Species	Habitat	Group size	Social system
Red-faced Black Spider Monkey *Ateles paniscus*	Subtropical and tropical moist forests (Rylands *et al.* 2003).	About 20 individuals (Mittermeier and van Roosmalen 1981).	Multimale-multifemale social system. Fission-fusion grouping pattern (Mittermeier and van Roosmalen 1981).
Bald uakari *Cacajao calvus*	White-water *várzea* forests and *terra firme* forests (Ayres 1986; this study).	30-200 individuals (Ayres 1986; Chapter 6).	Multimale-multifemale social system. Fission-fusion grouping pattern (Ayres 1986; Chapter 6).
Red-nosed saki *Chiropotes albinasus*	*Terra firme* forests (Veiga *et al.* 2006).	19-30 individuals (Ayres 1989). 50+ individuals (Veiga *et al.* 2006).	Multimale-multifemale social system. Fission-fusion grouping pattern (Veiga *et al.* 2006).
Stump-tailed macaque *Macaca arctoides*	Subtropical and tropical broadleaf evergreen forest (Fa 1989).	12-50 individuals usually 20 to 30 (Fooden *et al.* 1985).	Multimale-multifemale social system (Fooden *et al.* 1985).
Assamese macaque *Macaca assamensis*	Subtropical and tropical dry forest (Eudey *et al.* 2000).	10-50 individuals (Roonwal and Mohnot 1977).	Multimale-multifemale social system (Roonwal and Mohnot 1977).
Japanese Macaque *Macaca fuscata*	Wide range of habitats, including mountains, subtropical and temperate broad-leaved evergreen forests (Nakagawa *et al.* 1996).	5-70 individuals (Nakagawa *et al.* 1996).	Multimale-multifemale social system (Nakagawa *et al.* 1996; Napier and Napier 1985).
Rhesus macaque *Macaca mulatta*	Wide range of habitats including tropical and temperate habitats including semidesert, dry deciduous, mixed deciduous, bamboo, and temperate forests as well as in tropical forests and mangrove swamps (Seth and Seth 1986; Fooden 2000; Srivastava and Mohnot 2001).	6–90 individuals (Makwana 1978).	Multimale-multifemale social system (Makwana 1978).
Mandrill *Mandrillus sphinx*	Dense primary rainforest and sometimes secondary rainforest, gallery forest and coastal forest (Harrison 1988; Rowe 1996).	Up to 250 individuals (Jouventin 1975; Hoshino *et al.* 1984). Mean group size 150 individuals (Tutin *et al.* 1997).	Multimale-multifemale social system. Unimale mating system, although 'one-male units' may have one *or two* males (Jouventin 1975).

7.5 Summary

1. The age-sex classes were not evenly distributed through the groups, with males forming bachelor groups on the periphery of large groups.

2. *Adult males* were nearest neighbours of *adult males* in 68.6% of observations. Excluding infants, *adult females* were the commonest

neighbours for *adult females*. *Adult* and *subadult males* were more often found alone or more distant from other group members.

3. *Adult female* uakaris were often close to more than one *adult male*.

4. *Adult male* uakaris engaged in aggressive chasing and display behaviours. Display and chasing behaviours often appeared to be conducted in pairs or groups of 'affiliative males'.

5. Uakaris at Lago Preto were seasonal breeders, giving birth between August and November. Mating was observed on six occasions between late April and mid June.

6. Far fewer births occurred at Lago Preto in 2004 than in 2003 and 2005.

7. The uakari's shortened tail could have evolved to maintain contact in widely-spaced groups, and to communicate efficiently while foraging. The obvious importance of the tail in communication suggests selection pressures related to signalling effectiveness or efficiency, rather then the locomotory pressures generally implied.

8. The red facial skin of uakaris probably evolved because of extreme multi-male breeding conditions, with a short breeding season, affiliative males, large group sizes and a fission-fusion grouping pattern.

Chapter 8

Predicting the Impact of Timber and Non-Timber Plant Resource Extraction on Red Uakari Monkeys in the Iquitos-Yavarí Region.

8.1 Introduction

Protected areas are currently inadequate in size to protect the biological diversity found in tropical forests and, in many tropical countries, the greater area of timber production forests may provide critical habitat for wildlife (Fimbel *et al.* 2001). Selectively logged and second-growth forests are recognised for their value in the conservation of biological diversity (Chazdon *et al.* 1998). Conversely, the management of protected areas often includes provision for the extraction of natural resources. In the Tamshiyacu-Tahuayo Communal Reserve (TTCR) in Peru, communities have retained control over the management of natural resource use, and practice small scale farming, hunting, fishing and extraction of forest products within the reserve (Newing and Bodmer 2004). Similar systems operate in the Amanã Sustainable Development Reserve (ASDR) in Brazil, and the adjoining Mamirauá Sustainable Development Reserve (MSDR), where small-scale logging is also practised (Bowler *et al.* 2006). Reserves like the TTCR and MSDR have shown that controlled use of resources, including game hunting, can be compatible with the conservation of game populations and other wildlife (Bodmer and Puertas 1999). Where endangered or vulnerable animals are present it is necessary to consider how the extraction of timber or non-timber plant-resources will impact on these species.

Many species of forest wildlife thrive in selectively-logged forest (Frumhoff 1995). Some taxa, at some sites, show greater species richness and diversity in selectively-logged than in unlogged forests (Isabiriye-Basuta and Kasenene 1987; Nummelin and Borowiec 1991), while other studies have shown similar species richness in logged and unlogged forest (e.g. Clarke *et al.* 2005). These results often give an impression that selective logging has little impact or even beneficial consequences on wildlife. Frumhoff (1995) points out that such conclusions would be false, given that species able to colonise and persist in logged forests are often replacing others that require less disturbed habitat. While it appears that selective logging might be compatible with biodiversity conservation, and that populations of some animal species will benefit, other species will decline in logged habitats.

Primates show widely variable responses to logging (Plumptre and Grieser Johns 2001). Plumptre and Reynolds (1994) and Johns (1991) have shown that some primate species can occur at higher densities in selectively-logged forest, while others decrease in density. In African and Asian primates, Skorupa (1987) found that poor species survival was correlated with large home ranges, broad group spread and a high percentage of fruit, seeds and flowers in the diet. These findings are supported by similar analyses by Harcourt (1998) and Johns and Skorupa (1987), while Plumptre and Grieser Johns (2001) added that seed predators appear to be adversely effected by logging.

Results from Grieser Johns (1997) suggest that the Pitheciinae seed predators, particularly *Cacajao* and the closely-related *Chiropotes*, are adversely affected by intensive logging. *Cacajao melanocephalus*, for instance, declines in areas of degraded *Igapo* (Hernandez-Camach and Cooper 1976). However, Ayres and Johns (1987) found that moderate levels of logging in *várzea* forests do not result in population reduction for *Cacajao calvus calvus*. Ayres and Johns (1987) suggest that the lower levels of damage generally caused by timber extraction in *várzea*, compared to similar levels of extraction in *terra firme*, might allow *Cacajao* to persist in these logged areas. *Chiropotes,* which lives in *terra firme* forests, and does not appear to use *várzea* forest, showed very low tolerance to logging on the Araguia river (Ayres and Johns 1987). They noted that several important food source trees for *Chiropotes satanas* were removed by logging on the Araguaia River, but Ferrari *et al.* (2004) found that in the absence of hunting, *Chiropotes satanas* around the Tucurui Reservoir might be more tolerant to disturbance. Ayres and Johns (1987) considered the effects of timber extraction on *Cacajao calvus calvus* inhabiting exclusively seasonally flooded *várzea* forests, where selective logging had occurred in some areas. They suggested that the influence of logging on white uakaris would depend on the extent that felled timber trees were also the food trees used by the uakaris. Ayres and Johns found that few of the uakaris' food trees were logged commercially, with some important exceptions, notably *Piranhea trifoliate*. This species is seasonally infested with caterpillars that are an important food for *Cacajao calvus calvus* when other resources are scarce. Ayres and Johns (1987) warned that when the extraction of new timber species becomes commercially viable they can be removed from the accessible *várzea* forests very quickly. Since the publication of their paper, *Xylopia callophylum* has become important as a timber species. This species was recorded as particularly important in the diet of *Cacajao calvus calvus* by Ayres (1986). So, since 1998 a forestry programme promoting the sustainable use of timber inside Mamirauá Reserve has banned the exploitation of this particular tree species (Bowler *et al. 2006*).

The Yavarí has been subject to logging for many years, but timber extraction appears to have been limited to only the most valuable species. Resource extraction peaked in the 1970s and then began a slow decline. Valuable *Cedrela* timber became scarce close to the river, and timber companies found it too difficult to float the timber out on the small forest streams. Operations were then hit by outbreaks of malaria in the 1990s which led to most logging operations being abandoned (Bodmer and Puertas 2003; also see Chapter 2). New timber concessions on the Peruvian side of the Yavarí River, designated as a permanent production forest for selective timber extraction, were granted in 2004. These areas were divided into plots that logging companies could apply to manage for a 40-year period. Many of the companies controlling concessions are quite small and are hired by larger commercial firms that take the trunks by river to Petropolis and Islandia at the mouth of the Yavarí. Not all concessions were taken, and companies presumably selected only the most attractive concessions, based on the amount of valuable timber and ease of access (Bodmer *et al.* 2006).

The effect of logging and non-timber resource extraction on *Cacajao calvus ucayalii* in the Yavarí-Ucayali corridor will depend on which tree species or fruits are harvested, and the extent that these trees are used by *Cacajao calvus ucayalii.* The damage levels created by harvesting, and the level of hunting during the extraction of timber, will also determine the extent of the effects. Many of the most important non-timber forest products are palms, which are harvested for food and building materials. The importance of *Mauritia flexuosa* palms to the genus *Cacajao* is well known (Aquino 1999; Boubli 1999), but has never been adequately quantified. Bodmer *et al.* (1999) attempted to quantify the importance of palms for terrestrial animals and demonstrated that the removal of *Mauritia flexuosa* potentially results in a reduction in the biomass of a number of important game animals.

The effect of logging on *Cacajao calvus ucayalii* in the Yavarí River basin will also depend on the extent that logging concessions coincide with the patchy distribution of the monkey. Extensive surveys by Salovaara *et al.* (2003) and Bodmer *et al.* (2003) on the Yavarí and Yavarí-Mirín Rivers and around the TTCR close to Iquitos demonstrate a patchy distribution for *Cacajao calvus ucayalii* in this region. Its range coincides largely with logging concessions in the area (Figure 8.1). Using the values of timber in sawmills on the lower Yavarí and other areas, and by looking at current logging practices on the Yavarí, the species most likely to be removed from the logging concessions are determined. The overlap in the diet of *Cacajao calvus ucayalii* with timber and non-timber resource use is then examined to make predictions on how resource extraction in the Iquitos-Yavarí region might affect populations of this primate.

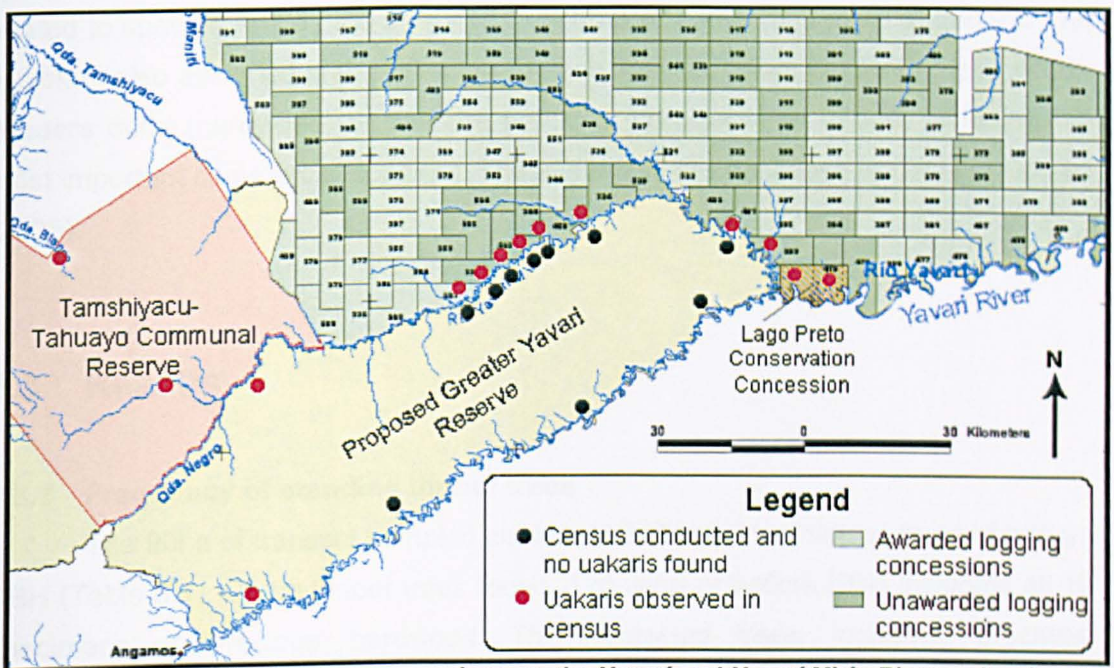

Figure 8.1 Map of the logging concessions on the Yavarí and Yavarí-Mirín Rivers, showing the distribution of *Cacajao calvus ucayalii* in the area. Red circles indicate sites where *Cacajao calvus ucayalii* has been observed. Black circles indicate sites where census work has been conducted and *Cacajao calvus ucayalii* has not been found.

8.2 Methods

8.2.1 Timber species in the Iquitos-Yavarí region

The timber species being extracted on the Yavarí were determined by observing logs being transported on the river, and conducting informal interviews with people from the village of Esperanza, where many logging operations were based. Sawmill staff at the mouth of the Yavarí were interviewed to attempt to predict which species were likely to be extracted in the future.

8.2.2 Tree composition and volume of standing timber

To assess the volume of timber species in *terra firme* forests on the Yavarí, surveys were conducted by Coales (2005) at a site about 45km upriver from Lago Preto called Santa Elena (S 4°39', W 72°04'). Four fixed-width transects 60m wide were surveyed; one of 2km, one of 3km and two of 5km (total area of 90ha). All commercial species within the transects with a diameter at breast height (DBH) of greater than 10cm were identified by a field assistant with experience in commercial timber surveys in Loreto. For all trees, the local name used by the assistant was recorded, and the tree was identified formally by a botanist. Some local names related to species, while others related to genera or sometimes pairs of genera. The assistant also assigned a classification to each species: 'Madera blanda' (softwood), 'Madera dura' (hardwood) or 'Madera preciosa' ('precious' hardwood, including the most important commercial species). These surveys are described in detail in Coales (2005).

8.3 Results

8.3.1 Frequency of standing timber trees

The 90ha of transect sampled contained 248 individual timber trees of >10cm DBH (Table 8.1). Of the timber trees found, 126 were of >40cm DBH including all 13 specimens of 'precious' hardwood. The hardwood trees, including 'precious' hardwoods occurred at a density of 0.478 trees/ha, and the softwoods at 0.922 trees/ha (Table 8.2).

8.3.2 Timber and non-timber plant-resource species in the diet of *Cacajao calvus ucayalii*

Several tree taxa in the diet of *Cacajao calvus ucayalii* at Lago Preto are also extracted by the timber industry, or as non-timber forest products (Table 8.3). The diet contained 3 palm species that are used as non-timber forest products in and around the TTCR, *Maurita flexuosa*, *Oenocarpus bataua* and *Astrocaryum chambira* (Table 8.3). Of these, *Mauritia flexuosa* is clearly the most important, being extracted in high volumes and making up 20% of the diet of *Cacajao calvus ucayalii.* Precious hardwoods did not feature in the diet, but some other, less-sought-after hardwoods (e.g. *Licania heteromorpha*, *Manilkara* sp.) did. Possibly the largest overlap between the diet of *Cacajao calvus ucayalii* and the potential for extraction is for trees in the family Myristicaceae, known locally as 'cumala'. This family makes up a relatively large part (4.2%) of the diet of *Cacajao calvus ucayalii*, and is one of the commonest families in Lago Preto (13.3% in *terra firme*, 8.7% in *várzea*, 12.0% in upland *aguajal* and 9.4% in floodplain *aguajal*).

Table 8.1 Frequencies of timber tree species of DBH>10cm in 90ha (from Coles 2005).

Type of timber	Local name	Scientific name	Number of individuals (n=248)
Precious hardwood	Tornillo	*Cedrelinga catenaeformis* FABACEAE	11
	Cedro	*Cedrela odorata* MELIACEAE	1
	Cedro blanco	*Cedrela fissilis* MELIACEAE	1
Hardwood	Guariuba	*Clarisia racemosa* MORACEAE	19
	Canela muena	*Ocotea aciphylla* LAURACEAE	14
	Quillosisa	*Erisma bicolor* VOCHYSIACEAE	8
	Cunchi muena	*Endlicheria krukovii* LAURACEAE	3
	Lagarto caspi	*Calophyllum brasiliensis* CLUSIACEAE	1
Softwood	Cumala roja	*Iryanthera* spp. MYRISTICACEAE	87
	Cumala colorado and aguanillo	*Otoba glycicarpa* and *Otoba parviflora* MYRISTICACEAE	52
	Pashaco roja	*Parkia panurensis* FABACEAE	33
	Cumala blanco	*Osteophloeum plotyspermum* and *Virola* sp. MYRISTICACEAE	8
	Pashaco blanco	*Parkia* sp. and *Macrolobium* sp. FABACEAE	3
	Cumala caupuri	*Virola* sp. MYRISTICACEAE	3
	Marupa	*Simarouba amara* SIMARUBACEAE	2
	Lapuna	*Chorisia integrifolia* and *Cieba pentandra* BOMBACEAE	1
	Pucuma caspi	*Iryanthera tricornis* MYRISTICACEAE	1

Table 8.2 Densities of trees of DBH>40cm of different timber types (from Coles 2005).

Type of timber	Number of trees in the total area surveyed (90ha)	Trees/ha
Precious wood	13	0.144
Hardwood	30	0.333
Softwood	83	0.922
Total timber trees	**126**	**1.400**

Table 8.3 Timber trees and exploited palms in the Iquitos-Yavarí region which also feature in the diet of *Cacajao calvus ucayalii*.

Local name	Scientific name	Use	Extraction in concessions on the Yavarí and Yavarí-Mirín	Importance in the diet of *Cacajao calvus ucayalii*
Trees				
Cumala roja and pucuma caspi	*Iryanthera* spp. Myristicaceae	Softwood	Currently low, but intensive extraction possible in the future.	2.8% of the diet. Unripe seeds eaten.
Cumala blanco and cumala caupuri	*Osteophloeum plotyspermum* and *Virola* spp. Myristicaceae	Softwood	Currently low, but intensive extraction possible in the future.	*Osteophloeum* 0.6% of the diet. Unripe seeds eaten. *Virola* 0.7% of the diet. Unripe seeds and ripe arils eaten.
Pashaco blanco and pashaco rojo	*Parkia* spp. and *Macrolobium* spp. Fabaceae	Softwood	Very low. Unlikely to be extracted in large quantities.	*Parkia* 2.3% of the diet. Unripe seeds and gums eaten, and possibly insects infesting old pods. *Macrolobium* 0.1% of the diet. Unripe seeds eaten.
No common name given	*Licania* spp. Chrysobalanaceae	Hardwood	Probably not extracted. Extraction possible in the future.	Very important (6.1% of the diet).
No common name given	*Manilkara* spp. Sapotaceae	Hardwood	Probably not extracted in great numbers. Extraction possible in the future.	Occasional (0.5% of the diet).
No common name given	*Brosimum* spp. Moraceae	Hardwood	Probably not extracted in great numbers. Extraction possible in the future.	Moderate (1.4% of the diet).
Palms				
Aguaje	*Mauritia flexuosa* Aracaceae	Fruits eaten raw, or made into sweet drinks and ice-cream.	Low	20% of the diet. Ripe pulp eaten. Unripe seeds very occasionally eaten.
Ungurahui	*Oenocarpus bataua* Aracaceae	Fruits made into sweet drinks and ice-cream.	Low	2.3% of the diet. Ripe pulp eaten.
Chambira	*Astrocaryum chambira* Aracaceae	Oil, fruit and fibre.	Very low	Occasional (<0.1% of the diet). Seeds eaten.

8.4 Discussion

The most striking thing about the diet of *Cacajao calvus ucayalii* at Lago Preto is the dominance of the aguaje palm *Mauritia flexuosa* for four months of the year.

This species comprised 20% of the total diet, and more than 50% of the diet in May, June, July and August. Aguaje is also the most important non-timber plant-resource harvested from the forest by the human population in Loreto. The fruits, which grow on large racemes, are eaten raw or made into sweet drinks and ice-cream. An estimated 20 tons of aguaje fruit is consumed each day in Iquitos alone (Castillo *et al.* 2006). Wild aguaje grows in tall stands, which are difficult and dangerous to climb (Uhl and Dransfield 1987), so the racemes are generally collected by felling the palm, reducing the fruit crop for subsequent years. Competition for wild aguaje means they are often harvested before they are ripe, and sold for a fraction of the value of ripe fruit (Bodmer *et al.* 1999). Given the importance of aguaje to *Cacajao calvus ucayalil*, extraction of this resource may impact on the densities of the species in some areas.

On the Yavarí, the human population is low, and markets are too distant to make extraction of aguaje commercially viable. Commercial extraction of *Mauritia flexuosa* from the concessions on the Yavarí and Yavarí-Mirín Rivers is therefore unlikely to occur on a large scale. Trees are likely to be felled by loggers to reach the fruits for subsistence, but probably only close to logging camps, and not at a level likely to impact populations of *Cacajao*. Closer to Iquitos, aguaje is extracted in large quantities and female palms are becoming increasingly scarce as people travel further afield to harvest the fruits (Bodmer *et al.* 1999; Meyer and Penn 2003). In and around the TTCR, aguaje has been extracted for many years, and the sustainable management of this palm was a concern before the creation of the reserve (Meyer and Penn 2003). The relationship between aguaje and many animals including *Cacajao calvus ucayalii* was identified several years ago by Bodmer (1990), Bodmer *et al.* (1990) and Aquino (1999). Bodmer *et al.* (1999, 1990) examined the relationships between palms, people and terrestrial mammals in the Pacaya-Samiria National Reserve (PSNR), and concluded that continued felling of aguaje in the reserve would lead to a reduction in the biomass of mammals. This research highlighted the potential effects of aguaje extraction in many parts of Loreto, and resulted in the initiation of an agroforestry project, where the communities of the TTCR plant aguaje in settlement zones (Meyer and Penn 2003). In open areas the palms trees grow relatively shorter, so they do not have to be cut down to retrieve the fruit. The goal is to plant enough aguaje in people's garden plots and fallows in the buffer zone so that they will not have to enter the reserve and destroy the naturally-occurring trees. Furthermore, because the trees in the buffer zone are 'owned' there is no competition to harvest the fruits first, and they can be cut from the tree when they are at their best. The findings in this thesis demonstrate the importance of projects like these and the sustainable use of aguaje palms in maintaining populations of *Cacajao calvus ucayalii* around more populous areas.

The second most important palm fruit in the diet of *Cacajao calvus ucayalii* is *Oenocarpus bataua*, known locally as 'ungurahui'. This species is not as economically important as aguaje, and has received far less attention. It is extracted for consumption by felling the tree and its use may impact on wildlife populations. While ungurahui made up 2.3% of the total annual diet of *Cacajao calvus ucayalii* at Lago Preto, its use peaked at 18.5% in September at a time when ripe aguaje fruits were running out and availability of fruit in the forest was low (see Chapter 4). Ungurahui palms grow in *terra firme* forests, and are more dispersed than aguaje palms. This probably makes intensive extraction less likely, but the extraction of ungurahui in Loreto requires more attention from conservationists. The third palm species *Astrocaryum chambira* featured in the diet of *Cacajao calvus ucayalii*, but it only made up a small proportion of the diet, and is not extracted intensively.

The effects of selective logging on *Cacajao calvus ucayalii* are more difficult to predict. Uakaris have socio-ecological and life-history traits that have been found to correlate with poor species survival in secondary forest (Skorupa 1987). These traits include an extremely large home range, a broad group spread and a diet of almost exclusively fruit, seeds and flowers. While these findings suggest that the species would not thrive in secondary forest, surveys by Ayres and Johns (1987) demonstrated that *Cacajao calvus calvus* could persist in moderately-logged forest. Ayres and Johns suggested that the effects of logging depend on the overlap in the species' diet and the species logged. Predicting what timber species are likely to be removed from the logging concessions between Iquitos and the Yavarí is problematic, and different species are likely to be removed from different areas depending on access and their distance from sawmills. Dawkins and Philip (1998) identified a growing trend toward polycyclic systems, which cut only the most valuable timber and then allow the forest to recover before the next harvest. Timber extraction in Amazonia generally follows this pattern, but the process is driven largely by the economics of the timber industry. The most valuable species, and the timber trees nearest to sawmills are removed first, and when local supplies are exhausted, companies start to look further afield. Timber companies often travel further to find the more valuable species, and extract timber of lower value (softwoods and timber for pulp) closer to the mill (Smith *et al.* 1995). The value of different timber species also changes as favoured species become scarce and the commercial properties of various species become better documented (Ayres 1987).

The value of timber trees is always offset by the cost of extracting the trees. Concessions on the Yavarí-Mirín are remote and it is time-consuming and expensive to bring the trees down to the mouth of the Yavarí. Forestry workers often have to wait many months for water levels to rise enough to float their logs out of the *várzea* forests, and it is unlikely that many valuable timber trees remain in accessible sites close to the Yavarí. Predicting which species will be logged in the Yavarí is problematic. The timber companies themselves are not always forthcoming with information on the species that they are using, perhaps due to widely ignored restrictions on the logging of certain species such as *Cedrela* spp. Furthermore, common names for timber sometimes apply to single species, but often encompass several species and sometimes several genera. Conversely, the commercial qualities of one species in a particular genus cannot be assumed to hold for other members of the genus.

In an informal interview, the owner of a small sawmill in Islandia at the mouth of the Yavarí stated that 'cumala' (family Myristicaceae) makes up at least 70% of the wood extracted for processing at his sawmill. This sawmill has been processing timber from three concessions it holds in Amazonas, but has recently been allocated three concessions on the Yavarí and Yavarí-Mirín rivers. A larger sawmill also stated that they were specifically targeting cumala now that a company in Islandia had agreed to buy the timber. Previously, there had been no market for the timber, which is of poorer quality than timber from families such as Lauraceae and Meliaceae. Myristicaceae makes up a relatively large proportion of the diet of *Cacajao calvus ucayalii*, and removing it would certainly lower the amount of food available to the species.

Observations in the upper Yavarí and Yavarí-Mirín rivers suggest that logging operations have been removing hardwood species described by the common name 'cedro' (*Cedrela* spp.) and possibly 'tornillo' (*Cedrelinga* spp). If only these species are harvested, our survey suggests that around one tree every seven hectares would be extracted. If other hardwood tree species found by Coales (2005) (Table 8.1) of DBH>40cm were also extracted, this Figure would rise to just over one tree every two hectares. Discussions with people from the communities of Esperanza and Carolina revealed that one of the logging companies in the area was starting to extract 'cumala' timber on the Yavarí-Mirín River. There are some restrictions on the logging of some Myristicaceae species in Brazil (H. Queiroz *pers comm.*), and it is possible this has increased demand for it in Peru. If softwood trees, like cumala, of DBH>40cm were also harvested on the Yavarí, then 1.4 trees/ha would be extracted.

With the associated damage disturbance caused by extraction, this constitutes a much greater impact on the forest.

The most important families in the diet of *Cacajao calvus ucayalii* at Lago Preto are Arecaceae, Sapotaceae, Fabaceae, Lecythidaceae and Chrysobalanaceae. Interviews with the owners of sawmills in Islandia suggest that most species in the families Sapotaceae and Lecythidaceae are not valuable timber trees. There were wide range of species from the family Fabaceae in the diet of *Cacajao calvus ucayalii*, but the genera *Inga* and *Parkia* made up a large proportion of these records. Few sources list *Inga* spp. as timber species, but some species in the genus *Parkia* are considered valuable as timber trees (e.g. Peters 1959). *Parkia* was classified as softwood timber in the timber surveys used for this research (Coales 2005). The timber qualities of species from the family Chrysobalanaceae are not well documented, but Pinedo-Vasquez *et al.* (1990) list one species from this family, *Licania heteromorpha,* as a hardwood timber species in areas of Amazonian Brazil, where high-value timbers have already been exhausted. Ayres and Johns (1987) also list *Licania amara* as a commercial hardwood near Tefé in Brazil, but also in an area which has been logged previously. *Licania heteromorpha* is common at Lago Preto, and the majority of feeding records on Chrysobalanaceae by *Cacajao calvus ucayalii* were on this species. These trees were not identified as commercial in Loreto by the timber surveyor employed on surveys used in this thesis (Coales 2005), or by sawmills in Islandia, but if logging were to follow the same trends on the Yavarí as in Brazil, *Licania* might eventually be extracted.

Cacajao calvus ucayalii is hunted in most parts of its range, but usually for subsistence, while larger-bodied mammals are sold in markets. Management plans for hunting in the TTCR (Newing and Bodmer 2003; Bodmer 2000; Puertas and Bodmer 1993) and community-based wildlife conservation have reduced the hunting of primates significantly over the years in the TTCR, since community-based wildlife management plans stipulate a reduction in the hunting of monkeys. However, Swanson Ward and Chism (2003) report hunting of *Cacajao calvus ucayalii* in the TTCR area, where densities of preferred primate species such as *Lagothrix*, *Ateles* and *Alouatta* have declined. On the Yavarí, *Cacajao calvus ucayalii* is only occasionally hunted, because larger-bodied game species still occur at high densities (Puertas and Bodmer 1993; Salovaara *et al.* 2003). *Cacajao calvus ucayalii* is one of the priorities in management plans being implemented in communities on the Yavarí-Mirín River. The indirect effect of increased hunting brought about by logging operations is widely reported (e.g. Robinson *et al.* 1999). Given the low intensity timber extraction likely in the near future on the Yavarí, the effects of hunting on

Cacajao calvus ucayalii might be the most important factor affecting populations of this primate within the logging concessions. Hunting in the concessions is subject to regulations by the Peruvian National Institute of Natural Resources (INRENA), but it is not clear how restrictions on hunting could be enforced. By the rules of the concessions, logging workers are permitted to hunt game in their concessions for subsistence, but primates may not be hunted. Peruvian law states that subsistence hunting may not be conducted without a wildlife management plan (Puertas *pers. com.*). In practice, uncontrolled hunting is likely to increase in the concessions on the Yavarí and probably also in adjoining areas. WCS has proposed a management plan for the Yavarí, which includes guidelines for hunting in the concessions.

While there are still healthy populations of large mammals in much of the area covered by the logging concessions (Salovaara *et al.* 2003), monkeys are likely to be particularly vulnerable to hunting by timbermen. They have low fecundity and are more easily located and shot than the large terrestrial mammals. The closest Peruvian communities to Lago Preto are Esperanza (179 residents) and Carolina (17 residents). WCS and DICE have been working with these communities since 1990, collecting information on resource use and its impact on species populations, and advising on sustainable levels of hunting. These communities keep hunting registers for all species, while DICE and WCS collect density data for all large wildlife. The people of Carolina, whose hunting grounds abut the Lago Preto study area, have stated that they do not need to hunt the red uakari monkey. Hunting in the area is currently quite selective, with hunters targeting larger commercial species to sell at markets downriver. Timbermen are likely to be less experienced hunters and may be less inclined to spend time looking for more-difficult-to-find species. Also, they may not have a long term interest in game populations. The result of this may be that the more-easily-targeted primates are taken more frequently.

Putz *et al.* (2001) assert that "more studies with titles like 'The effects of logging on species X' may be less than effective in promoting the transformation from purely-exploitative logging to sustainable forest management if they do not address silvicultural and financial alternatives". In the case of this study, it is possible that relatively simple conservation strategies may be enough to ensure the persistence of *Cacajao calvus ucayalii* in the area. Given an economically-enforced low intensity of extraction, ensuring that concession owners log only *within* their concessions might be enough to maintain healthy populations of *Cacajao calvus ucayalii*, at least in the short term. This approach would also preserve Peruvian national timber resources from what is essentially illegal extraction outside concession areas that ultimately takes income away from the Peruvian government. Controlling hunting will also be of key importance.

Recommendations to ban the extraction of certain uakari food trees within the distribution of *Cacajao calvus ucayalii*, should be considered. This strategy has proven successful for *Cacajao calvus calvus* in Mamiraurá, Brazil (Bowler *et al.* 2006), where the extraction of *Xylopia callophylum* has been banned. Other restrictions on timber extraction in Brazil could have knock-on effects in Peru. The ban on the extraction of cumala (Myristicaceae) timber in Brazil could well be promoting extraction in Peru. The effects of bans on particular timber species on extraction rates and sustainability of forestry in Peru should be assessed, and possible action considered.

Cacajao calvus ucayalii is absent from much of the area between the Yavarí and Yavarí-Mirín Rivers. The highest densities are found in the Lago Preto Conservation Concession, but this reserve is small and surrounded by logging concessions where uakari groups from the Lago Preto study area regularly range. The persistence of *Cacajao calvus ucayalii* in the Yavarí-Ucayali corridor depends largely on populations that occur in logging concession areas, and those in and around the TTCR that are subject to higher levels of hunting and palm removal. Long-term persistence of *Cacajao calvus ucayalii* in and around the TTCR depends largely on existing game management and agroforestry projects, particularly for the aguaje palm. In the short term, while only the most valuable hardwoods are being exploited, it appears that populations of *Cacajao calvus ucayalii* close to the Yavarí and Yavarí-Mirín might survive relatively intact, and that these concession areas might continue to be one of the main strongholds for the species. Where removal of other timber species occurs, particularly of the family Myristicaceae, there will also be a reduction in the food available for *Cacajao calvus ucayalii.* There will also be higher levels of habitat disturbance and associated hunting, which may have a greater impact on uakari numbers.

8.5 Summary

1. The diet of *Cacajao calvus ucayalii* at Lago Preto contained 3 palm species that are used as non-timber plant forest products; *Maurita flexuosa*, *Oenocarpus bataua* and *Astrocaryum chambira*. Of these, *Mauritia flexuosa* is the most important, being extracted in high volumes and making up 20% of the diet.

2. Precious hardwoods did not feature in the diet of *Cacajao calvus ucayalii* at Lago Preto but some less-sought-after timber trees did. Possibly the largest overlap between the diet of *Cacajao calvus ucayalii* and the potential for extraction is for trees in the family Myristicaceae, known locally as 'cumala'. This family makes up a relatively large part (4.2%) of the diet of *Cacajao calvus ucayalii*, and is one of the commonest families in the Amazon Basin.

3. On the Yavarí River, extraction of palms is very low and is unlikely to have any impact on uakari populations.

4. On the Yavarí River, the economics of timber extraction mean that only the most valuable 'precious hardwood' species are extracted. These species occur at low density so extraction itself is unlikely to impact uakari numbers. However, logging operations consume large quantities of wild meat and hunting pressure on uakaris is likely to increase on the Yavarí during timber extraction.

Chapter 9

Protected Areas and the Geographical Distribution of *Cacajao calvus ucayalii*

9.1 Introduction

Geographic distribution and abundance are key determinants of global population size and global extinction risk in primates (Cowlishaw and Dunbar 2000). While humans can have an enormous influence on the distribution, abundance and rarity of primates, it is important to understand the natural causes of variation in these characteristics before addressing the added effects of human actions (Cowlishaw and Dunbar 2000). The most obvious constraints on the distribution of primates are physical barriers such as oceans, mountain ranges and rivers, but changes in habitat type have also been shown to limit distribution (e.g. Oates 1988). In Amazonia, the most obvious barriers to primate distribution are major rivers, something described by several authors (notably Hershkovitz 1977; Wallace 1852, 1876). Ayres (1986) and Ayres and Clutton-Brock (1992) considered the importance of river boundaries in delimiting the distributions of Neotropical primates, demonstrating that primate communities were less similar on opposite sides of a river when the river was wider or faster flowing. Ayres and Clutton-Brock (1992) suggested that this might be because of an increased risk of drowning in faster rivers. Alternatively, slower rivers meander more, leading to increased chances of arboreal bridges (because the river becomes longer, increasing the probability of these bridges forming), or to increased formation of oxbow lakes resulting in connections between opposite banks. Ayres and Clutton-Brock (1992) also found that larger-bodied primates were less constrained by rivers than small-bodied species.

Rodman (1978) found that local distributions of primates in Kalimantan were correlated with diet. Primate species were most likely to be found in areas where fruit or leaf availability resembled the diet of that species. While food availability is clearly an important constraint on distribution and abundance, food may not always be limiting at all times, and seasonal 'nutritional bottlenecks' of low fruit availability may be responsible for limiting primate populations (Emmons 1984; Peres 1994). Terborgh (1986) introduced the idea that during lean periods, primates often have to rely on 'keystone' food resources. McFarland Symington (1988) explained variation in spider monkey abundance between sites by the availability of keystone resources., but generally, testing hypotheses regarding keystone species can be problematic, because it is difficult to identify which dietary components play a crucial role, especially given the flexibility in feeding in most species (Peres 2000; Cowlishaw and Dunbar 2000).

Food availability for primates would appear to be determined, at least in part, by soil quality and available nutrients. There is little evidence for this in African or Asian primates (Oates *et al.* 1990; Marsh and Wilson 1981), but in South America Peres (1997) and Emmons (1984) compared primate abundances between *terra firme* forests on nutrient-poor soils and floodplain forests with nutrient-rich soils resulting from sedimentation during seasonal flooding. Primate abundance was higher in floodplain forests than in *terra firme* forests, consistent with the theory that higher production results from higher soil fertility and leads to higher primate abundance. In addition to productivity, there is evidence that tree-species diversity can influence the availability of food resources and primate abundance in Asia (Caldecott 1980) and Africa (Thomas 1991; Lawes 1992).

9.2 The geographical distribution of *Cacajao*

Cacajao is distributed through western Amazonia, and is replaced by *Chiropotes* in eastern Amazonia (Chapter 1; Hershkovitz 1987). The ranges of the 6 or 7 subspecies of *Cacajao* are bounded by major rivers (Figure 1.1), as is common with most Amazonian primate taxa (Hershkovitz 1977), but the distributions of some subspecies have been shown to cross some major rivers (e.g. *Cacajao calvus calvus* [Sousa e Silva Júnior and Martins 1999]). As discussed in Chapter 6, the proposition that the *terra firme* habitat acts as a barrier to the distribution of *Cacajao*, and accounts for its unusually-small geographic range (Ayres 1986, 1989; Ayres and Clutton-Brock 1992), does not appear to hold, since populations are found in both flooded and *terra firme* habitats. Competition with *Chiropotes* is probably a factor in defining the eastern boundary of the distribution of *Cacajao*. It is thought that the ranges of the two genera do not overlap, although mixed groups of *Cacajao melanocephalus melanocephalus* and *Chiropotes satanas* have been observed in the contact zone by Boubli (2002). Differences between types of seasonally flooded forest also influence the ecology and the geographical ranges of *Cacajao*. Barnett and Brandon-Jones (1997) highlighted the habitat divergence between the two species. *Cacajao melanocephalus* is exclusive to black-water rivers, avoiding areas of *várzea* flooded forest, while *Cacajao calvus* inhabits the white-water forests.

Ayres (1986) also considered the importance of rivers in delimiting the geographical distribution of *Cacajao*, reasoning that *Cacajao* has a higher probability of crossing major rivers than would be expected for its body size, because of its preference for riverine habitats. This observation may be supported by new information on the distribution of some of the subspecies (Chapter 1), which are present on both sides of some major rivers. While monkeys are occasionally seen crossing rivers in Amazonia, most observations have been of *Alouatta* spp. (Ayres 1986). Any propensity of *Cacajao* to cross rivers is probably not due to swimming, because it is relatively small-bodied and has long thick fur. More likely it is due to a tendency to become isolated on river islands of flooded forest that effectively move to opposite banks as the rivers change their courses. Because of higher sedimentation, white-water rivers generally change course more quickly than black-water rivers. *Cacajao calvus* lives along white-water rivers, and might be expected to cross rivers more frequently than *Cacajao melanocephalus*, which lives in forests alongside black water rivers.

A third explanation for the distribution of the Pitheciinae offered by M. Ayres is being published posthumously (Ayres and Prance in press), and concerns the abundance of Lecythidaceae trees, especially of the genera *Lecythis* and *Eschweilera*. Ayres (1986) identified these genera as of key importance to *Cacajao* and *Chiropotes*. Ayres and Prance (in press) documented a close correlation between the distribution of the two monkey genera and the distribution and densities of *Lecythis* and *Eschweilera* in a number of Neotropical forests. Stevenson (2001) found similar relationships with the Pitheciinae at a number of sites; both Pitheciinae biomass and the number of Pitheciinae species were positively correlated with the abundance of *Eschweilera* trees. It should be noted that neither of these studies demonstrate causality, and that the density of the Pitheciinae monkeys may be dependent on another factor that co-varies with the density of *Eschweilera* trees, such as plant species richness. Both Ayres and Prance's (in press) and Stevenson's (2001) studies only included one site where *Cacajao* occurs. In both cases this was Lake Teiú and *Cacajao calvus calvus*. In addition to a restricted distributions (Chapter 1), *Cacajao calvus ucayalii* has a patchy distribution between the Yavarí and Ucayali Rivers (Salovaara *et al.* 2003). River boundaries, the distribution of habitats and the abundance of *Eschweilera* or other key genera are examined to see if they might explain the patchiness in the distribution of *Cacajao calvus ucayalii* on the Yavarí and Yavarí-Mirín Rivers.

9.3 The influence of major rivers on the distribution of *Cacajao calvus ucayalii* in the Yavarí-Ucayali interfluvium

Cacajao calvus ucayalii is found in *terra firme* and seasonally-inundated forests at various sites between the Yavarí and the Ucayali Rivers. Within this area it has a very patchy distribution, and in most areas in its range it occurs at very low densities. At Lago Preto, densities of the species are conspicuously high. It is possible that the range of *Cacajao calvus ucayalii* is unusual in extending into *terra firme* forest, but only *Cacajao calvus ucayalii* and *Cacajao calvus calvus* have been studied in any detail. It may be that the latter is the unusual subspecies in terms of its habitat preferences.

While the range of *Cacajao calvus* crosses some large rivers, it has not appeared to have had much success in crossing the Yavarí, where it is present on the Peruvian (west) bank, but not the Brazilian (east) bank. It is possible (if records are confirmed) that it occurs on the Brazilian side in the headwaters where the river is narrower, and at the mouth where some records indicate that its historical range may have extended into Brazil. *Cacajao calvus ucayalii* also occurs on the north bank of the Yavarí-Mirín, but not the south bank (except in the headwater region), and is also absent from long stretches of the mid section of the Yavarí (figure 8.1).

The range of *Cacajao calvus* does cross some rivers. Generally, these are rivers that change their courses relatively rapidly, and where channels and large islands are common. Examples include the Solimões where *Cacajao calvus calvus* has been confirmed on both sides, and potentially on the Ucayali (if records are confirmed) where the course of the river changes rapidly at the confluence of the Ucayali and Marañon Rivers, creating large fluvial islands. The Yavarí on the other hand does not appear to change course particularly rapidly (Chapter 2.3) and has few, if any, islands along its length. There is a large island at the mouth of the Yavarí, where indeed *Cacajao calvus ucayalii* may have crossed in the past, resulting in the historical distribution reported by Hershkovitz (1987a).

9.4 Large-seeded tree families and the distribution of *Cacajao calvus ucayalii* in the Yavarí-Ucayali interfluvium

Ayres and Prance (in press) identified *Eschweilera* and the similar *Lecythis*, both in the family Lecythidaceae, as the most important genera in the diets of *Cacajao* and *Chiropotes*. Lecythidaceae was also important at Lago Preto, making up 7% of the diet (Chapter 5), but so were several other tree families. Arecaceae was the most important, and the species eaten are common and widely distributed in the Yavarí-Ucayali interfluvium. The next most important families were Sapotaceae, Fabaceae, Lecythidaceae and Chrysobalanaceae. All of these families have large-seeded fruits, and Sapotaceae, Lecythidaceae and Chrysobalanaceae also have hard shells.

There are few data on the densities of tree genera and families in the Yavarí-Ucayali interfluvium, particularly on the Yavarí and Yavarí-Mirín Rivers. Data were collated from seven plots in five sites in continuous forest in this area. *Cacajao calvus ucayalii* occurred at three of the five sites (Table 9.1). Botanical information from Curacinha and Buenavista, both on the upper Yavarí, and Quebrada Blanco close to the Tamshiyacu-Tahuayo Communal Reserve were collected by N. Pitman (unpublished data). Data from Lago Santa Elena on the Yavarí were collected by WCS-Peru (Ahuite 2004). Data from Lago Preto were collected for this study (Chapter 4). All these plots were in *terra firme* forest except for one plot at Lago Preto which was in *várzea*. No other data were available for *várzea* plots.

The two sites where *Cacajao calvus ucayalii* does not occur, Buenavista and Lago Santa Elena, also have the lowest densities of *Eschweilera* and Lecythidaceae, and the lowest combined densities of the 'hard-shelled, large-seeded' families Lecythidaceae, Sapotaceae and Chrysobalanaceae. Densities of these taxa were considerably higher at Lago Preto and at Quebrada Blanco. The densities of *Eschweilera* and Lecythidaceae in *terra firme* at Buenavista and Lago Santa Elena are considerably lower than the densities found at other sites in the Yavarí-Ucayali interfluvium, but they are similar to the densities found in *várzea* at Lake Teiú, where *Cacajao calvus calvus* is found, and to several other sites where *Chiropotes* spp. are found (Ayres and Prance in press).

Table 9.1 Densities of the genus *Eschweilera*, the family Lecythidaceae and of 'hard-shelled, large-seeded families' at sites on the Yavarí-Ucayali interfluvium relative to the presence of *Cacajao calvus ucayalii*.

Site	***Cacajao calvus ucayalii***	**Plot area (ha)**	**Total trees DBH>10cm in plot**	**Plot habitat**	**Soil**	**Density (trees/ha) of *Eschweilera***	**% of total trees DBH>10cm that are *Eschweilera***	**Density (trees/ha) of Lecythidaceae**	**% of total trees DBH>10cm that are Lecythidaceae**	**Density (trees/ha) of large seeded Families: Sapotaceae, Chrysobalanaceae and Lecythidaceae**	**% of total trees DBH>10cm that are Sapotaceae, Chrysobalanaceae and Lecythidaceae**
Curacinha (N. Pitman unpublished data)	yes	1	669	*terra firme*	nutrient poor	33	4.9	42	6.3	124	18.5
Buenavista (N. Pitman unpublished data)	no	1.0	544	*terra firme*	nutrient richer	23	4.2	26	4.8	90	16.5
Quebrada Blanco 1 (N. Pitman unpublished data)	yes	1	548	*terra firme*	Sandy, nutrient poor	73	13.3	75	13.7	134	24.6
Quebrada Blanco 2 (N. Pitman unpublished data)	yes	1	536	*terra firme*	Sandy, nutrient poor	88	16.4	91	17	154	28.7
Lago Preto *terra firme* (Chapter 4)	yes	0.9	558	*terra firme*	nutrient poor	61.3	9.9	63.5	10.2	146	23.4
Lago Preto *várzea* (Chapter 4)	yes	0.8	528	*várzea*	alluvial silt	61.6	8.9	76	11.1	166.3	24.1
Lago Santa Elena (Ahuite 2004)	no	1	528	*terra firme*	nutrient richer	29	5.5	29	5.5	44	8.3

While these results appear to support the findings of Stevenson (2001) and Ayres and Prance (in press), that Pitheciinae distributions might be affected by the densities of these key plant taxa, there are too few data and too many other variables to conclude that the patchy distribution of *Cacajao calvus ucayalii* in the Yavarí-Ucayali interfluvium is determined by the densities of these tree species. In particular, few vegetation plots have been completed in *várzea*, which is an important habitat for many populations of *Cacajao calvus ucayalii.* Stevenson (2001) also cautions that the patterns found in his study do not prove causality.

The highest densities of *Eschweilera* trees occurred in the two Quebrada Blanco plots. While data on *Eschweilera* and uakari densities are sparse, it is possible to speculate that the high densities of *Eschweilera* at Quebrada Blanco enable *Cacajao calvus ucayalii* to occur in an area where there is little *várzea*, a habitat that appears to provide an important seasonal abundance of food for *Cacajao calvus ucayalii* at Lago Preto. Although there were higher densities of *Eschweilera* at Quebrada Blanco than in the *terra firme* plot at Lago Preto, Lago Preto had higher densities of the other 'hard-shelled, large-seeded' families; Sapotaceae and Chrysobalanaceae. The *várzea* plot had even higher densities of these two families, but there are no other *várzea* plots for comparison, and these densities might be typical for the habitat. This suggests that it could be the occurrence of large-seeded tree species in general rather than *Eschweilera* in particular that determine the distribution and abundance of the Pitheciinae.

9.5 Soil fertility and the distribution of *Cacajao calvus ucayalii* in the Yavarí-Ucayali interfluvium

Differences in vegetation composition are often due to differences in soil composition. Other studies have correlated mammal distributions or densities with soil fertility (Emmons 1984) or vegetation types (e.g. Peres 1997). Although the sample size is very small, *Cacajao calvus ucayalii* occurs at sites where the *terra firme* soil is nutrient poor (Table 9.1), and not at the nutrient-richer sites. Higher densities of *Eschweilera* and the other 'hard-shelled, large-seeded' families also occur at the 'nutrient-poor soil' sites. This is a pattern observed across Amazonia by ter Steege *et al.* (2006), who suggest that species that have large seeds grow slowly and do better in less dynamic forests with a low turnover of individuals, a characteristic of low soil fertility. *Cacajao* is also associated with seasonally inundated habitats, where *Eschweilera* and other large-seeded tree genera are also common.

Large-seeded fruits are of considerable importance to *Cacajao* and other primates in the subfamily Pitheciinae (Chapter 5), and soil fertility may have considerable influence on the abundance of these fruits. Further analysis might reveal a relationship between soil fertility in the forests of the Yavarí-Ucayali interfluvium and the distribution of *Cacajao calvus ucayalii.* Further relationships between the densities of the Pitheciinae, large-seeded tree species density and soil fertility might also exist, but Salovaara *et al.* (2005) recorded soil types on a section of the Yavarí-Mirín River, where *Cacajao calvus ucayalii* occurred on the north bank, but not the south. Here, the predominant forest type was *terra firme* growing on relatively nutrient-rich clay to loamy soils. On the south side of the river, where *Cacajao calvus ucayalii* was not present, there were several areas of terrace forests of *terra firme*, apparently more similar to the forest at Lago Preto, growing on relatively nutrient-poor loamy soils. The influence of the relatively small areas of nutrient-rich *várzea*, where large-seeded trees are abundant may also be important in determining the distribution of *Cacajao calvus ucayalii* on the Yavarí.

9.6 Proportions of available habitat

Given the evidence for seasonal migration between habitats, or at least seasonal differences in the use of habitats, particularly at Lago Preto (Chapter 6), it appears that the habitat types available to *Cacajao calvus ucayalii* might be important. *Cacajao calvus ucayalii* at Lago Preto used *aguajal*, *várzea* and *terra firme*, and it might be inferred that the subspecies requires all or at least one of these habitats. This theory does not appear to hold however. In some areas *Cacajao calvus ucayalii* does not have access to all these habitats. For example, at Quebrada Blanco, they use only *terra firme* with patches of upland *aguajal*, unless there is seasonal migration over considerable distances (E. Heymann Pers. com.). *Cacajao calvus calvus* at Lake Teiú live exclusively in *várzea*, and one would expect *Cacajao calvus ucayalii* to be able to do the same. On the upper Yavarí-Mirín and upper Yavarí Rivers where there are populations of *Cacajao calvus ucayalii*, the flooded forests are influenced more by local rainfall, and probably differ significantly from the *várzea* at Lago Preto and further downstream. Furthermore, on examining satellite images, areas in the Yavarí-Ucayali interfluvium where *Cacajao calvus ucayalii* does not occur appear to have habitats in similar proportions to those areas where *Cacajao calvus ucayalii* does occur. It is possible that it is the overall abundance of large-seeded tree species that is the important factor in determining the distribution of *Cacajao*. The required abundance could be fulfilled by the high densities of these tree species in either nutrient-poor *terra firme* or seasonally-flooded forest. Lago Preto has both nutrient-poor *terra firme* and relatively large areas of seasonally-flooded *várzea* forest created by the meandering river below the mouth of the Yavarí-Mirín.

9.7 Past hunting

Another possibility for the absence of *Cacajao calvus* in the Yavarí-Yavarí-Mirín interfluvium is that it was over hunted in the past when the region was more populous (see Chapter 2). This seems unlikely, because large-bodied taxa, such as *Alouatta*, *Lagothrix* and *Ateles* are generally the first to disappear in heavily-hunted areas (Peres 1990; Puertas and Bodmer 1993; Bennett *et al.* 2001), and these species are relatively common in the area. However, it is possible that *Cacajao calvus ucayalii* might be vulnerable to local extinctions, because it naturally occurs at low densities, and because populations may be restricted to certain areas of habitat. Other primate species may have been better able to survive in inland *terra firme* forest without needing to migrate to alternative forest types at certain times of the year. Additionally, it is possible that *Cacajao calvus ucayalii* has been particularly slow to re-colonise areas while other species have not, perhaps not crossing some of the smaller rivers and streams that drain into the Yavarí, but the particularly large home ranges of *Cacajao calvus ucayalii* (Chapter 6) should make it easy for them to move into new areas of suitable habitat.

9.8 Competitive exclusion

Interspecific competition can also have an effect on the abundance of a primate species (Cowlishaw and Dunbar 2000), although in practice the effects of competition are difficult to separate from the effects of habitat preference (Glanz 1990). Where *Cacajao calvus ucayalii* does occur between the Yavarí and Ucayali Rivers, it does not replace another primate species, but occurs in addition to 12 other species. The possibility that another primate species excludes *Cacajao calvus ucayalii* from certain areas seems unlikely. The other possible competitors for *Cacajao calvus ucayalii* are squirrels and large parrots. There is no indication that additional species or higher numbers of parrots occur where *Cacajao calvus ucayalii* is absent, although densities of squirrels are inversely correlated with densities of *Cacajao calvus ucayalii* (Chapter 5).

9.9 Patchiness, partial barriers and metapopulations

One of the areas where *Cacajao calvus ucayalii* is most conspicuously absent is in the interfluvium between the Yavarí and Yavarí-Mirín. *Cacajao calvus ucayalii* is only present in the upper reaches of the two rivers. These populations inhabit forests that are apparently continuous with areas where there are no *Cacajao calvus ucayalii* (Figure 8.1). It is unlikely that the habitat on one side of the river is uniformly poor for uakaris, while the other side is uniformly good. Indeed, Salovaara *et al.* (2005) found apparently-suitable habitats and soils on the south bank of a section of the Yavarí-Mirín, where uakaris were only present on the north bank. It seems possible that there is some sort of barrier stopping uakaris colonising otherwise suitable habitat. Barriers could be ecological or physical. For example Peres *et al.* (1996) suggested that *várzea* forests were an ecological barrier to tamarins, restricting gene flow between populations. A band of unsuitable habitat in the *terra firme* forests between the Yavarí and Yavarí-Mirín Rivers, perhaps with low abundance of large-seeded tree species, as suggested by the limited survey work in Table 9.1, could be enough to present a barrier to *Cacajao calvus ucayalii*. This could be preventing *Cacajao calvus ucayalii* from colonising the south-west bank of the Yavarí-Mirín.

Alternatively, the forest between the Yavarí and Yavarí-Mirín is drained by a number of smaller streams and rivers. While there is continuous *terra firme* forest connecting the two sides of all these streams well inland from the major rivers, it is not known if *Cacajao calvus ucayalii* lives away from *várzea* forests in these areas. These streams may form partial barriers for groups of *Cacajao calvus ucayalii* and groups living close to the banks of the Yavarí and Yavarí Mirín. Many of these streams are bordered by *chavascal* habitat, which *Cacajao calvus ucayalii* does not like to enter, reducing the likelihood that the barrier will be crossed. If there are one or more major streams acting as barriers in this way, groups might not cross with enough frequency for large viable populations to colonise areas. The species generally occurs at low density, and local extinctions of partially-isolated populations may occur, perhaps assisted historically by human hunting. The part played by chance in populations crossing natural barriers and persisting in suitable habitat should be considered. Partial isolation of parts of the population between the Yavarí and Ucayali with source and sink areas and local extinctions would mean that the population is acting as a metapopulation as defined by Hanski (1998).

9.10 Why are there so many uakaris at Lago Preto?

Mammal censuses at Lago Preto consistently give high densities of *Cacajao calvus ucayalii* relative to other areas using the DISTANCE method (Table 2.2). During this study, repeat counts revealed that at least 160 (and possibly more than 200) uakaris were using the Lago Preto study area at one time. On several occasions, researchers were sure that there where no uakaris in the area, but the groups always returned after a maximum of five days. For several consecutive months between August and October 2004 researchers got the impression that fewer red uakaris were using the area than in these months in 2003, but large groups of uakaris were nearly always present in the area throughout the study period. This is unusual. In other areas in the Yavarí-Ucayali interfluvium, when uakaris are recorded in census work they are usually seen once or twice before they disappear from the area (R. Bodmer *pers. com.*). Group sizes in these other areas can be as large as those typically seen at Lago Preto, so it is the regularity with which large uakari groups are encountered at Lago Preto that makes the area unusual.

While it is possible that the proportions of preferred habitat are ideal for uakaris at Lago Preto, or that the habitats there are rich in species favoured in the diet of the monkeys, habitat topography may also be an important factor. Lago Preto is situated at the confluence of the Yavarí and Yavarí-Mirín Rivers, and is bordered to the south and west by wide rivers. A large, particularly-open 'purer' *aguajal* borders the east side of the study site. In these patches the palms are widely spaced, and there is little other cover. Uakaris were not seen using these areas during the study, and this habitat may have been something of a barrier to the study groups. North of this, a large stream bordered by a wide band of low scrubby *chavascal* vegetation extends into the *terra firme*. Uakaris were observed crossing this *chavascal* on only one occasion. It is conspicuous that *Cacajao calvus ucayalii* rarely crossed large *aguajal* swamps when there was no ripe *Mauritia flexuosa* fruit available. This may be due to increased risk from predators in the open habitat, because travel was more difficult in these areas, or simply because they did not want to leave favourable habitat. To the north there is extensive *terra firme*, and at certain times of the year the uakaris do head north into this area, but they always seem to return. Additionally the study area contains one of the few locations (possibly the only one) in the larger Lago Preto Conservation Concession where *terra firme* forest borders *várzea* forest with no *aguajal* or other 'open-canopied' swamp habitat in between. This relatively narrow point of easy access to *terra firme* from the *várzea* forest was frequently used by the uakaris. Ayres (1986) also found that habitat topography was important in the ranging patterns of *Cacajao calvus calvus* at Lake Teiú where they foraged along long strips of *restinga* vegetation, avoiding *chavascal* vegetation much of the time.

There are large *aguajal* palm-swamps at Lago Preto that have mixed canopies allowing easier and more secure access to *Mauritia flexuosa* palms. These are adjacent to *várzea* and *terra firme* forests, and there is an area where uakaris can cross from *terra firme* habitat into *várzea* without crossing open *aguajal* or *chavascal* habitats. In many other areas there are wide areas of *aguajal* between the *terra firme* and *várzea* habitats. Uakaris can therefore pass between all three habitats at Lago Preto without crossing large areas of unfavourable habitat. It may also be that foraging uakaris are conveniently channelled into a narrow 'corner' of *terra firme* forest by unfavourable 'open' habitats to the east and west. Uakaris often foraged along the edges of habitat. This may simply be because they neither wanted to retrace their steps nor enter a different habitat type. Uakaris doing this in *terra firme* at Lago Preto inevitably looped around in an almost enclosed area of *terra firme* forest bordered by other forest types.

The high densities of uakaris at Lago Preto could therefore be the result of a combination of factors. Habitats could be present in optimal proportions to allow a large population to move between habitats seasonally within a relatively small area without exhausting food supplies. Soils in the terra firme forests at Lago Preto are poor, which may have resulted in relatively high densities of large-seeded tree species important in the diet of uakaris. Additionally, the topography of the area may mean that uakaris use the area because seasonally-favourable habitats can be accessed without crossing unfavourable habitats.

9.11 *Cacajao calvus ucayalii* in protected areas

The rarity of *Cacajao calvus ucayalii* and its potential as a flagship species make it a focus for conservation efforts in the Peruvian Amazon. While managing hunting is seen as the priority in this region (Bodmer 1995), protected areas play an important part in national and regional conservation strategies and conservation projects often focus around these areas. The patchy distribution of *Cacajao calvus ucayalii* makes the siting of these areas particularly important for the conservation of the species. The motivation behind the establishment of most of the existing reserves in the Peruvian Amazon has not been the protection of *Cacajao calvus ucayalii*.

Cacajao calvus ucayalii occurs in only two departments of Peru; Loreto and Ucayali. Most of the protected areas in these departments are situated outside the recognised geographical distribution of uakaris, including all five of the National Parks and Reserves. Until recently the only protected area known to contain the species in Peru was the regional Tamshiyacu-Tahuayo Communal Reserve. New protected areas have been proposed and created in recent years. The presence of *Cacajao calvus ucayalii* has become part of the justification for 3 areas either under proposal or newly created, and persistent sightings by local people suggest that Loreto's Pacaya-Samiria National Reserve might also contain a small population of the species.

9.11.1 The Tamshiyacu-Tahuayo Communal Reserve

The Tamshiyacu-Tahuayo Communal Reserve (TTCR) extends over an area of 322,500 hectares, and is situated close to the city of Iquitos in the upland forests between the Amazon and the Yavarí (Newing and Bodmer 2004). The reserve was created as a result of a strong alliance between local people and conservationists. Government agencies and non-government groups took particular interest in the area because of its unique biodiversity; fourteen primate species have been confirmed to occur sympatrically in the reserve and no other protected areas included *Cacajao calvus ucayalii* (Puertas and Bodmer 1993). Economic activities for both the financial income and subsistence of rural inhabitants are permitted within the TTCR. The most important are agriculture, agroforestry, fishing, hunting, harvesting timber and extraction of non-timber plant products. Game selection by hunters in the area is influenced primarily by the value of game meat in the towns near Iquitos. Community-based wildlife conservation has reduced the hunting of primates significantly over the years in the TTCR, since the community-based wildlife management plans stipulate a reduction in the hunting of monkeys (Bodmer and Puertas 1999).

Uakari densities in the TTCR are relatively low, at 2.5 individuals/km² (Puertas & Bodmer 1993). Hunting of *Cacajao calvus ucayalii* has occurred in and around the reserve (Bodmer *et al.* 2003; Swanson Ward and Chism 2003), and larger species have been impacted. *Cacajao calvus ucayalii* populations in the Tamshiyacu-Tahuayo Communal Reserve are also threatened by non-timber plant-resource extraction (Chapter 8).

9.11.2 Sierra del Divisor Reserved Zone

The Sierra del Divisor Reserved Zone is located in northeastern Peru in the departments of Loreto and Ucayali. It covers over 1.5 million hectares and adjoins a protected area in the Alto Juruá region of Acre state in Brazil creating a total area of nearly 3.2 million hectares (The Nature Conservancy 2006). In April 2006 the Sierra del Divisor was delclared a Reserved Zone (The Nature Conservancy 2006). Reserved zones are transitional categories used while official status is evaluated, and proposals can still be rejected by the government. Sierra de Divisor's consortium of Peruvian partners includes Pro Naturaleza, the Center for Conservation Data (CDC-UNALM), the Peruvian Society for Environmental Law (SPDA) and Instituto del Bien Común (IBC).

The Sierra del Divisor region has an extremely high diversity in primates. There are 18 species, including *Cacajao calvus ucayalii* and Goeldi's monkey (*Callimico goeldii*) (The Nature Conservancy 2006), but the 18 species are not all sympatric, and the figure is reached partially because the Reserved Zone is large and incorporates several inferfluvial areas, where species composition is different.

The presence of *Cacajao calvus ucayalii* in the area was used as part of the justification for the reserve, although it appears that abundances and distributions in the Reserved Zone are known only at three sites surveyed by Aquino *et al.* (2005). More work is required to determine the distribution and density of the species to assess the reality of the reserve's value to *Cacajao calvus ucayalii*.

9.11.3 Pacaya-Samiria National Reserve

The Pacaya-Samiria National Reserve is an area protected for the conservation of biological diversity and the sustainable use of animal and plant-resources, aquatic or terrestrial. Commercial exploitation of natural resources is permitted under approved management plans supervised by national authorities (Bodmer *et al.* 1999).

Isolated reports of red uakari monkeys on the Yanayacu River in the Pacaya-Samiria National Reserve have occurred for a number of years (P. Puertas pers. com.), but no primatologist has confirmed its presence in the area. The species is not included in the inventories for the reserve. Descriptions of the geographical range of the red uakari monkey have always described the Ucayali River as the western boundary of the species range, but the Pacaya-Samiria National Reserve is on the western side of this river. Most recent reports of red uakaris on the Yanayacu River come from the area around Yarina, a relatively new village on the Yanayacu River founded in the mid 1980's. Few of the adult residents have lived in the area all their lives. Primates are not widely hunted, and only two members of the community regularly hunt in the area. Apparently healthy game populations mean that these hunters do not have to travel far to find game animals. Residents state that only peccary and large rodents are hunted, and that strict quotas are adhered to. The

NGO 'Pro Naturaleza' has been working with the communities on the Yanayacu to manage wildlife for many years, and appears to be having considerable success, with populations of paiche and river turtles on the increase (J. Noriega Murrieta *pers. com.*).

In September 2006, a short expedition was made to conduct interviews in Yarina and search the site for red uakari monkeys. Although red uakaris were not encountered during this expedition, several residents of Yarina reported seeing red uakari monkeys, usually in small groups on the banks of the river. Only two residents of Yarina regularly hunt, and both reported infrequent observations of groups of 20 or more uakaris. In addition to the recent observations, 3 older men (one from Yarina and two from the small village of Araquipa) claim to have seen red uakari monkeys years ago, when they used to make hunting and fishing expeditions into the forest. There was a high level of consistency between interviews, and considerable detail was given within some of the interviews. The observations were virtually all within an area of about 200km^2 (20,000ha) bounded by a large bend in the Yanayacu River, and by *chavascal* on the south side. Many of the interviewees were able to observe the monkeys for several minutes and described the short tail and red face in addition to the less diagnostic red fur. This is not a monkey that is easily confused with other species if it is seen well.

The Ucayali forms a significant barrier to primates, but the constantly-changing course of the river means that very large islands of forest big enough to support small primate populations effectively cross from one side of the river to the other as oxbow lakes are formed, particularly near the mouth of the river where it meets the Amazon. It is not impossible that a population of uakaris was pinched off on a river island in the past and has persisted on the west side of the Ucayali ever since. Since the species occurs at low densities in most areas where it is present, it is possible that it has escaped the notice of biologists.

The confirmation of red uakari monkeys in the Pacaya-Samiria National Reserve would add a new primate to the species list for the reserve, bringing the total number of species to 13. This would be an extremely diverse primate community and one unequalled in areas of extensive *várzea*. If present, the population must be extremely small and probably experiencing inbreeding. It will require special consideration if it is to persist. The striking appearance of this monkey would likely prove a draw for tourism, even though sightings of the monkeys would be very infrequent. Tourism already appears to be working well within the successful management plans for the area overseen by Pro Naturaleza (J. Noriega Murrieta pers. com.).

Interviews suggest that the species may have been present at higher densities in the past. High levels of activity on this river in the past from illegal loggers, and from people crossing the forest from the Ucayali River to extract resources, might have reduced densities of this primate by hunting. The population would be the only known population of the subspecies *Cacajao calvus ucayalii* occurring in the complete absence of non-flooding *terra firme* forests. Establishing the size of this population, and monitoring the population in the long term might give an idea about how this species might fare when its densities are low.

9.11.4 Lago Preto Conservation Concession and the proposed Greater Yavarí Reserve

The history, fauna and flora of the Lago Preto Conservation Concession are described in detail in Chapters 2 and 4. The 9926ha Concession is unique amongst the protected areas discussed in this Chapter, in that its location was determined by the densities of *Cacajao calvus ucayalii* on the Yavarí. *Cacajao calvus ucayalii* is the most abundant primate in the Lago Preto Conservation Concession, and densities are considerably higher than those in any other areas (Chapter 2). However, the concession is very small, and cannot protect the region's populations of *Cacajao calvus ucayalii* on its own. Conservative estimates suggest that about 350 red uakari monkeys might have been using the entire conservation concession area in June and July 2005 (Barton 2006).

Because the area is surrounded by logging concessions, and WCS-DICE works with the rural communities on the Yavarí and Yavarí-Mirín Rivers, Lago Preto is used as a base for research and conservation work in the area. This enables WCS-DICE to maintain an almost constant presence in the area and monitor the logging and hunting going on around the concession. Over the past two years at Nuevo Esperanza, after several years of data collection and liaison with the community, WCS and DICE have been implementing community-based wildlife management. The management actions include stopping or greatly reducing the hunting of primates, and red uakaris are very much part of the management plan. This is just the beginning of a long process, so it will take time to see the true results.

These studies and conservation actions can be seen as a model for some proposals that are in progress to designate a large protected area between the Yavarí and Yavarí-Mirín rivers. This would link the TTCR reserve with Lago Preto, creating a very large area of continuous protected forest. Uakaris are absent from a large proportion of this reserve, but occur at the western end. It is not known how far east into the area under proposal the population extends.

9.12 Conclusions

There are various reasons why *Cacajao calvus ucayalii* has the patchy distribution observed on the Yavarí and Yavarí-Mirín. The two major rivers themselves are certainly barriers to *Cacajao calvus ucayalii*, but the importance of smaller streams has yet to be investigated. Because large immature seeds are so important to *Cacajao*, the distribution of *Eschweilera* and other large-seeded tree species might have some influence on the distribution and density of *Cacajao*. Because densities of large-seeded tree species appear to be strongly negatively correlated with soil fertility, soil fertility might ultimately be responsible for much of the disjunct distribution of *Cacajao*. More research into the densities of tree families, soil types, tree diversity and the distribution of vegetation types in the Yavarí-Ucayali interfluvium is required to understand the patchy distribution of *Cacajao calvus ucayalii* fully. These studies could be combined with studies to find the limit of the distribution of *Cacajao calvus ucayalii* on the upper Yavarí, where distribution data are lacking.

Cowlishaw and Dunbar (2000) identified the general rule that ecologically-specialised species tend to have more restricted ranges, and it is conceivable that local distribution might also be affected by specialisation. Species that are less specialised might be able to achieve higher densities because they have a wider range of resources available to them (Cowlishaw and Dunbar 2000). *Cacajao* is generally described as a specialist seed predator, but it also consumes considerable amounts of ripe pulp (Chapter 3). It also consumes the seeds of a large number of plant species. Oates *et al.* (1990) suggested that eating seeds might allow colobine monkeys to live at higher abundances than they could if they where more folivorous. Robinson and Ramirez (1982) looked at the effects of diet type and body size on primate abundance in Neotropical primates, and found that abundance declines with body size, and that folivores tended to be more abundant than frugivores. Folivores and frugivores were both more abundant than insectivores. Seed-eating was not examined, but Salovaara *et al.* (2003) and Bodmer *et al.* (2003) found that the seed-eating specialist *Cacajao calvus ucayalii* has low abundance in most areas.

Gaston *et al.* (1997) identified an association between population abundance and geographic distribution. Species with large geographic distributions also tend to have high abundances within their distribution. Gaston *et al.* (1997) suggested that the most important factor might be the degree of ecological specialisation, with generalists being able to achieve high abundance and large distributions owing to the wide range of resources available to them. Since *Cacajao calvus ucayalii* lives at low densities, the population size it can achieve is also restricted. Low population size leads to a higher extinction risk, and vulnerability to environmental stochasticity (Cowlishaw and Dunbar 2000). A patchy distribution might result from low density populations because some of these will become extinct by chance, especially if migration between subpopulations within the metapopulation is restricted by physical or ecological barriers. Marshall (2006) found that lower-quality habitats acted as demographic sinks for white-bearded gibbons (*Hylobates albibarbis*) and red langurs (*Presbytis rubicunda rubida*). Some areas of lower quality habitat for *Cacajao calvus* might act as sink areas, where the population is maintained in part by migration from source areas. If migration into these areas is restricted, local extinction is more likely. Alternatively, some populations in less than perfect habitats may occur, because they are easily 'fed' by source populations. Since logging is occurring over large areas of the geographic range of uakaris, consideration of habitat quality for the species, and not just 'presence or absence' is required in identifying areas for conservation. Efforts to conserve marginal populations will be wasted if the habitats in source areas are degraded or over-hunted.

Whatever the reasons for the patchy distribution of *Cacajao calvus ucayalii*, much of its range occurs outside protected areas. It appears that some of the most important areas for the species are the designated logging concessions between the Yavarí and Yavarí-Mirín Rivers. In these areas, the effects of timber extraction and the management of hunting by local communities and logging workers is likely to be important for the persistence of healthy populations of *Cacajao calvus ucayalii*. Other areas, where good densities of *Cacajao calvus ucayalii* are known, are few. The Lago Preto Conservation Concession is small, and organisations involved with proposals for further protected areas should make efforts to determine the distributions and densities of this important flagship species, especially if they are intending to use *Cacajao calvus ucayalii* as justification for the declaration of the reserve.

Chapter 10

Conclusions

10.1 The biology of *Cacajao calvus ucayalii*

A wide range of aspects of the biology of *Cacajao calvus ucayalii* and the environment where it lives has been discussed in this thesis, including the diet, ranging, grouping system and social behaviour of this primate. This ecological information is useful in formulating conservation strategies. The population growth of a species, and its ability to recover from changes in population size caused by hunting or habitat degradation, depend on its life history characteristics. These in turn are determined in part by the feeding behaviour, competition with other species, and availability of food resources. Social and reproductive behaviour also have direct effects on the demography of populations (Veiga 2004).

The diet and feeding ecology of *Cacajao calvus ucayalii* were key components of this research. What the uakaris were eating and when, paying particular attention to the physical characteristics of the food items used, are described in Chapter 5. Understanding the diet of *Cacajao calvus ucayalii* is the first step to understanding how it competes with other primates for resources. Where species compete for limited resources they are likely to affect each others population densities. The ripe pulp of *Mauritia flexuosa* was the most eaten item at Lago Preto, and was important to *Cacajao calvus ucayalii* when there was a seasonal shortage of other fruit. To a lesser extent the palm *Oenocarpus bataua* was also important during seasonal shortages. Many other primate species also fed on *Mauritia flexuosa* at Lago Preto, and the species is considered a keystone species in western Amazonian forests (Bodmer *et al.* 1990; 1999). There may be competition for *Mauritia flexuosa* and *Oenocarpus bataua* palm fruits, but the fruits were abundant during their respective fruiting seasons. The main resources for *Cacajao calvus ucayalii* outside the *Mauritia flexuosa* fruiting season were immature and unripe seeds. Most important of these are large-seeded, hard-shelled species, largely from the families Lecythidaceae, Sapotaceae and Chrysobalanaceae. *Cebus apella*, *Cebus albifrons* and *Lagothrix lagotricha* are known to feed on seeds (Peres 1991), but these species have less specialised dentition than *Cacajao*, and are not able to open hard fruits. A large proportion of the diet of *Pithecia* is made up of unripe seeds, but Chapter 5 suggests that *Cacajao* is likely to be able to exploit several very-hard-shelled species that the sympatric *Pithecia* is not. It was not possible to quantify the degree of competition occurring between *Cacajao calvus ucayalii* and *Pithecia monachus* at Lago Preto, but there did not appear to be a relationship between the densities of *Pithecia monachus* and *Cacajao calvus ucayalii* on the Yavarí.

It has been demonstrated that *Cacajao calvus ucayalii* at Lago Preto move seasonally between habitats, ranging over *terra firme*, *várzea* and *aguajal* palm-swamps. The most used habitat at the site was *terra firme.* This shows that Ayres (1989) did not need to try to explain the 'non-occurrence' *of Cacajao calvus calvus* in *terra firme. Cacajao* and *Chiropotes* have similar diets (Ayres 1989), occupying similar niches in their respective ranges, though *Chiropotes* lives exclusively in *terra firme* forests. Ayres (1989) suggested that *Chiropotes* could live in *terra firme* forests because primate diversity is lower in eastern Amazonia where *Chiropotes* occurs, and competition was lower in *terra firme* for this reason. However, *Cacajao calvus ucayalii* appears more flexible in its habitat requirements than previously thought, and does not appear to have a problem living in *terra firme* forests with 12 other primate species. *Chiropotes* and *Cacajao* are both able to switch to immature seeds during periods of scarcity of ripe pulps. This may help both of these primates avoid competition with species specialising in fruit pulps. The finding that *Cacajao calvus ucayalii* uses *terra firme* more than any other habitat at Lago Preto may explain why the ranges of *Cacajao* and the ecologically-similar *Chiropotes* do not overlap.

The unusually flexible grouping patterns observed in *Cacajao calvus ucayalii* are discussed in Chapter 6, where group size varies from a few individuals to several hundred. This 'fission-fusion' grouping system could have direct impacts on the ability of the species to inhabit certain areas. The ranging behaviour of *Cacajao calvus ucayalii* in different habitats at Lago Preto enabled testing of Ayres' (1989) theory on the fission-fusion foraging strategies adopted by *Chiropotes* and *Cacajao.* When foraging in *várzea* forests *Cacajao calvus ucayalii* behaved like *Cacajao calvus calvus,* foraging in smaller groups. When foraging in *terra firme* forest *Cacajao calvus ucayalii* foraged in larger groups as is typical in *Chiropotes.* When *Cacajao calvus ucayalii* forages in the *aguajal* habitat, group sizes are of a similar size to those in *terra firme.* Stands of *Mauritia flexuosa* palms can be considered extremely large food patches able to accommodate the entire troop. The groups do not need to fission when foraging in this habitat. This is consistent with Ayres' (1989) explanation of the grouping system of *Cacajao*, and with the theory that foraging group sizes are determined by the patch sizes of the resources being used.

The large group sizes and flexible grouping patterns of *Cacajao* must impact on the social organisation and mating system of the species. The fission-fusion pattern enables groups to react to short term ecological pressures while maintaining large social groups. Large groups can occur year round, even when the distribution of resources demands that foraging groups are smaller. The consequences these patterns have had on the evolution of communication and social behaviour in

Cacajao calvus were discussed in Chapter 7. Two competing theories on how social groups are organised in the species were considered. Garber and Kowalewski (in press) hypothesise that *Cacajao* has a multi-male breeding system in which males are likely to be tolerant of each other's sexual activity, and females are likely to be promiscuous. The closely-related *Chiropotes satanas* appears to have this kind of social organisation (Veiga and Silva 2005). Knogge *et al.* (2006) put forward an alternative theory on the social organisation of *Cacajao calvus*, predicting that the social organisation of *Cacajao calvus ucayalii* would follow the pattern observed in other species that form very large groups, and be organised into 'one-male units'. Elements of both theories appeared to be present at Lago Preto. The high degree of male affiliation in *Cacajao* hints at a system akin to that of *Ateles* and *Chiropotes,* but aggression was commoner in *Cacajao calvus ucayalii* at Lago Preto than in *Chiropotes satanas* observed by Veiga and Silva (2005). Bachelor groups were common and adult male uakaris engaged in aggressive chasing behaviours, apparently in cooperating groups. Males at Lago Preto were certainly affiliative with other males, and the impression gained was that males travelling with adult females were also associating with other males. *Cacajao* may differ from *Chiropotes* in that it forms smaller social units within large groups, but more convincing data are required to demonstrate whether these are one-male or, at least sometimes, include two or more affiliative males.

10.2 The conservation of *Cacajao calvus ucayalii*

10.2.1 Resource extraction

The Yavarí is a stronghold for *Cacajao calvus ucayalii*, and is the only place known where this subspecies can be encountered regularly. The history of the Yavarí River and surrounding areas was reviewed in Chapter 2. Human populations have had considerable influence on the Yavarí and continue to play a part in the development of the area. The commercial extraction of resources has been of particular importance in the Yavarí. At the start of the data collection for this thesis in 2003, human population levels on the Yavarí were probably at their lowest levels in recorded history. The population has swelled slightly since 2003 with the incursion of several timber companies who have been awarded new logging concessions on the Yavarí and Yavarí-Mirín Rivers. The changing emphasis on the exploitation of different natural resources along the Yavarí was traced, leading up to the present day and the establishment of the concessions. Logging on the Yavarí is a commercial activity with an economic return likely to exceed that of the sale of wild meat and peccary skins (Bodmer *et al.* 2006), but which poses a threat to wildlife in the area.

The threats to *Cacajao calvus ucayalii* posed by timber extraction were considered in Chapter 8. Since the extraction is selective, the effects will depend on the overlap between the diet of *Cacajao calvus ucayalii* and the species logged. Data on the vegetation on the Yavarí River and red uakari diet at Lago Preto were brought together with information on logging practices and the extraction of other resources in key areas of the monkey's range. The effects of selective logging on *Cacajao calvus ucayalii* are difficult to predict. Extraction depends of the value of different timber species, which changes as favoured species become scarce and the commercial properties of new species become better documented (Ayres 1987). Observations in the upper Yavarí and Yavarí-Mirín Rivers suggest that logging operations have been removing only the most valuable hardwood species, with some extraction of softwoods starting in some concessions. The fruits and seeds of some softwood timber species feature in the diet of *Cacajao calvus ucayalii.* For this reason, combined with increased habitat disturbance caused by the extraction of more trees, the extraction of softwoods is likely to have a much greater impact on *Cacajao calvus ucayalii.*

In the short term, while only the most valuable hardwoods are being exploited, it appears that populations of *Cacajao calvus ucayalii* close to the Yavarí and Yavarí-Mirín might survive relatively intact, and that these concession areas might continue to be one of the main strongholds for the species. Where removal of other timber species occurs, particularly of the family Myristicaceae, there will be a reduction in the food available for *Cacajao calvus ucayalii.* There will also be higher levels of habitat disturbance and associated hunting, which may have a greater impact on uakari numbers. The findings in Chapter 8 suggest that restrictions on the extraction of certain uakari food trees within the distribution of *Cacajao calvus ucayalii* might be appropriate. This strategy has proven successful for *Cacajao calvus calvus* in Mamiraurá, Brazil (Bowler *et al.* 2006), where the extraction of *Xylopia calophylla* has been banned. Restrictions on timber extraction in Brazil could have knock-on effects in Peru. The ban on the extraction of cumala (Myristicaceae) timber in Brazil could well be promoting extraction in Peru. The effects of bans on timber species in other countries on the extraction rates and sustainability of forestry in Peru should be assessed, and possible action considered.

The effects of non-timber resource extraction on *Cacajao calvus ucayalii* were considered in Chapter 8. *Mauritia flexuosa* is the most important non-timber plant-resource harvested from the forest by the human population in Loreto (Castillo *et al.* 2006), and it was conspicuous that *Mauritia flexuosa* was also the most important species in the diet of *Cacajao calvus ucayalii* at Lago Preto. Given the importance of *Mauritia flexuosa* to *Cacajao calvus ucayalii*, extraction of this resource may impact on the densities of the species in some areas. On the Yavarí, the human population is low, and markets are too distant to make extraction of *Mauritia flexuosa* commercially viable. Closer to Iquitos, *Mauritia flexuosa* is extracted in large quantities (Bodmer *et al.* 1999, Meyer and Penn 2003), and the findings presented in Chapter 8 demonstrate the importance of the sustainable use of aguaje palms in maintaining populations of *Cacajao calvus ucayalii* around more populous areas.

10.2.2 Hunting and conservation of *Cacajao calvus ucayalii*

The ability of a species to sustain a certain level of hunting depends largely on its life history characteristics. Social, ranging and reproductive behaviour can also have clear demographic consequences (Veiga 2004). *Cacajao calvus ucayalii* lives at low densities, so the population size it can achieve is also restricted. Low population size leads to a higher extinction risk, and vulnerability to environmental stochasticity (Cowlishaw and Dunbar 2000). Although *Cacajao calvus ucayalii* lives at low densities, it moves in large social groups. Hunting could reduce group sizes for this species, and it is not known if social groups with fewer individuals would be viable. Smaller groups could experience increased predation pressure or reduced breeding success. For these reasons reducing hunting in this species is particularly important.

The hunting practices of the people on the Yavarí were introduced in Chapter 2, and Chapters 8 and 9 discussed hunting in relation to the Tamshiyacu-Tahuayo Communal Reserve and the logging concessions on the Yavarí. The conclusions reached were that increased hunting around logging concessions was probably the greatest threat to *Cacajao calvus ucayalii* on the Yavarí, at least in the short term. Hunting and its sustainability were outside the scope of the data collection at Lago Preto, and long-term research on mammal populations and hunting in the region were used (e.g. Bodmer *et al.* 2003; Bodmer 1995; Bodmer and Puertas 2005; Puertas and Bodmer 1993). *Cacajao calvus ucayalii* is hunted in most parts of its range, but usually for subsistence, while larger-bodied mammals are sold in markets. Management plans and community-based wildlife conservation in the Tamshiyacu-Tahuayo Communal Reserve have reduced the hunting of primates significantly over the years, since the community-based wildlife management plans stipulate a reduction in the hunting of monkeys (Newing and Bodmer 2003; Bodmer 2000; Puertas and Bodmer 1993).

On the Yavarí, *Cacajao calvus ucayalii* is only occasionally hunted, because larger-bodied game species still occur at high densities (Puertas and Bodmer 1993; Salovaara *et al.* 2003). *Cacajao calvus ucayalii* is one of the priorities in management plans being implemented by DICE-WCS in communities on the Yavarí-Mirín River. The indirect effect of increased hunting brought about by logging operations is widely reported (e.g. Robinson *et al.* 1999), and the effects of hunting on *Cacajao calvus ucayalii* might be more important than the effects of timber extraction within the logging concessions. Despite regulations on hunting imposed by the Peruvian National Institute of Natural Resources (INRENA), uncontrolled hunting is likely to increase in the concessions on the Yavarí and adjoining areas. WCS has proposed a management plan for the Yavarí that includes guidelines for hunting in the concessions. It is possible that relatively simple conservation strategies may be enough to ensure the persistence of *Cacajao calvus ucayalii* in the area. Ensuring that concession owners log only *within* their concessions, and don't hunt *Cacajao calvus ucayalii* might be enough to maintain healthy populations of this primate, at least in the short term.

10.2.3 Distribution of *Cacajao calvus ucayalii* and protected areas

Cacajao calvus ucayalii has a patchy distribution, which has important consequences for the conservation of this species. The various reasons why *Cacajao calvus ucayalii* has the patchy distribution observed on the Yavarí and Yavarí-Mirín Rivers were reviewed in Chapter 9. Some areas of lower-quality habitat for *Cacajao calvus* might act as sink areas, where the population is maintained in part by migration from source areas. Some populations in less than perfect habitats may occur because they are easily 'fed' by source populations. Consideration of habitat quality for the species, and not just 'presence or absence' is required in identifying areas for conservation.

Whatever the reasons for the uneven distribution of *Cacajao calvus ucayalii*, much of its range occurs outside protected areas. The Tamshiyacu-Tahuayo Communal Reserve contains populations of this species and these are protected by the management plans that are in place there. *Cacajao calvus ucayalii* is absent from much of the area between the Yavarí and Yavarí-Mirín Rivers, but exceptionally high densities are found in the Lago Preto Conservation Concession. This protected area is small and surrounded by logging concessions where uakari groups from the Lago Preto study area regularly range. The persistence of *Cacajao calvus ucayalii* in the Yavarí-Ucayali corridor depends largely on populations that occur in logging concession areas, and those in and around the Tamshiyacu-Tahuayo Communal

Reserve. Proposals and newly-designated protected areas are described in Chapter 9, and the presence of *Cacajao calvus ucayalii* is used as partial justification for their designation. Salovaara *et al.* (2003) and Bodmer *et al.* (2003) have shown that densities of *Cacajao calvus ucayalii* are very variable; even where it occurs densities can be extremely low. New reserves containing *Cacajao calvus ucayalii* will be valuable for the conservation of the primate and should be encouraged, but, since resources and the political will for new protected areas have limits, organisations involved with proposals for further protected areas should make efforts to determine the distributions and densities of this important flagship species. This would ensure that areas selected for protection on the basis of the presence of *Cacajao calvus ucayalii* are actually protecting good-sized populations of this flagship species.

10.3 Wider lessons for conservation biology

With a total of 230 globally-threatened primate species, conservationists must consider the reasons why such a large proportion of the order is threatened, in order to formulate appropriate strategies to conserve endangered primates and prioritise areas or species for conservation. The sheer numbers of endangered primates distributed across numerous countries with their own different economic and political problems require a variety of solutions that must be carefully considered for each threatened population. Advances in the field of primate conservation biology will need to be combined with species-specific research into the ecology and in some cases behaviour of threatened species to develop appropriate conservation strategies.

Different primate species in Amazonia are threatened by different pressures. For the larger-bodied primates, the major threat is often hunting, while small-bodied primates are barely affected by hunting, and habitat degradation and deforestation are more important threats (Bodmer 1995). Furthermore, some primates are more at risk than others due to patchy populations or restricted ranges. Habitat specialists or specialist feeders, such as seed predators, might also be more sensitive to habitat modification (Plumptre and Grieser Johns 2001), whilst complex life histories or social systems might influence a species' ability to survive in small fragmented populations, or to recover after a reduction in population size. *Cacajao calvus ucayalii* has a number of characteristics that make it suitable as a case study on how various aspects of its biology can contribute to the conservation of a primate species. It is a specialist feeder, with complex habitat requirements, has a patchy distribution and is threatened by hunting and habitat disturbance. Furthermore, it has a complex social and grouping system, which could affect the demography of populations.

In examining a primate facing multiple threats it has become clear that the threats are not equally important in all parts of the range. In many parts of the range, hunting is probably the main threat. In the Tamshiyacu-Tahuayo Communal Reserve the hunting of primates has been reduced and the extraction of aguaje may be one of the chief concerns for uakari populations. On the Yavarí, the distance to markets means that large-scale commercial extraction of aguaje is not likely. Habitat disturbance from timber extraction on the Yavarí is a threat to uakaris, but, while timber extraction occurs at lower intensities, the main threat appears to be increased hunting to feed a population swelled by logging activities in remoter parts of the range. This may change, however, as extraction of new species of timber becomes commercially viable. Habitat disturbance might then take on increased importance. When setting conservation strategies it is important to understand how the threats vary in different parts of the range, and how threats are likely to change through time.

10.4 Recommendations for further ecological research on *Cacajao calvus ucayalii*

Collecting up-to-date information on the current distribution of *Cacajao calvus ucayalii* has to be a priority for research. The last detailed census on the tributaries of the Ucayali was conducted between 1979 and 1986 by Aquino (1988) and it is likely that the range has been reduced since. While detailed census work has been conducted on parts of the Yavarí-Mirín, the distribution on much of the Yavarí is only partially known. Given the locations of existing and proposed protected areas, priorities must include determining the extent of the distribution of *Cacajao calvus ucayalii* in the proposed Yavarí reserve, and in the Sierra del Divisor Reserved Zone. Relative densities of the species must also be calculated for these areas. The presence of a reminant population in the Pacaya-Samiria National Reserve requires confirmation. This population is likely to be small, but if it exists, its persistence is required to maintain the integrity of the primate assemblage in the reserve.

Because large immature seeds are so important to *Cacajao*, the distribution of *Eschweilera* and other large-seeded tree species might have some influence on the distribution and density of *Cacajao*. Because densities of large-seeded tree species appear to be strongly negatively correlated with soil fertility, soil fertility might ultimately be responsible for much of the disjunct distribution of *Cacajao*. More research into the densities of tree families, soil types, tree diversity and the distribution of vegetation types in the Yavarí-Ucayali interfluvium is required to understand the patchy distribution of *Cacajao calvus ucayalii* fully. These studies could be combined with research to better determine the distribution of *Cacajao calvus ucayalii.*

Cacajao calvus clearly has a multi-male social system, but Ayres (1986), Knogge *et al.* (2006) and Garber and Kowalewski (in press) have differing ideas about whether the breeding system of the species is multi-male or single-male. It is also not known whether females, males or both sexes disperse from the natal groups. The demography of *Cacajao calvus* populations may depend on these factors. More data on the nearest neighbours of adult males that are associating with females are required to help determine the breeding system of *Cacajao calvus ucayalii.*

Breeding in *Cacajao calvus ucayalii* at Lago Preto is seasonal. Very young animals can be counted between January and April with the knowledge that the majority of the season's young have been born between August and December. Long term data on the number of births each year could be collected, and would yield information valuable in understanding the demography of the population.

Bibliography

Abegglen, J.J. 1984. *On socialization in Hamadryas Baboons: A field study.* Lewisburg, Pennsylvania: Bucknell University Press.

Ahuite, M. 2004. Composición de Árboles y Estructura de un Bosque del Valle del Río Yavarí, Loreto-Perú. Unpublished Report. WSC-Peru, Iquitos.

Almeida, F.B., Deane, L.M. 1970. *Plasmodium brasilianum* reencontrado em seu hospedeiro original, o Macaco uacari branco, *Cacajao calvus. Bol. Inst. Nac. Pesq. Amazonia* 4:1-9.

Altmann, J. 1974. Observational study of behaviour: Sampling methods. *Behaviour* 48: 1-41.

Altmann, S.A., Altmann, J. 1979. Demographic constraints on behavior and social organization. In: *Primate ecology and human origins: Ecological influences on social organization,* ed. I. S. Bernstein E. O. Smith, eds. New York: Garland STPM Press.

Altmann, J. 1990. Primate males go where the females are. *Animal Behaviour.* 39:193-195.

Aquino, R. 1988. Preliminary survey on the population densities of *Cacajao calvus ucayalii. Primate Conservation.* 9: 24-26.

Aquino, R. 1995. Concervacion de *Cacajao calvus ucayalii* en la Amazonia Peruana. *Neotropical Primates.* 3: 40-42.

Aquino, R. 1998. Some observations on the ecology of *Cacajao calvus ucayalii* in the Peruvian Amazon. *Primate Conservation.* 18: 21-24.

Aquino, R. 1999. Observaciones preliminares sobre la dieta de *Cacajao calvus ucayalii* en el Nor-Oriente Peruano. *Neotropical Primates* 7(1): 1-5.

Aquino, R., Alvarez, J. and Mulanovich, A. 2005. Diversidad y estado de conservación de primates en las Sierras de Contamana, Amazonía peruana. *Revista Peruana de Biología* 12(3): 427-434.

ARKive. 2006. Bald-headed uakari (*Cacajao calvus*) Wildscreen. http://www.arkive.org/species/GES/mammals/Cacajao_calvus Downloaded on 17 October 2006.

Ayres, J.M. 1981. Observations sobre a ecologia e o comportamento dos cuxius (*Chiropotes albinasus* y *Chiropotes satanas*), Cebidae: Primates. Unpublished Master's Thesis. Universidade do Amazonas: Manaus, Brazil.

Ayres, J.M. 1986. The White Uakaris and the Amazonian Flooded Forests. Unpublished PhD thesis, Cambridge University.

Ayres, J.M. 1989. Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes. Journal of Human Evolution* 18(7): 697-716,

Ayres, J.M. and Clutton-Brock. T.H. 1992. River boundaries and species range size in Amazonian Primates. *American Naturalist* 140:531-537.

Ayres, J.M. and Johns, A.D. 1987. Conservation of white uacaries in Amazonian *várzea. Oryx.* 21(2): 74-80.

Ayres, J.M. and Prance, G.T. (in press) On the distribution of Pitheciine monkeys and Lecythidaceae trees in Amazonia. In: *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris,* eds. Barnett, A. and Viega, L. Cambridge, Cambridge University Press.

Baldwin, J.D. and Baldwin, J.I. 1972. The ecology and behaviour of squirrel monkeys (*Saimiri sciureus*) in a natural forest in western Panama. *Folia Primatol.* 18:161-184.

Barnett A.A. 2004. The meanings of *Cacajao* and uacari: folk etymology in Neotropical primate taxonomy. *Neotropical Primates* 12:147-152.

Barnett, A.A. and Ross, C. (in preparation) The naked red head of *Cacajao calvus*: facts, fantasies and filaria.

Barnett, A.A., Borges, S. and de Castilho, C.V. 2000. Golden-backed uacari, *Cacajao melanocephalus ouakary*, in Jaú National Park, Amazonia, Brazil. *Primate Eye* 70:33-37.

Barnett, A.A., de Castilho C.V., Shapley R.L and Anicácio A. 2005. Diet, habitat selection, and natural history of the golden-backed uacari, *Cacajao melanocephalus ouakary*, in Jaú National Park, Brazil. *International Journal of Primatology* 26: 961-981.

Barnett, A.A. and Brandon-Jones, D. 1997. The ecology, biogeography and conservation of the uakaris, *Cacajao* (Pitheciinae). *Folia Primatologica*. Vol. 68, 223- 235.

Barnett, A.A. and da Cunha, A.C. 1991. The golden-backed uakari on the upper Rio Negro, Brazil. *Oryx*. 25: 80-88.

Barton, C. 2006. The ecology and population viability of *Cacajao calvus ucayalii* in Lago Preto, Peru. Unpublished BSc thesis DICE University of Kent at Canterbury, UK

Bartecki, U., Heymann, E.W. 1987. Sightings of red uakaris, *Cacajao calvus rubicundus*, at the Río Blanco, Peruvian Amazonia. *Primate Conservation* 8: 34-36.

Bates, H.W. 1863. *The Naturalist on the River Amazon*. John Murray, London.

Beckerman, S. 1983. Does the swidden ape the jungle? *Human Ecology* 11: 69-84

Bennett, C.L., Leonard, S. and Carter, S. 2001. Abundance, diversity, and patterns of distribution of primates on the Tapiche River in Amazonian Peru. *American Journal of Primatology*. 54:119-126.

Begazo, A.J. and R.E. Bodmer 1998. Use and conservation of the Cracidae (Aves Galliformes) in the Peruvian Amazon. *Oryx*, 32: 301-309.

BirdLife International. 2000. *Threatened birds of the world*. Barcelona and Cambridge, UK: Lynx Edicions and BirdLife International.

Bodmer, R.E., T.G. Fang and L. Moya I. 1990. Fruits of the forest. *Nature* 343: 109.

Bodmer, R.E. (1990). Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). *Journal of Zoology* 222: 121-128.

Bodmer, R.E. 1995. Susceptibility of mammals to overhunting in Amazonia. In: *Integrating People and Wildlife for a Sustainable Future*, eds. J. Bissonette and P. Krausman The Wildlife Society, Bethesda, Maryland, pp. 292-295.

Bodmer, R.E. 2000. Integrating hunting and protected areas in the Amazon. In: *Future Priorities for the Conservation of Mammals: Has the Panda had its Day?* Eds. N. Dunstone and A. Entwistle. Cambridge University Press, UK.

Bodmer, R.E., Eisenberg, J.F. and Redford K.H.1997. Hunting and the likelihood of extinction of Amazonian mammals. *Conservation Biology* 11:460-466.

Bodmer, R.E., Allen, C.M., Penn, J.W., Aquino, R. and Reyes, C. 1999. Evaluating the sustainable use of wildlife in the Pacaya-Samiria National Reserve, Peru. *America Verde Working Paper No. 4 Latin America and Caribean Region*. The Nature Conservancy.

Bodmer, R.E., T.G. Fang, L. Moya I. and R. Gill. 1994. Managing wildlife to conserve Amazonian forests: population biology and economic considerations of game hunting. *Biological Conservation* 67: 29-35.

Bodmer, R.E. & Pezo Lozano, E. 2001. Rural Development and Sustainable Wildlife Use in the Tropics. *Conservation Biology*, 15, 1163-1170.

Bodmer, R.E. and Puertas, P.E. 1999. Community-based comanagement of wildlife in the Peruvian Amazon. In: *Hunting for Sustainability in Tropical Forests*. eds. J.G. Robinson and E.L. Bennet. Columbia University Press, New York.

Bodmer, R.E. and Puertas, P. 2003. A brief history of the Yavarí valley. In: *Peru: Yavari. Rapid Biological Inventories* Report 11. eds. Pitman, N.C. Vriesendorp, D. Moskovits.Chicago, IL: The Field Museum.

Bodmer, R.E., Puertas, P. and Antúnez, M. 2003. Use and sustainability of wildlife hunting in and around the proposed Yavarí reserved zone. In: *Peru: Yavari.*

Rapid Biological Inventories Report 11. eds. Pitman, N.C. Vriesendorp, D. Moskovits. Chicago, IL: The Field Museum.

Bodmer, R.E., Puertas, P., Rios, C., Fang, T. and Ryan, E. 2006. Investigación sobre la facilibilidad de implementar un manejo de fauna silvestre en concesiones forestales en la Amazonia Peruana. Unpublished Technical Report. DICE-WCS.

Boubli, J.P. 1993. Southern expansion of the geographical distribution of *Cacajao melanocephalus melanocephalus. International Journal of Primatology.* 14(6): 933-937.

Boubli, J.P. 1994. The black uakari monkey in the Pico da Neblina National Park. *Neotropical Primates.* Vol. 2, 11-12.

Boubli, J.P. 1997 Feeding ecology of one group of Humbolt's black uakari, *Cacajao melanocephalus melanocephalus*, in the Pico da neblina national park, brazil. *Neotropical Primates* 2(3):113-115.

Boubli, J. P. 1998. A study of the black uakari *Cacajao melanocephalus melanocephalus* in the Pico de Neblina National Park, Brazil. *Neotropical Primates* 5(4):111–113.

Boubli, J. P. 1999. Feeding ecology of black-headed uakaris (*Cacajao melanocephalus melanocephalus*) in the Pico de Neblina National Park, Brazil. *International Journal of Primatology.* 20:719–749.

Boubli, J. P. 2002 Western extension of the range of bearded sakis: A possible new taxon of *Chiropotes* sympatric with *Cacajao* in the Pico da Neblina National Park, Brazil. *Neotropical Primates.* 10(1): 1-4.

Boubli, J. P. and Ditchfield, A. 2000. The time of divergence between the two species of uacari monkeys, *Cacajao calvus* and *Cacajao melanocephalus. Folia Primatologica* 71:387–391.

Bowler, M. 2003. The ecology and conservation of the red uakari monkey *Cacajao calvus ucayalii* in the Yavari Valley of Peru. [Abstract] *Primate Eye.* 79: 3-4.

Bowler, M., Queiroz, H., Bodmer, R.E. and Puertas, P.E. 2006. Uakaris for real: conservation initiatives in Peru and Brazil. [Abstract] *International Journal of Primatology.* 27(Suppl 1). Abst #521.

Buchanan, D.B., Mittermeier, R.A. and van Roosmalen, M.G.M. 1981. The saki monkeys, genus Pithecia. In: *Ecology and behaviour of Neotropical primates. Vol. 1.* eds. A. F. Coimbra-Filho R. A. Mittermeier. Rio de Janeiro: Academia Brasileira de Ciencias. 391-417.

Caldecott, J.O. 1980. Habitat quality and populations of two sympatric gibbons (Hylobatidae) on a mountain in Malaya. *Folia Primatologica.* 33:291-309.

Canavez, F.C., Moreira, M.A.M., Ladasky J.J., Pissinatti A., Parham P. and Seuánez H.N. 1999. Molecular Phylogeny of New World Primates (Platyrrhini). *Molecular Phylogenetics and Evolution.* 12(1) 74-82.

Castillo, D. del., Otárola, E. and Alvarado, L. 2006. *Aguaje: la maravillosa palmera de la Amazonía, Aguaje: the amazing palm tree of the Amazon. Iquitos*: Instituto de investigaciones de la Amazonía peruana. IIAP - Comisión europea.

Castro, R. and Soini, P. 1977. Field studies on *Saguinus mystax* and other callitrichids in Amazonian Peru. In: *The Biology and Conservation of the Callitrichidae*, D.G. Kleiman ed. Pp. 73-78. Smithsonian Institution Press, Washington, D.C.

CBBC. 2005. Serious Amazon. Episode 6. Children's BBC. London.

Chapman, C. A., White, F. J. & Wrangham, R. W. 1993. Defining subgroup size in fission-fusion societies. *Folia primatologica.* 61: 31-34.

Chapman, C.A., Wrangham, R.W. and Chapman, L.J. 1995. Ecological constraints on group size. An analysis of chimpanzee and spider monkey subgroups. *Behavioral Ecology and Sociobiology.* 36:59-70.

Chazdon, R. L., R. K. Colwell, J. S. Denslow and M. Guariguata. 1998. Statistical estimation of species richness of woody regeneration in primary and secondary rainforests of NE Costa Rica. In: *Forest Biodiversity in North, Central, and*

South America and the Caribbean: Research and Monitoring. eds. Dallmeier, F., and J. Comisky. Parthenon Press, Paris.

Cheney, D.L., Wrangham, R.W. 1987. Predation. In: *Primate Societies.* eds. B.B. Smuts D.L. Cheney R.M. Seyfarth R.W. Wrangham T.T. Struhsaker. Chicago: University of Chicago Press.

Chivers, D.J., Hladik, C.M. 1984. Diet and gut morphology in primates. In: *Food acquisition and processing in primates.* eds. D. J. Chivers B. A. Wood A. Bilsborough, New York: Plenum Press.

Changizi, M.A., Zhang, Q., Shimojo, S. 2006. Bare skin, blood and the evolution of primate colour vision. *Biology letters* 2(2): 217-221.

CITES. 2006. Convention on International Trade in Endangered Species of Wild Fauna and Flora. http://www.cites.org. Downloaded 17 October 2006.

Clarke, F.M., Pio, D.V. Racey, P.A. 2005. A Comparison of Logging Systems and Bat Diversity in the Neotropics. *Conservation Biology* 19(4):1194-1204.

Clinebell, R.R., Phillips, O.L., Gentry, A.H., Stark, N. and Zuuring, H. 1995. Prediction of Neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation* 4: 56-90.

Clutton-Brock, T.H. and Harvey, P.H. 1976. Evolutionary rules and primate societies. In: *Growing points in ethology.* eds. P.P.G. Bateson, R.A. Hinde, Cambridge: Cambridge University Press.

Clutton-Brock, T.H. and Harvey, P.H. 1977. Species differences in feeding and ranging behaviour in primates. In: *Primate Ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes.* ed. T.H. Clutton-Brock, New York: Academic Press.

Coales, K. 2005. Assessing the commercial value of standing timber in an area of proposed rainforest reserve in Yavarí, Peru. Unpublished BSc thesis DICE University of Kent at Canterbury, UK

Cowlishaw, G., and Dunbar, R. 2000. *Primate conservation biology.* Chicago: University of Chicago Press.

Cracraft, C. 1983. Species concepts and speciation analysis. *Ornithology.* 1: 159-187.

Cunha, A. da and Barnett, A. 1989. Project Uakari: First Report: The Preliminary Survey, Part One: Zoology. Pronatura, Río de Janeiro, Brazil and WWF-Netherlands, Amsterdam.

Cunningham, E.P. and Janson, C.H. 2006. *Pithecia pithecia*'s behavioral response to decreasing fruit abundance. *American Journal of Primatology.* 68(5): 491-497.

D'Acuna, C. 1698. *A relation of the great river of Amazons in South-America.* London: S. Buckley.

Davies, C.R., Ayres, J.M., Dye, C. and Deane, L.M. 1991. Malaria Infection Rate of Amazonian Primates Increases with Body Weight and Group Size. *Functional Ecology,* 5(5):655-662.

Dawkins, H.C. and M.S. Philip. 1998. *Tropical Moist Forest Silviculture and Management: A history of success and failure.* Wallingford, United Kingdom: CAB Centre for Agriculture and Bioscience.

de Castelnau, F. 1850-51. Expédition dans les partes centrales de l'Amérique du Sud, de Rio de Janeiro a Lima, et de Lima au Para. Paris: Chez P. Bertrand.

Defler, T.R. 1989. The status and some ecology of primates in the Colombian Amazon. *Primate Conservation.* Vol. 10 51-56.

Defler, T.R. 1991. *Cacajao melanocephalus* (Humboldt, 1811) Primates, Cebidae. Trianea. *Acta Cient. Tecn. Inderena* 4: 557-558.

Defler, T.R. 1996. Aspects of the ranging pattern in a group of wild woolly monkeys (*Lagothrix lagotricha*) *American Journal of Primatology.* 38:289-302.

Defler, T.R. 1999. Fission-fusion in the black-headed uacari (*Cacajao melanocephalus*) in eastern Colombia. *Neotropical Primates.* Vol. 7, 5-8.

Defler, T.R. 2001. *Cacajao melanocephalus ouakary* densities on the lower Apaporis River, Colombian Amazon. Primate Report.

Defler, T.R. 2003. *Primates de Colombia.* Conservation International, Bogota, D.C., Colombia.

De la Cruz, B.N. et al. 1999. Boletín No. 134, Serie A: Carta Geológica Nacional. Lima: Instituto Geologico, Minero y Metalúrgico.

Del Campo, H. Valverde, Z. Calle, A. and Wali, A. 2003. Human Communities. In: *Peru: Yavari. Rapid Biological Inventories* Report 11. eds. Pitman, N.C. Vriesendorp, D. Moskovits. Chicago, IL: The Field Museum.

Dietz, J.M., Dietz, L.A., and Nagagata, E.Y. 1994. The effective use of flagship species for conservation: The example of the lion tamarin. In *Creative conservation Interactive management of wild and captive animals.* eds. P.J.S. Olney, G.M. Mace, and A.T.C. Feistner, 32-49. London: Chapman and Hall.

Di Fiore, A., Campbell, C.J. 2007. The Atelines: variations in ecology, behavior, and social organization. In *Primates in Perspective* eds. Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M. and Bearder, S.K. New York: Oxford University Press.

Dixson, A.F. 1983. Observations on the evolution and behavioral significance of "sexual skin" in female primates. *Advances in the Study of Behaviour.* 13:63-106.

Drage, J. 2003. Armadillo abundance in Lago Preto. Unpublished BSc thesis DICE University of Kent at Canterbury, UK.

Dunbar, R.I.M. 1984. *Reproductive decisions: An economic analysis of gelada baboon social strategies.* Princeton: Princeton University Press.

Dunbar, R.I.M. 1996. Determinants of group size in primates: A general model. In: *Evolution of social behaviour: Patterns in primates and man.* eds. G. Runciman, J. Maynard Smith, and R. Dunbar, 33-58. New York: Oxford University Press.

Egoavil, E. O. 1992. Perfil demografico de la region Loreto. Instituto de Investigaciones de la Amazonia Peruana, Iquitos, Peru.

Emmons, L.H. 1984. Geographic variation in densities and diversities of non-flying mammals in Amazonia. *Biotropica* 16:210-222.

Emmons, L.H., and Feer, F. 1997. *Neotropical Rainforest Mammals.* The University of Chicago Press. Chicago and London.

Encarnación, F. 1993. El bosque y las formaciones vegetales en la llanura amazónica del Perú. *Alma Mater* 6: 95-114.

Entwistle, A.C., Mickleburgh, S. & Dunstone.N. 2000. Mammal conservation: current contexts and opportunities. In: *Future Priorities for the Conservation of Mammals - Has the Panda had its Day?* eds. Entwistle, A. & Dunstone. N. Cambridge: Cambridge University Press.

Eudey, A. and Members of the Primate Specialist Group 2000. Macaca assamensis. In: IUCN 2006. 2006 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 13 November 2006.

Fedigan, L.M., Baxter, M.J. 1984. Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*). *Primates.* 25(3): 279-294.

Fernandes, M.C.A.G. 1990. Distribuicao de primates nao-humanos no estado de Acres e vizinhancas: Um estudo preliminar. Monograph, Departmento de Ciencias da Natureza, Universidade Federal do Acre, Rio Branco.

Fernandes, M. E. B. 1993. Tail-wagging as a tension-relief mechanism in Pithecines. *Folia Primatologica.* 61: 52–56.

Ferrari, S.F., E.M. Lima, S.S.B da Silva, and L.M. Veiga. 2004. Conservation of remnant populations of bearded sakis (*Chiropotes satanas*) in the Tucuruí Reservoir, southeastern Amazônia. *Folia Primatologica*, 75(suppl. 1): 260-261.

Fimbel, R.A., A. Grajal and J.G. Robinson. 2001. Logging and wildlife in the tropics: impacts and options for conservation. In: The Cutting Edge: Conserving Wildlife in Logged Tropical Forests. eds. R.A. Fimbel, A. Grajal and J.G. Robinson. Columbia University Press, New York, 667-695.

Flores, W. 2006. Aspectos ecológicos de Crácidos en Lago Preto, río Yavarí. Tesis de Biólogo, UNAP.

Fontaine, R., and F. V. Du Mond. 1977. The red ouakari in a seminatural environment: potentials for propagation and study. eds. Rainier III and Bourne. 167-236.

Fontaine, R. 1979. Survey of the Red Uakari (*Cacajao calvus rubicundus*) in eastern Peru. Report of the New York Zoological Society on the Project New York, USA.

Fontaine, R. 1981. The Uakaris, Genus Cacajao. in Ecology and Behavior of *Neotropical Primates*. eds. A.F. Coimbra-Filho and R.A. Mittermeier. Academia Brasileira de Ciencias.

Fooden, J., Quan, G.Q., Wang, Z.R. and Wang, Y.X. 1985. The stumptail macaques of China. *American Journal of Primatology*. 8(1):11-30.

Foster, R.B. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island. In: *The Ecology of a Tropical Forest*. eds. Leigh, E.G., A.S. Rand, and D.M. Windsor, Smithsonian Press, Washington, D.C.

Frumhoff, P. 1995. Conserving wildlife in tropical forests managed for timber. *Bioscience* 45:456–464.

Galetti, M., de Carvalho, O. 2000. Sloths in the Diet of a Harpy Eagle Nestling in Eastern Amazon. *The Wilson Bulletin*: 112(4): 535–536.

Garber, P.A. 1997. One for all and breeding for one: Cooperation and competition as a tamarin reproductive strategy. *Evolutionary Anthropology*. 5(6): 187-199

Garber, P.A. and Kowelewski, M. (in press) Male cooperation in Pitheciines: The reproductive costs and benefits to individuals of forming large multimale-multifemale groups. In Evolutionary Biology and Conservation of Titis, Sakis and Uacaris. eds. Barnett, A. and Viega, L. Cambridge, Cambridge University Press.

Garrett, L. 2002. The behaviour and ecology of the red uakari monkey (*Cacajao calvus rubicundus*) in the Yavari Valley, Amazonian Peru. Unpublished BSc thesis DICE University of Kent at Canterbury, UK.

Gaston, K.J., Blackburn, T.M. and Lawton, J.H. 1997. Interspecific abundance-range size relationships: An appraisal of mechanisms. *Journal of Animal Ecology*. 66:579-601.

Gautier, L., and R. Spichiger. 1986. Ritmos de reproducción en el estrato arbóreo del Arborétum Jenaro Herrera (provincia deRequena, departamento de Loreto, Perú): Contribución al estudio de la flora y de la vegetación de la Amazonía peruana X. Candollea 41(1): 193-207.

Gentry, A. H. 1988. Tree species richness of upper Amazonian forests. *Proc. Nat. Acad. Sci.* 85: 156-159.

Gentry, A.H. 1990. Floristic similarities and differences between southern central America and upper and central Amazonia. In: *Four Neotropical Rainforests*. ed. A.H. Gentry New Haven: Yale University Press.

Geoffroy Saint-Hilaire, I. 1847. Note sur un singe américain appartenant au genre Brachyure. Comptes Rendus Hebdomadaires des Séances de l'Academie des Sciences, Paris, série D 23: 576.

Geoffroy Saint-Hilaire, I. and Deville, E. 1848. Note sur un huit espècies nouvelles de singes américaine, faitent parties des collections de M. de Castelnau et Emile Deville. Comptes Rendus Hebdomadaires des Séances de l'Academie des Sciences, Paris, série D 27: 497–499.

Glander, K. 1987. Reproduction and population growth in free-ranging mantled howling monkeys. *American Journal Physical Anthropology*. 53:25-36.

Glanz, W.E. 1990. Neotropical mammal densities: How unusual is the community on Barro Colorado Island, Panama? In: *Four Neotropical Forests*, ed. A.H. Gentry, 287-313. New Haven: Yale University Press.

Goodall, J. 1986. *The Chimpanzees of Gombe*. Belknap Press, Cambridge, Mass.

Goodman, M., Porter, C. A., Czelusniak, J., Page, S. L., Schneider, H., Shoshani, J., Gunnell, G., and Groves, C. P. (1998). Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. *Mol. Phyl. Evol.* 9: 585–598.

Grieser Johns 1997. *Timber Production and Biodiversity Conservation in Tropical Rain Forests.* Cambridge, United Kingdom: Cambridge University Press.

Goulding, M. 1980. *The fishes and the forest: Explorations in Amazonian natural history.* University of California Press, Los Angeles.

Goulding, M. 1989. *Amazon, the flooded forest.* London: BBC Books.

Groves, C. P. 2001. *Primate Taxonomy.* Smithsonian Institution Press, Washington, DC.

Hamilton, W.D., Zuk M., 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218: 384-387.

Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41–49.

Harcourt, A.H. 1998. Ecological indicators of risk for primates, as judged by species' susceptibility to logging. In: *Behavioural Ecology and Conservation Biology.* Ed. T. Caro. New York: Oxford University Press.

Harcourt, A.H., Harvey, P.H., Larson, S.G., Short, R.V. 1981. Testis weight, body weight and breeding system in primates. *Nature.* 293:55-57.

Hernandez-Camacho, J. and Cooper, R.W. 1976. The non-human primates of Colombia. In: *Neotropical Primates: Field Studies and Conservation.* eds. Thorington, R.W., Eltne, P.G. Cambridge, Cambridge University Press. 35-69.

Hershkovitz, P. 1972. Notes on New World monkeys. *International Zoo Yearbook.* 12:3-12.

Hershkovitz, P. 1977. *Living New World monkeys (Platyrrhini) with an introduction to Primates.* Vol. 1. University of Chicago Press. Chicago.

Hershkovitz, P. 1985. A preliminary taxonomic review of the South American bearded saki monkeys, genus Chiropotes (Cebidae, Platyrrhini), with a description of a new sub-species. *Fieldiana, Zool.* 27: 1–23.

Hershkovitz, P. 1987a. Uacaries, New World monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): A preliminary taxonomic review with the description of a new subspecies. *American Journal of Primatology.* Vol.12, 1-53.

Hershkovitz, P. 1987b. The taxonomy of South American sakis, genus *Pithecia* (Cebidae, Platyrrhini): a preliminary report and a description of a new species and a new subspecies. *American Journal of Primatology* 12:44, 387-468.

Hart, N.S, 2001. The visual ecology of avian photoreceptors. *Prog Retinal Eye Res* 20:675–703.

Heymann, E.W. 1990. Further field notes on red uakaris, *Cacajao calvus ucayalii*, from the Quebrada Blanco, Amazonian Peru. *Primate Conservation* 11, 7-8.

Heymann, E.W. 1992. The red uakari (*Cacajao calvus ucayalii*): Some field observations and speculations on a little-known species. *Primate Eye.* Vol. 47.

Heywood, V.H. 1995. Global Biodiversity Assessment. Cambridge University Press, Cambridge.

Hick, U. 1968. The collection of saki monkeys at Cologne Zoo. *International Zoo Yearbook.* 8:192-194.

Hill, C. A. 1965. Maintenance of facial colour in the red uakari (*Cacajao rubicundus*). *International Zoo Yearbook.* 5:140–141.

Hoshino, J., Mori, A., Kudo, H. and Kawai, M. 1984. Preliminary report on the grouping of mandrills (*Mandrillus sphinx*) in Cameroon. *Primates.* 25(3):295-307.

Horovitz, I., Zardoya, R. and Meyer, A.. 1998. Platyrrhine systematics: A simultaneous analysis of molecular and morphological data. *American Journal of Physical Anthropology* 106:261-281.

Humboldt, A., de. 1811-1812. Recueil d'observations de zoologie et d'anatomie comparée, faites dans l'océan Atlantique et dans l'Intériour du nouveau continent et dans la Mer du Sud pendant les années 1799, 1800, 1801, 1802 et 1803. eds. Humboldt, A. de & Bonpland, A. Levrault Schoell, Paris. 2 vols.

Isabirye-Basuta, G. and J. M. Kasenene. 1987. Small rodent populations in selectively felled and mature tracts of Kibale forest, Uganda. *Biotropica* 19:260–266.

IUCN 2006. 2006 IUCN Red List of Threatened Species. http://www.iucnredlist.org. Downloaded on 17 October 2006.

Ivlev, V.S. 1961. *Experimental ecology of the feeding of fishes.* Yale University Press, New Haven.

Izawa, K. 1976. Group sizes and compositions of monkeys in the upper Amazon basin. *Primates.* 17: 367-399.

Jacobs, G. H. 1993. The distribution and nature of color vision among the mammals. *Biological Reviews.* 68:413–471.

Janson C.H. and Emmons S. 1990. Ecological structure of the non-flying mammal community at Cocha Cashu biological station, Manu National Park, Peru. In: *Four Neotropical rainforests.* ed. A.H. Gentry, Yale University Press. 627 pp / pp. 314-338.

Joffe, T.H and Dunbar, R.I.M. 1997. Visual and social-cognitive information processing in primate brain evolution. *Proceedings of the Royal Society of London.* B264(1386):1303-1307.

Johns, A. 1986. Notes on the ecology and current status of the buffy saki, *Pithecia albicans. Primate Conservation.* 7: 26-29.

Johns, A 1991. Forest disturbance and Amazonian primates. Primate Responses to Environmental Change. H. O. Box, ed. Chapman & Hall: London, United Kingdom. pp. 115–135.

Johns, A. 1992. Species conservation in managed tropical forests. In: *Tropical Deforestation and Species Extinction.* eds. T.C Whitmore. And J.A Sayer, Chapman & Hall: London. pp 15-53.

Johns, A. and Skorupa, J.P. 1987. Responses of rainforest primates to habitat disturbance: A review. *International Journal of Primatology.* 8: 157-191.

Jouventin, P. 1975. Observations of the social ecology of mandrill. *Terre et la vie.* 29: 493-532.

Kahn, F and Henderson, A. 1999. An overview of the palms of the Várzea in the Amazon region. In: *Várzea: diversity, development, conservation of Amazonia's whitewater floodplains.* eds. C. Padoch., J.M Ayres, M, Pinedo and M. Vasquez, New York Botanical Garden Press: Bronx, USA. pp. 187-193.

Kay, R.F., Plavcan, J.M., Glander, K.E. and Wright, P.C. 1988. Sexual selection and canine dimorphism in New World monkeys. *American Journal of Physical Anthropology.* 77(3):385-397.

Kinzey, W.G. 1992. Dietary and dental adaptations in the Pitheciinae. *American Journal of Physical Anthropology.* 88 : 499-514.

Kinzey, W.G. 1997. Cacajao. In: *New World Primates: Ecology, Evolution, and Behavior.* eds. Warren G. Kinzey and Aldine de Gruyter, New York.

Kinzey, W.G and Cunningham, E.P. 1994. Variability in platyrrhine social organization. *American Journal of Primatology.* 34(2):185-198.

Kinzey, W.G. and Norconk, M.A. 1990. Hardness as a basis of fruit choice in two sympatric primates. *American Journal of Physical Anthropology* 81 : 5-15.

Kinzey, W.G. and Norconk, M.A. 1993. Physical and chemical properties of fruit and seeds eaten by Pithecia and Chiropotes in Surinam and Venezuela. *International Journal of Primatology.* 14(2) : 207-227.

Knogge, C., Zinner, D. and Heymann, E. 2006. Evidence for harem units as the base for the multilevel organisation of red uakaris *Cacajao calvus ucayalii* [Abstract] Tagung der Gesellschaft für Primatologie, Max-Planck Institute for Evolutionary Anthropology in Leipzig, The Junior Research Group Integrative Primate Socio-Ecology (IPSE).

Kuchikura, Y. 1988. Efficiency and focus of blowpipe hunting among Semaq Beri hunter-gatherers of peninsular Malaysia. *Human Ecology.* 16 :271-305.

La Condamine, C.M. de 1751. *Journal du voyage fait par ordre du Roi, a l'Equateur.* Paris: Imprimerie Royale.

Lane, D.F. Pequeno, T. and Flores Villar, J. 2003. Birds In: Peru: Yavari. Rapid Biological Inventories Report 11 eds. Pitman, N.C. Vriesendorp, D. Moskovits, Chicago, IL: The Field Museum.

Lange, A. 1912. *In the Amazon jungle: Adventures in remote parts of the upper Amazon River, including a sojourn among cannibal Indians.* New York: G. P. Putnam's Sons.

Larrabure y Correa, C. 1905-09. Coleccion de leyes, decretos, resoluciones y otros documentos oficiales referentes al Departamento de Lorteo. Lima: La Opinión Nacional.

Lasry, J.E., Sheridan, B.W. 1965. Chagas' myocarditis and heart failure in the red uakari *Cacajao rubicundus. International Zoo Yearbook.* 5: 182-184.

Lawes, M.J. 1992. Estimates of population density and correlates of the status of the samango monkey *Cercopithecus mitis* in Natal, South Africa. *Biological Conservation.* 60:197-210.

Leclerc, M.C., Hugot, J.P., Durand, P. and Renaud, F. 2004. Evolutionary relationships between 15 Plasmodium species from New and Old World primates (including humans): An 18S rDNA cladistic analysis. *Parasitology.* 2004. 129(6): 677-684

Lehman, S.M. and Robertson, K.L. 1994. Preliminary survey of *Cacajao melanocephalus melanocephalus* in southern Venezuela. *International Journal of Primatology.* 15(6) : 927-934.

Leighton, M and Leighton, D.R. 1982. The relationship of size of feeding aggregates to size of food patch: Howler monkeys (*Alouatta palliata*) feeding in Trichilia cipo fruit trees on Barro Colorado island. *Biotropica.* 14(2):81-90.

Leonard, S. and Bennett, C. 1996. Associative behavior of *Cacajao calvus ucayalii* with other primate species in Amazonian Peru. *Primates.* 37(2):227-230.

Lesson, R. P. 1840. Species de Mammiferes Bimanes et Quadrimanes: Suivi d'un Memoire sur les Orycteropes. J. B. Balliére, Paris.

Lim, C.S., Tazi, L. and Ayala, F.J. 2005. *Plasmodium vivax*: recent world expansion and genetic identity to *Plasmodium simium. Proceedings Of The National Academy Of Sciences* Of The USA. 102(43):15523-15528.

Lima, D. 1991. Kin saints and the forest: the study of Amazonian caboclos in the middle Solimões region. Ph.D. Thesis, University of Cambridge.

Lopes, J.P., Albuquerque, H., Silva, Y. and Shrimpton, R. 1980. Aspectos nutritivos de algunos frutos da Amazonia. *Acta Amazonica.* 10:755-758.

Macdonald, D. W. (ed.). 2001. *The New Encyclopedia of Mammals.* Oxford University Press: Oxford, UK.

Magurran A. E. 1988 Ecological diversity and its measurement. Cambridge University Press: Cambridge, UK.

Makwana, S.C. 1978. Field ecology and behaviour of the rhesus macaque (*Macaca mulatta*): I. Group composition, home range, roosting sites, and foraging routes in the Asarori forest. *Primates* 19:483-492.

Marengo, J. A. 1998. Climatología de la zona de Iquitos. In: Geoecología y desarrollo Amazónico: Estudio integrado en la zona de Iquitos, Perú. eds. R. Kalliola and S. Flores-Paitán Turku, Finland: Annales Universitatis Turkuensis Ser A II 144.

Marengo 2006: Tropical South America East of the Andes, in State of the Climate in 2005. Shein, K.A., ed., *Bulletin of the American Meteorological Society.* 87: S56-S57.

Marsh, C.W. and Wilson, W.L. 1981. A survey of primates in peninsular Malaysian forest. Kuala Lumpur: Universiti Kebangsaan Malaysia; Cambridge: Cambridge University Press.

Marshall, A.J. 2006. Simian sources and sinks: Incorporating spatial information on habitat quality into conservation plans for endangered primates. [Abstract] *International Journal of Primatology.* 27(Suppl 1).

Martin, L.B., Olejniczak, A.J and Maas, M.C. 2003. Enamel thickness and microstructure in Pitheciin primates, with comments on dietary adaptations of the middle Miocene hominoid Kenyapithecus. *Journal of Human Evolution.* 45(5) : 351-367.

McFarland, M.J. 1986. Ecological determinants of fission-fusion sociality in *Ateles* and *Pan.* In: *Primate Ecology and Conservation*, vol. II. eds. J. Else and P. C. Lee, Cambridge: Cambridge University Press. pp. 181-190.

McFarland-Symington, M. 1988. Environmental determinants of population densities in *Ateles. Primate Conservation.* 9:74-79.

McFarland-Symington, M. 1990. Fission-fusion social organisation in *Ateles* and *Pan. International Journal of Primatology.* 11(1): 47-61

Meyer, D. and Penn, J. 2003. An overview of the Tamshiyacu-Tahuayo Communal Reserve. In: Peru: Yavari. Rapid Biological Inventories Report 11 eds. N.C, Pitman, D, Vriesendorp, Moskovits. Chicago, IL: The Field Museum

Mitani, J.C., Gros-Louis, J and Manson, J.H. 1996. Number of males in primate groups: Comparison tests of competing hypotheses. *American Journal Of Primatology.* 38(4):315-332.

Mittermeier, R.A. 1988. Primate diversity and the tropical forest. In: *Biodiversity.* E.O. Wilson, ed. Washington, D.C.: National Academy Press. pp 145-154.

Mittermeier, R.A and van Roosmalen, M.G.M. 1981. Preliminary observations on habitat utilization and diet in eight Surinam monkeys. *Folia Primatologica.* 36: 1-39.

Mittermeier, R.A., Myers, J.B., Thomsen, J.B., Fonseca, G.A.B., Olivieri, S. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology.* 12 : 516-520.

Mittermeier, R. A., Valladares-Pádua, C., Rylands, A.B., Eudey, A.A., Butynski, T.M., Ganzhorn, J.U., Kormos, R., Aguiar, J.M., Walker, S. 2005 Primates in Peril: The World's 25 Most Endangered Primates 2004–2006 Special Report IUCN/SSC Primate Specialist Group (PSG), International Primatological Society (IPS), Conservation International (CI).

Nakagawa, N., Iwamoto, T., Yokota, N., & Soumah, A.G. 1996. Inter-regional and inter-seasonal variations of food quality in Japanese macaques: constraints of digestive volume and feeding time. In: Evolution and ecology of macaque societies, eds. J.E. FA., & D.G. Lindburg pp. 207-234. New York, NY: Cambridge University Press.

Napier, J.R and Napier, P.H. 1985. *The Natural History of the Primates.* London: British Museum (Natural History). pp 200.

Newing, H and Bodmer, R. 2004. Collaborative wildlife management and adaptation to change: the Tamshiyacu-Tahuayo Communal Reserve, Peru. *Nomadic Peoples.* 7: 110-122.

Newman, G. 2006. Fish populations and diversity in oxbow lakes in the Peruvian Amazon. Unpublished BSc thesis DICE University of Kent at Canterbury, UK

Nishida, T. 1968. The social group of wild chimpanzees in the Mahali Mountains. *Primates.* 9 :167-224.

Nishimura, A. Reproductive behaviors of woolly monkeys, 1992. *Lagothrix lagotricha. Reichorui Kenkyu / Primate Res.* 8(2): 188.

Nishimura, A. Social interaction patterns of woolly monkeys (*Lagothrix lagotricha*): A comparison among the atelines. 1994. *Doshisha Daigaku Rikogaku Kenkyu Hokoku / Sci Engrg Rev Doshisha Univ..* 35(2) : 235-254.

Nixon, K. C. & Wheeler, Q. D. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6, 211-223.

Nogueira-Neto, P. 1992. Ecological stations: a saga of ecology and environmental policy. Empresa das Artes, Sao Paulo.

Norconk, M.A. 1996. Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. In: Adaptive Radiations of Neotropical Primates. eds. M.A. Norconk, A.L. Rosenberger and P.A. Garber, New York: Plenum Press. pp: 403-423 & 547-548.

Norconk, M.A., Conklin-Brittain, N.L. 2004. Variation on frugivory: The diet of Venezuelan white-faced sakis. *International Journal of Primatology* 25(1):1-26.

Norconk, M.A., Wertis, C and Kinzey W.G. 1997. Seed predation by monkeys and macaws in eastern Venezuela: Preliminary findings. *Primates*. 38(2): 177-184.

Norconk, M.A., B.W. Grafton & N.L. Conklin-Brittain. 1998. Seed dispersal by neotropical seed predators. *American Journal of Primatology*, 45:103-126.

Nummelin, M. and L. Borowiec. 1991. Cassidinae beetles in primary and managed forest in Kibale Forest, Western Uganda. *African Journal of Ecology*. 30 :10–17.

Oates, J.F. 1988. The distribution of *Cercopithecus* monkeys in West African forests. In: A primate radiation: Evolutionary biology of the African guenons. eds. A. Gautier-Hion, F. Bourliere, J.P. Gautier and J. Kingdon, Cambridge: Cambridge University Press. pp 79-103.

Oates JF. 1996. Habitat alteration, hunting. and the conservation of folivorous primates in African forests. *Australian Journal of Ecology*. 21(1) :1–9.

Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Dasilva, G.L. and Mole, S. 1990. Determinants of variation in tropical forest primate biomass: New evidence from west Africa. *Ecology*. 71 : 328-343.

Onern. 1976. Inventario, evaluación e integración de los recursos naturales de la Selva: Zona Iquitos, Nauta y Colonia Angamos. Lima: Oficina Nacional de Evaluación de Recursos Naturales.

Ortega, H., Hidalgo, M. and Bértiz, G. 2003. Fishes In: Peru: Yavari. Rapid Biological Inventories Report 11. eds. Pitman, N.C. Vriesendorp, D. Moskovits. Chicago, IL: The Field Museum.

Padoch, C. 1988. People of the Floodplain and forest. In: *People of the Tropical Forest*. eds. J.S. Denslow and C. Padoch, University of California Press: Berkeley. pp 127-141.

Padoch, C. and de Jong, W. 1987. Traditional agroforestry practices of native and ribereño farmers in the lowland Peruvian Amazon. In: Agroforestry: Realities, Possibilities and Potentials. ed. H.L. Gholz. Martinus Nijhoff/Dr W. Junk Publishers, Dordrecht.

Pascoe, J. 2002. Primate Diversity in the Yavari Valley, Amazonian Peru. Unpublished BSc thesis DICE University of Kent at Canterbury, UK.

Peetz, A. 2001. Ecology And Social Organization Of The Bearded Saki Chiropotes Satanas Chiropotes (Primates: Pitheciinae) in Venezuala. Bonn: Society of Tropical Ecology. 170.

Peres, C.A. 1988. Primate community structure in Brazilian Amazonia. *Primate Conservation*. 9 : 83-87.

Peres, C.A. 1990. Effects of hunting on western Amazonian primate communities. *Biological Conservation*. 54: 47-59.

Peres, C.A. 1991. Seed predation of Cariniana micrantha (Lecythidaceae) by brown capuchin monkeys in central Amazonia. *Biotropica*. 23(3): 262-270.

Peres, C.A. 1993 Notes on the ecology of buffy saki monkeys (*Pithecia albicans*, Gray 1860): A canopy seed-predator. *American Journal Of Primatology*. 31: 129-140.

Peres, C.A. 1994. Primate responses to phenological changes in an Amazonian terra firme forest. *Biotropica*. 26(1): 98-112.

Peres, C.A. 1996. Use of space, spatial group structure, and foraging groups size of gray woolly monkeys (*Lagothrix lagotricha cana*) at Urucu, Brazil: A review of the Atelinae. Adaptive Radiations Of Neotropical Primates. M.A. Norconk A.L. Rosenberger P.A. Garber, eds. New York: Plenum Press. pp: 467-488 & 550.

Peres, C.A. 1997. Primate community structure at twenty Amazonian flooded and unflooded forests. *Journal of Tropical Ecology*. 13: 381-405.

Peres, C.A. 2000. Identifying keystone plant-resources in tropical forests. *Journal of Tropical Ecology*. 16: 287-317.

Peres, C.A., J.L. Patton, and M.N.F. da Silva. 1996. Riverine barriers and gene flow in Amazonian saddle-back tamarins. *Folia Primatologica*. 67(3): 113-124.

Pérez, P., Bodmer, R. and Puertas, P. 2004. Anuros y Saurios del Interfluvio Yavarí-Tahuayo y su comparación con las Áreas Naturales Protegidas en la Región Loreto, Perú. Memoria VI Congreso sobre Manejo de Fauna Silvestre en la Amazonía y Latinoamérica.

PERU. 2001 Reglamento de la Ley Forestal y de Fauna Silvestre, DS No. 014.2001-AG. Delo 9 de abril.

Peters, C.M., Gentry, A.H., Mercelot, R.O. 1959. Valuation of an Amazon rainforest. *Nature*. 339 : 655-656.

Pinedo-Vasquez, M., Zarir, D., Jipp, P., Ctota-Irunea, J. 1990. Use-values of tree species in a commercial forest reserve in Northeast Peru. *Conservation Biology*. 4: 405-416.

Pires, J. M. and Prance, G. T. 1985. The vegetation types of the Brazilian Amazon. In: *Amazonia*. eds. G. T. Prance and T. E. Lovejoy, Pergamon Press: New York. pp. 109-145.

Pitman, N.C. Vriesendorp, D. Moskovits (eds.) 2003. Peru: Yavari. Rapid Biological Inventories Report 11. Chicago, IL: The Field Museum

Plumptre, A.J., and Johns. A. 2001. Changes in primate communities following logging disturbance. In: *The cutting edge: conserving wildlife in logged tropical forests.* eds. R. A. Fimbel, A. Grajal, and J.G. Robinson, New York: Columbia University Press. pp 71-92.

Plumptre, A.J. and Reynolds, V. 1994. The impact of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *Journal of Applied Ecology*. 31 : 631-641.

Podolsky, R.D. 1990. Effects of mixed-species association on resource use by *Saimiri sciureus* and *Cebus apella*. *American Journal of Primatology*. 21: 2. p147-158.

Prance, G. T. 1985. *Amazonia* G. T. Prance and T. E. Lovejoy, eds. Pergamon: Oxford. pp 146–165.

Puertas, P. and Bodmer, R.E. 1993. Conservation of a high diversity primate assemblage. *Biodiversity and Conservation*. 2 : 586-593.

Puertas, P., Bodmer, R., Escobedo, A., Ríos, C., Pérez, P. and Antúnez, M. 2006. Propuesta Técnica de la Wildlife Conservation Society (WCS) para la Concesión de Conservación de Lago Preto-Paredón, en el Río Yavarí, Nor-oriente del Perú. Unpublished Proposal.

Putz, F.E., L.K. Sirot, and M.A. Pinard. 2001. Tropical forest management and wildlife: silvicultural effects on forest structure, fruit production, and locomotion of non-volant arboreal animals. In: *The Cutting Edge: Conserving Wildlife in Managed Tropical Forests*. eds. R. Fimbel, A. Grajal, and J. Robinson, Columbia University Press: New York.

Raimondi, A. 1874-79. El Perú: Historia de la geografía del Perú. Lima: Imprenta del Estado.

Räsänen, M., Linna, A., Irion, G., Rebata, L. Vargas, R. & Wesselingh F. 1998: Geologia y geoformas del area de Iquitos, Peru. Geoecología y desarrollo de la zona de Iquitos, Perú. eds. R. Kalliola & R. Paredes, Annales Universitatis Turkuensis, Ser. A II: 60-136.

Recharte, M. and Bodmer, R. 2004. Recuperación del Lobo de río en el Yavarí Mirí: CITES Historia de Éxito. Memoria VI Congreso sobre Manejo de Fauna Silvestre en la Amazonía y Latinoamérica.

Robinson, J.G. 1988. Group size in wedge-capped capuchin monkeys, *Cebus olivaceous. Behavioral Ecology and Sociobiology.* 23 (3): 187-197.

Robinson, J.G. and Bodmer R.E. 1999. Towards wildlife management in tropical forests. *Journal of Wildlife Management.* 63:1-13.

Robinson, J.G. and Ramirez, C.J. 1982. Conservation biology of Neotropical primates. In: *Mammalian biology in South America.* M.A. Mares and H.H. Genoways, eds. Pittsburgh: University of Pittsburgh Press. pp 329-344.

Robinson, J. G., Redford, K. H., Bennett, E. L. 1999. Wildlife Harvest in Logged Tropical Forests. *Science.* 284(5414) : 595-7.

Robinson S. 1994. Habitat selection and foraging ecology of raptors in Amazonian Peru. *Biotropica* 26 :443–458.

Robinson J,G and Janson, C.H. 1987. Capuchins, squirrel monkeys and atelines: Sociological convergence with Old World primates. In: *Primate Societies.* eds. B.B. Smuts D.L. Cheney R.M. Seyfarth R.W. Wrangham T.T. Struhsaker, Chicago: University of Chicago Press. pp 69-82.

Rodríguez L.O., and Knell, G. 2003. Amphibians and Reptiles. In: Peru: Yavari. Rapid Biological Inventories Report 11. eds. Pitman, N.C. Vriesendorp, D. Moskovits Chicago, IL: The Field Museum.

Rodman, P.S. 1978. Diets, densities and distributions of Bornean primates. In: *The ecology of arboreal folivores,* ed. G. Montgomery, 465-478. Washington, D.C.: Smithsonian Institution Press.

Roonwal, M. L. and Mohnot. S. M. 1977. *Primates of South Asia: Ecology, Sociobiology, and Behavior.* Cambridge, Massachusetts. USA : Harvard University Press.

Rosenzweig M,L. 1995. *Species Diversity in Space and Time.* Cambridge: Cambridge University Press.

Rowe, N. 1996. *The Pictorial Guide to the Living Primates.* East Hampton, New York: Pogonias Press. p 263.

Ruck, L. and Montreuil, V. 2004. Evaluación de paiche, *Arapaima gigas*, en Lago Preto - Paredón. Río Yavarí. Memoria VI Congreso sobre Manejo de Fauna Silvestre en la Amazonía y Latinoamérica.

Ruokolainen, K., and H. Tuomisto. 1998. Vegetación natural de la zona de Iquitos. In: Geoecología y desarrollo amazonico: Estudio integrado en la zona de Iquitos, Perú. Annales Universitatis Turkuensis Ser A II eds. R. Kalliola and S. Flores Paitán, 114. pp 253-344.

Rylands, A.B., Bampi, M.I., Chiarello, A.G., da Fonseca, G.A.B., Mendes, S.L., Marcelino, M. & Heymann, E.W. 2003a. *Ateles chamek.* In: IUCN 2006. 2006 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 07 October 2006.

Rylands, A.B., Bampi, M.I., Chiarello, A.G., da Fonseca, G.A.B., Mendes, S.L. & Marcelino, M. 2003b. *Cacajao calvus.* In: IUCN 2006. 2006 IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 07 October 2006.

Salovaara, K., Bodmer, R.E., Recharte, M. Reyes, F. 2003. Diversity and Abundance of Mammals. In: Peru: Yavari. Rapid Biological Inventories Report 11 eds. Pitman, N.C. Vriesendorp, D. Moskovits. Chicago, IL: The Field Museum.

Salovaara, K.J., Cárdenas, G.G. and Tuomisto, H. 2004. Forest classification in an Amazonian rainforest landscape using pteridophytes as indicator species. *Ecography* 27 (6) : 689-700.

Salovaaraa, K.J., Thesslerb, S., Malikc, R.N and Tuomistoa, H. 2005. Classification of Amazonian primary rain forest vegetation using Landsat ETM+ satellite imagery. *Remote Sensing of Environment* 97: 39-51

Sanchez, F.A. et al. 1999, Boletín No. 132, Serie A: Carta Geológica Nacional. Lima: Instituto Geologico, Minero y Metalúrgico.

Schneider H and Rosenberger A,L 1996. Molecules, morphology, and platyrrhine systematics. In: *Adaptive Radiations of Neotropical Primates*. eds. M.A. Norconk, A.L. Rosenberger, P.A. Garber, New York: Plenum Press. pp: 3-19 & 533.

Schneider, H., Sampaio, I., Harada, M.L., Barroso, C. M. L., Schneider, M. P. C., Czelusniak, J and Goodman, M. 1996. Molecular phylogeny of the New World Monkeys (Platyrrhini, Primates) based on two unlinked nuclear genes: IRBP intron 1 and epsilon-globin sequences. *American Journal of Physical Anthropology* 100:153-179.

Setz, E. 1994. Feeding ecology of golden-faced sakis. *Neotropical Primates*. 2 : 13-14.

Setz, E.Z ., Pinto, L.P., Bowler, M., Vie J and Barnett A. 2006. Pitheciines: comparing use of time and space. [Abstract] *International Journal of Primatology*. 27(Suppl 1). Pgs: Abst #515.

Silvus, K.M. and Fragoso, J.M.V. 2003 Red-rumped Agouti (*Dasyprocta leporina*) Home range use in an Amazonian forest: Implications for the aggregated distribution of forest trees. *Biotropica* 35(1): 74-83.

Smith, N.J.H., Alvim, P. de, Adilson, E., Serrão, S. and Falesi, I.C. 1995. Amazonia. In: Regions at risk: comparisons of threatened environments. eds. J X. Kasperson, R.E. Kasperson, and B. L. Turner. United Nations University Press: Paris.

Soini, P. 1986. A synecological study of the primate community in the Pacaya-Samiria National Reserve, Peru. *Primate Conservation* (7) :63-71.

Sousa e Silva Jr., J. de, and Martins, E. de S. 1999. On a new white bald uakari population in Southwestern Brazilian Amazonia. *Neotropical Primates*. 7 (4) : 119–121.

Spix, J.B.von. 1823. Simiarum et Vespertilionum Brasiliensium Species Novae: ou histoire naturelle des espèces nouvelles des singes et de chauve-souris observées et recueillies pendant le voyage dans l'intérieur du Brésil. F. S. Hübschmann, Monaco.

Stammbach, E. 1987. Desert, forest and montane baboons: Multilevel-societies. In: *Primate Societies*. eds. B.B, Smuts, D.L, Cheney, R.M, Seyfarth, R.W, Wrangham R. and Struhsaker, T.T. Chicago. University of Chicago Press. pp: 112-120.

Steenbeek, R., Sterck, E.H.M., de Vries, H. and van Hooff J.A.R.A.M. 2000. Costs and benefits of the one-male, age-graded, and all-male phases in wild Thomas's langur groups. Primate Males: Causes And Consequences Of Variation In Group Composition. P.M Kappeler, eds. Cambridge: Cambridge University Press: pp: 130-145.

Stevenson P,R. 2001. The relationship between fruit production and primate abundance in neotropical communities. *Biological Journal of the Linnean Society*. 72(1):161–178.

Stevenson, P.R., Quinones, M.J., Ahumada, J.A. 1998. Annual variation of fruiting patterns using two different methods in a lowland tropical forest at Tinigua National Park, Colombia. *Biotropica*. 30: 129-134.

Stevenson, P.R., Quiñones, M.J., Ahumada, J.A. 2000. Influence of Fruit Availability on Ecological Overlap among Four Neotropical Primates at Tinigua National Park, Colombia. *Biotropica*. 32:3 533-544.

Stickel, L.F. 1954. A comparison of certain methods of measuring home range of small mammals. *Journal of Mammology*. 35: 1-15.

Strier, K.B. 1989. Effects of patch size on feeding associations in muriquis (*Brachyteles arachnoids*). *American Journal of Primatology*. 23:113-126.

Strier, K.B., Dib, L.T and Figueira, J.E.C. 2002. Social dynamics of male muriquis (*Brachyteles arachnoides hypoxanthus*). *Behaviour*. 139(2-3): 315-342.

Sumner, P. and Mollon, J.D. 2003. Colors of primate pelage and skin: Objective assessment of conspicuousness. *American Journal of Primatology.* 59(2): 67-91.

Swan, N. 2006. Population status and ecology in three caiman species in Lago Preto, Peru. Unpublished BSc thesis: DICE University of Kent at Canterbury, UK

Swanson Ward, N. and Chism, J. 2003. A report on a new geographic location of red uakaris (*Cacajao calvus ucayalii*) on the Quebrada Tahuaillo in Northeastern Peru. *Neotropical Primates.* 11(1): 19-22.

Symington, M.M. 1988. Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). *Behaviour.* 105 (1-2) :117-134.

Symington, M.M. 1990. Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology.* 11(1) :47-61.

Terborgh, J. 1983. *Five New World primates: A study in comparative ecology.* Princeton: Princeton University Press. pp: xiv, 260

Terborgh, J. 1986. Keystone plant-resources in the tropical forest. In: *Conservation biology: The science of scarcity and diversity.* ed. M.E. Soule, Sinauer Associates: Massachusetts. pp 330-344.

ter Steege, H., Sabatier, D., Castellanos, H., van Andel, T., Duivenvoorden, J., Adalardo de Oliveira, Ek, A., Lilwah, R., Maas, P. and Mori, S. 2000. An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *Journal of Tropical Ecology.* 16: 801–828.

ter Steege, H., Pitman, N., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.F. Pre´vost, M.F., Spichiger, R., Castellanos, H. von Hildebrand, P. and Va´squez, R. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature.* Vol 443:28.

The Nature Conservancy. 2006. New protected area furthers conservation of 4 million acres of the Amazon rainforest between Peru and Brazil http:// www.nature.org/success/art17761.html

Thomas, O. 1928. The Goodman-Thomas Expedition to Peru. VII. The mammals of the Rio Ucayali. *Annals and Magazine of Natural History.* 2: 249-265.

Thomas, S.C. 1991. Population densities and Patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. *Biotropica.* 23 :68-83.

Thorén, S., Lindenfors, P and Kappeler, P.M. 2006. Phylogenetic analyses of dimorphism in primates: evidence for stronger selection on canine size than on body size. *American Journal of Physical Anthropology.* 130(1): 50-59.

Tutin, C.E.G., Ham, R.M., White, L.J.T and Harrison, M.J.S. 1997. The primate community of the Lope Reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology.* 42(1): 1-24.

Uhl, N.W. and Dransfield, J. 1987. *Genera Palmarum: A classification of palms based on the works of Harold E. Moore, Jr. Lawrence.* Kansus: Allen Press, Inc.

Valqui, M. 2001. Mammal diversity and ecology of small mammals in Western Amazonia. Ph.D. dissertation, University of Florida, USA.

van Roosmalen M.G.M., Mittermeier, R.A., Fleagle, J.G. 1988. Diet of the northern bearded saki (*Chiropotes santanas chiropotes*): A neotropical seed predator. *American Journal of Primatology.* 14(1) : 11-35.

van Roosmalen M.G.M., Mittermeier, R.A., Milton, K. 1981. The bearded sakis, genus *Chiropotes*. In: *Ecology and Behaviour of Neotropical Primates.* eds. Coimbra-Filho, A.F., Mittermeier, R.A. Rio de Janeiro: Academia Brasileira de Ciencias. 1: 419-441.

van Roosmalen, M.G.M. 1984. Subcatorgorizing food in primates. In: *Food Acquisition and processing in primates.* eds. D. J. Chivers B. A. Wood A. Bilsborough, New York: Plenum Press. pp: 167-175.

van Schaik, C.P. 2000. Social counterstrategies against infanticide by males in primates and other mammals. In: *Primate Males: Causes and Consequences*

Of Variation In Group Composition. ed. P.M Kappeler, Cambridge: Cambridge University Press. pp 34-54.

Vásquez-Martínez, R., and O. L. Phillips. 2000. Allpahuayo: Floristics, Structure, and Dynamics of a High-Diversity Forest in Amazonian Peru. *Annals of the Missouri Botanical Garden.* 87(4): pp 499-527.

Veiga, L.M. 2004. Pitheciines at the behaviour-conservation interface: Using behavioural knowledge in the conservation of the southern bearded saki (*Chiropotes satanas*), In Anais do XXII Encontro Anual de Etologia, Campo Grande, Brazil. Pgs CD:ROM.

Veiga, L.M. & S.S.B Silva. 2005. Relatives or just good friends? Affiliative relationships among male southern bearded sakis (*Chiropotes satanas*), Livro de Resumos, XI Congresso Brasileiro de Primatologia, Porto Alegre. p 174.

Veiga L.M., Bowler, M., Cunningham, E., Di Fiore, A. and Fernandez-Duque, E. 2006. Variability in Pitheciine social organization. [Abstract] *International Journal of Primatology.* 27(Suppl 1). Pgs: Abst #516.

von Spix, J. B., and von Martius, C.F.Ph. Reise in Brasilien. 2 Bde Munich: M. Lindauer: 1823-31.

Waitt, C., Little, A.C., Wolfensohn, S., Honess, P., Brown, A.P., Buchanan-Smith, H.M. and Perrett, D.I. 2003. Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. *Proceedings of the Royal Society of London.* B270(Suppl 2). pp S144-S146.

Walker, S.E. and Ayres, J.M. 1996. Positional behavior of the white uakari (*Cacajao calvus calvus*). *American Journal of Physical Anthropology.* 101(1): 161-172.

Wallace, A.R. 1852. *Proceedings of the Royal Society of London.* 20: 107-110.

Wallace, A.R. 1876. *The Geographical Distribution of Animals.* MacMillan. London.

Wallace, S. 2003. Into the Amazon. *National Geographic Magazine.* August 2003. The National Geographic Society.

Ward, N. S. and J, Chism. 2003. A report on a new geographic location of red uakaris (*Cacajao calvus ucayali*) on the Quebrada Tahuaillo in northeastern Peru. Neotropical Primates 11(1):19-22.

Wrangham, R.W. 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes.* ed. T.H Clutton-Brock, New York: Academic Press. pp 503-538.

Zinner, D., Knogge, C., Heymann, E., Kappeler, P.M. 2001 Large Primate aggregations: Limits to Female – Female Networks? *Primate Report.* (Special issue 60-1): 47-48.

Appendix 1 Complete list of species on the tree transects at Lago Preto with frequencies for each of the four habitats.

Family	Species	*Terra firme*		*Várzea*		Upland *aguajal*		Floodplain *aguajal*		**Total**	
		Freq.	%	Freq.	%	Freq.	%	Freq.	%	**Freq.**	**%**
ANACARDIACEAE	*Tapirira* cf. *guianensis*	5	0.90							**5**	**0.34**
ANACARDIACEAE	*Tapirira* sp. *(a)*			8	1.52			1	0.35	**9**	**0.61**
ANACARDIACEAE	Unidentified Anacardiaceae	1	0.18							**1**	**0.07**
ANNONACEAE	*Anonna iquitensis*			7	1.33					**7**	**0.48**
ANNONACEAE	*Bocageopsis mattogrossensis*							4	1.40	**4**	**0.27**
ANNONACEAE	*Bocageopsis* sp. *(a)*			1	0.19			1	0.35	**2**	**0.14**
ANNONACEAE	*Crematospema* sp. *(a)*			3	0.57					**3**	**0.20**
ANNONACEAE	*Cymbopetalum* sp. *(a)*							1	0.35	**1**	**0.07**
ANNONACEAE	*Diclinanona tessmannii*	4	0.72							**4**	**0.27**
ANNONACEAE	*Duguetia quitarensis*			5	0.95					**5**	**0.34**
ANNONACEAE	*Duguetia spixiana*			2	0.38					**2**	**0.14**
ANNONACEAE	*Duguetia* sp. *(a)*			2	0.38					**2**	**0.14**
ANNONACEAE	*Guatteria decurrens*			2	0.38					**2**	**0.14**
ANNONACEAE	*Guatteria* cf. *elata*			2	0.38					**2**	**0.14**
ANNONACEAE	*Guatteria megalophylla*			1	0.19					**1**	**0.07**
ANNONACEAE	*Guatteria* cf. *olivacea*	1	0.18	4	0.76			4	1.40	**9**	**0.61**
ANNONACEAE	*Guatteria* sp. *(a)*	1	0.18							**1**	**0.07**
ANNONACEAE	*Guatteria* sp. *(b)*	1	0.18							**1**	**0.07**
ANNONACEAE	*Malmea diclina*			4	0.76			6	2.10	**10**	**0.68**
ANNONACEAE	*Oxandra espintana*			4	0.76					**4**	**0.27**
ANNONACEAE	*Oxandra xylopioides*	1	0.18							**1**	**0.07**
ANNONACEAE	*Pseudoxandra polypheba*			13	2.46			2	0.70	**15**	**1.02**
ANNONACEAE	*Rollinia edulis*	1	0.18							**1**	**0.07**
ANNONACEAE	*Tetrameranthus* cf. *laomae*	1	0.18							**1**	**0.07**
ANNONACEAE	*Xylopia excellens*	3	0.54			1	1.09			**4**	**0.27**
ANNONACEAE	Unidentified Annonaceae (1 or 2 spp.)	2	0.36							**2**	**0.14**
ANISOPHYLLEACEAE	*Anysophyllea guianensis*	2	0.36							**2**	**0.14**
APOCYNACEAE	*Aspidosperma desmanthum*	1	0.18							**1**	**0.07**
APOCYNACEAE	*Aspidosperma excelsum*			10	1.89			3	1.05	**13**	**0.89**
APOCYNACEAE	*Aspidosperma* sp. *(a)*	1	0.18							**1**	**0.07**
APOCYNACEAE	*Couma macrocarpa*	2	0.36							**2**	**0.14**
APOCYNACEAE	*Malouetia tamaquarina* or *M. peruviana*			6	1.14			4	1.40	**10**	**0.68**
APOCYNACEAE	*Paranchornia peruviana*	2	0.36			2	2.17			**4**	**0.27**
APOCYNACEAE	*Rhigospira quadrangularis*	2	0.36							**2**	**0.14**
AQUIFOLIACEAE	*Ilex* sp. *(a)*	1	0.18							**1**	**0.07**
AQUIFOLIACEAE	*Ilex* (unidentified spp.)	2	0.36							**2**	**0.14**
ARALIACEAE	*Dendropanax macropodus*	1	0.18							**1**	**0.07**
ARECACEAE	*Astrocaryum chambira*	4	0.72							**4**	**0.27**
ARECACEAE	*Astrocaryum* cf. *juruana*			1	0.19			1	0.35	**2**	**0.14**
ARECACEAE	*Euterpe precatoria*	3	0.54	1	0.19	10	10.87	66	23.08	**80**	**5.46**
ARECACEAE	*Mauritia flexuosa*					15	16.30	23	8.04	**38**	**2.60**
ARECACEAE	*Oenocarpus bataua*	11	1.97			4	4.35			**15**	**1.02**
ARECACEAE	*Socratea exorrhiza*	1	0.18							**1**	**0.07**
BOMBACACEAE	*Eriotheca macrophylla*					2	2.17			**2**	**0.14**
BOMBACACEAE	*Matisia* cf. *malacocalyx*	5	0.90							**5**	**0.34**
BOMBACACEAE	*Pachira* cf. *acuatica*			2	0.38					**2**	**0.14**
BOMBACACEAE	*Pachira insignis*			1	0.19			3	1.05	**4**	**0.27**
BORAGINACEAE	*Cordia nodosa*			2	0.38					**2**	**0.14**
BORAGINACEAE	*Cordia ucayalensis*	1	0.18							**1**	**0.07**
BURSERACEAE	*Crepidospermum prancei*	4	0.72							**4**	**0.27**
BURSERACEAE	*Protium apiculatum*	3	0.54							**3**	**0.20**
BURSERACEAE	*Protium* cf. *carnosum*	1	0.18							**1**	**0.07**
BURSERACEAE	*Protium crassipetalum*	2	0.36							**2**	**0.14**
BURSERACEAE	*Protium gallosum*	3	0.54							**3**	**0.20**
BURSERACEAE	*Protium grandifolium*	2	0.36							**2**	**0.14**
BURSERACEAE	*Protium* sp. *(a)*	1	0.18							**1**	**0.07**
BURSERACEAE	*Protium* sp. *(b)*			1	0.19					**1**	**0.07**
BURSERACEAE	*Protium* (unidentified spp.)	2	0.36							**2**	**0.14**
CARYOCARACEAE	*Caryocar glabrum*	1	0.18							**1**	**0.07**
CECROPIACEAE	*Cecropia distachya*	1	0.18							**1**	**0.07**
CECROPIACEAE	*Cecropia latiloba*			2	0.38					**2**	**0.14**
CECROPIACEAE	*Cecropia* sp. *(a)*							2	0.70	**2**	**0.14**
CECROPIACEAE	*Cecropia* (unidentified sp.)	1	0.18							**1**	**0.07**
CECROPIACEAE	*Coussapoa nitida*			4	0.76					**4**	**0.27**
CECROPIACEAE	*Pourouma bicolor*	2	0.36							**2**	**0.14**
CECROPIACEAE	*Pourouma cecropiifolia*	2	0.36							**2**	**0.14**
CECROPIACEAE	*Pourouma* cf. *cucura*	1	0.18							**1**	**0.07**
CECROPIACEAE	*Pourouma mollis*			1	0.19					**1**	**0.07**
CECROPIACEAE	*Pourouma ovata*	9	1.61							**9**	**0.61**
CECROPIACEAE	*Pourouma* sp. *(a)*	1	0.18							**1**	**0.07**
CECROPIACEAE	*Pourouma* sp. *(b)*			2	0.38					**2**	**0.14**

CECROPIACEAE	*Pourouma (unidentified* spp.)	3	0.54							**3**	**0.20**
CELASTRACEAE	*Maytenus* sp. *(a)*			1	0.19					**1**	**0.07**
CHRYSOBALANACEAE	*Couepia* cf. *bractiosa*	1	0.18							**1**	**0.07**
CHRYSOBALANACEAE	*Couepia* cf. *obovata*	1	0.18							**1**	**0.07**
CHRYSOBALANACEAE	*Couepia paraensis*		0	4	0.76					**4**	**0.27**
CHRYSOBALANACEAE	*Couepia parillo*	2	0.36							**2**	**0.14**
CHRYSOBALANACEAE	*Hirtella elongata*			3	0.57					**3**	**0.20**
CHRYSOBALANACEAE	*Hirtella* sp. *(a)*			4	0.76					**4**	**0.27**
CHRYSOBALANACEAE	*Licania britteniana*	1	0.18							**1**	**0.07**
CHRYSOBALANACEAE	*Licania egleri*	3	0.54							**3**	**0.20**
CHRYSOBALANACEAE	*Licania heteromorpha*	26	4.66							**26**	**1.78**
CHRYSOBALANACEAE	*Licania latifolia*	2	0.36							**2**	**0.14**
CHRYSOBALANACEAE	*Licania licaniiflora*			11	2.08					**11**	**0.75**
CHRYSOBALANACEAE	*Licania longistyla*			2	0.38					**2**	**0.14**
CHRYSOBALANACEAE	*Licania oblongifolia*	3	0.54							**3**	**0.20**
CHRYSOBALANACEAE	*Licania octandra*			2	0.38					**2**	**0.14**
CHRYSOBALANACEAE	*Licania* sp. *(a)*			10	1.89					**10**	**0.68**
CHRYSOBALANACEAE	*Licania* sp. *(b)*	1	0.18							**1**	**0.07**
CHRYSOBALANACEAE	*Parinari* cf. *parilis*			1	0.19					**1**	**0.07**
CHRYSOBALANACEAE	Unidentified Chrysobalanaceae (up to 5 spp.)	5	0.90							**5**	**0.34**
CLUSIACEAE	*Calophyllum brasiliense*			3	0.57			7	2.45	**10**	**0.68**
CLUSIACEAE	*Caraipa densifolia*			11	2.08	1	1.09			**12**	**0.82**
CLUSIACEAE	*Caraipa grandifolia*					17	18.48			**17**	**1.16**
CLUSIACEAE	*Caraipa* sp. *(a)*	3	0.54							**3**	**0.20**
CLUSIACEAE	*Garcinia* cf. *madruno*			2	0.38					**2**	**0.14**
CLUSIACEAE	*Symphonia globulifera*							13	4.55	**13**	**0.89**
CLUSIACEAE	*Tovomita* cf. *spruceana*					1	1.09	3	1.05	**4**	**0.27**
CLUSIACEAE	*Tovomita* sp. *(a)*							2	0.70	**2**	**0.14**
CLUSIACEAE	*Tovomita* sp. *(b)*	1	0.18							**1**	**0.07**
CLUSIACEAE	*Tovomita* sp. *(c)*	2	0.36							**2**	**0.14**
CLUSIACEAE	*Tovomita* (unidentified sp.)	1	0.18							**1**	**0.07**
CLUSIACEAE	*Vismia angusta*			3	0.57			2	0.70	**5**	**0.34**
CLUSIACEAE	Unidentified Clusiaceae	1	0.18							**1**	**0.07**
COMBRETACEAE	*Buchenavia* cf. *seriocarpa*	3	0.54					5	1.75	**8**	**0.55**
COMBRETACEAE	*Buchenavia* sp. *(a)*	1	0.18							**1**	**0.07**
COMBRETACEAE	*Buchenavia* sp. *(b)*			1	0.19					**1**	**0.07**
COMBRETACEAE	*Buchenavia* (unidentified sp.)	1	0.18							**1**	**0.07**
COMBRETACEAE	*Terminalia dichotoma*							6	2.10	**6**	**0.41**
CONNARACEAE	*Connarus* sp. *(a)*			1	0.19					**1**	**0.07**
DICHAPETALACEAE	*Tapura acreana*			13	2.46			1	0.35	**14**	**0.96**
DICHAPETALACEAE	*Tapura coriaceae*	2	0.36							**2**	**0.14**
EBENACEAE	*Diospyros* cf. *subrotata*			1	0.19					**1**	**0.07**
EBENACEAE	*Diospyros poeppigiana*			1	0.19			1	0.35	**2**	**0.14**
ELAEOCARPACEAE	*Sloanea floribunda*	2	0.36							**2**	**0.14**
ELAEOCARPACEAE	*Sloanea* aff. *pubescens*	1	0.18							**1**	**0.07**
ELAEOCARPACEAE	*Sloanea* cf. *sinemariensis*	5	0.90					2	0.70	**7**	**0.48**
ELAEOCARPACEAE	*Sloanea tuerckheimii*	1	0.18	1	0.19			1	0.35	**3**	**0.20**
ELAEOCARPACEAE	*Sloanea MR1137*	1	0.18	2	0.38					**3**	**0.20**
ELAEOCARPACEAE	*Sloanea sp 2*			1	0.19					**1**	**0.07**
ELAEOCARPACEAE	*Sloanea 'RG1794'*	2	0.36							**2**	**0.14**
EUPHORBIACEAE	*Alchornea latifolia*			5	0.95			1	0.35	**6**	**0.41**
EUPHORBIACEAE	*Alchornea* cf. *triplinernia*	2	0.36							**2**	**0.14**
EUPHORBIACEAE	*Alchorneopsis floribunda*	2	0.36							**2**	**0.14**
EUPHORBIACEAE	*Amanoa guyanensis*			2	0.38					**2**	**0.14**
EUPHORBIACEAE	*Amanoa* sp. *(a)*					2	2.17			**2**	**0.14**
EUPHORBIACEAE	*Aparisthmium cordatum*	1	0.18							**1**	**0.07**
EUPHORBIACEAE	*Conceveiba rhytidocarpa*	3	0.54					1	0.35	**4**	**0.27**
EUPHORBIACEAE	*Croton* cf. *cuneatus*			1	0.19					**1**	**0.07**
EUPHORBIACEAE	*Dydimocistus chrysadenius*	4	0.72							**4**	**0.27**
EUPHORBIACEAE	*Glycidendron amazonicum*	1	0.18	2	0.38					**3**	**0.20**
EUPHORBIACEAE	*Hevea guianensis*	13	2.33	2	0.38	3	3.26	2	0.70	**20**	**1.37**
EUPHORBIACEAE	*Hyeronima oblonga*	7	1.25							**7**	**0.48**
EUPHORBIACEAE	*Mabea angularis*	1	0.18							**1**	**0.07**
EUPHORBIACEAE	*Mabea speciosa*	1	0.18							**1**	**0.07**
EUPHORBIACEAE	*Maprounea guianensis*	1	0.18							**1**	**0.07**
EUPHORBIACEAE	*Micranda siphonoides*			14	2.65			12	4.20	**26**	**1.78**
EUPHORBIACEAE	*Nealchorna yapurensis*	2	0.36							**2**	**0.14**
EUPHORBIACEAE	*Richeria* cf. *grandis*	1	0.18	1	0.19					**2**	**0.14**
EUPHORBIACEAE	*Richeria* sp. *(a)*			1	0.19	1	1.09			**2**	**0.14**
EUPHORBIACEAE	Unidentified Euphorbiaceae (1 or 2 spp.)	1	0.18	5	0.95					**6**	**0.41**
FABACEAE	*Abarema* sp. *(a)*			3	0.57			1	0.35	**4**	**0.27**
FABACEAE	*Abarema* sp. *(b)*	1	0.18							**1**	**0.07**
FABACEAE	*Bauhinia brachycalyx*			4	0.76					**4**	**0.27**
FABACEAE	*Campsiandra angustifolia*			7	1.33			2	0.70	**9**	**0.61**
FABACEAE	*Crudia glaberrima*							5	1.75	**5**	**0.34**
FABACEAE	*Cynometra* cf. *spruceana*			4	0.76					**4**	**0.27**

FABACEAE	*Enterolobium barnebianum*	1	0.18							**1**	**0.07**
FABACEAE	*Inga brachyrhachis*							1	0.35	**1**	**0.07**
FABACEAE	*Inga* cf. *cinnamomea*			2	0.38					**2**	**0.14**
FABACEAE	*Inga gracilifolia*	1	0.18							**1**	**0.07**
FABACEAE	*Inga heterophylla* Wiild.	1	0.18							**1**	**0.07**
FABACEAE	*Inga marginata*	2	0.36	1	0.19			5	1.75	**8**	**0.55**
FABACEAE	*Inga* cf. *pruriens*	1	0.18							**1**	**0.07**
FABACEAE	*Inga thibaudina*	1	0.18							**1**	**0.07**
FABACEAE	*Inga* sp. *(a)*	1	0.18							**1**	**0.07**
FABACEAE	*Inga* sp. *(b)*	1	0.18							**1**	**0.07**
FABACEAE	*Inga* sp. *(c)*	2	0.36							**2**	**0.14**
FABACEAE	*Inga* sp. *(d)*							4	1.40	**4**	**0.27**
FABACEAE	*Inga* sp. *(e)*			3	0.57					**3**	**0.20**
FABACEAE	*Inga* sp. *(f)*			1	0.19					**1**	**0.07**
FABACEAE	*Inga* sp. *(g)*	1	0.18							**1**	**0.07**
FABACEAE	*Inga* sp. *(h)*					2	2.17			**2**	**0.14**
FABACEAE	*Inga* (unidentified sp.)	2	0.36							**2**	**0.14**
FABACEAE	*Macrolobium angustifolium*	2	0.36	9	1.70			9	3.15	**20**	**1.37**
FABACEAE	*Macrolobium* cf. *limbatum*	1	0.18			5	5.43			**6**	**0.41**
FABACEAE	*Macrolobium multijugum*							2	0.70	**2**	**0.14**
FABACEAE	*Marmaroxylon basijugum*	8	1.43							**8**	**0.55**
FABACEAE	*Parkia igneiflora*	1	0.18							**1**	**0.07**
FABACEAE	*Parkia nitida*	1	0.18							**1**	**0.07**
FABACEAE	*Parkia panurensis*	4	0.72			1	1.09			**5**	**0.34**
FABACEAE	*Pterocarpus amazonum*			5	0.95			3	1.05	**8**	**0.55**
FABACEAE	*Swartzia cardiosperma*	1	0.18							**1**	**0.07**
FABACEAE	*Swartzia pendula*					1	1.09	1	0.35	**2**	**0.14**
FABACEAE	*Swartzia schunkei*							1	0.35	**1**	**0.07**
FABACEAE	*Swartzia* sp. *(a)*	1	0.18							**1**	**0.07**
FABACEAE	*Swartzia* sp. *(b)*	1	0.18							**1**	**0.07**
FABACEAE	*Tachigali macbridei*	7	1.25							**7**	**0.48**
FABACEAE	*Tachigali tessmannii*			3	0.57			1	0.35	**4**	**0.27**
FABACEAE	*Tachigali* sp. *(a)*			1	0.19					**1**	**0.07**
FABACEAE	*Tachigali* sp. *(b)*	1	0.18							**1**	**0.07**
FABACEAE	*Tachigali* sp. *(c)*	2	0.36							**2**	**0.14**
FABACEAE	*Taralea oppositifolia*							2	0.70	**2**	**0.14**
FABACEAE	*Vatairea guianensis*			2	0.38			11	3.85	**13**	**0.89**
FABACEAE	*Zygia longifolia*	1	0.18	3	0.57			4	1.40	**8**	**0.55**
FABACEAE	*Zygia* sp. *(a)*	3	0.54							**3**	**0.20**
FABACEAE	*Zygia* sp. *(b)*			6	1.14					**6**	**0.41**
FABACEAE	Unidentified Fabaceae (3 spp.)	4	0.72							**4**	**0.27**
FLACOURTIACEAE	*Casearia* cf. *arborea*	2	0.36							**2**	**0.14**
FLACOURTIACEAE	*Casearia* sp. *(a)*							1	0.35	**1**	**0.07**
FLACOURTIACEAE	Unidentified Flacourtiaceae			3	0.57					**3**	**0.20**
HUMIRIACEAE	*Saccoglottis ceratocarpa*	1	0.18							**1**	**0.07**
HUMIRIACEAE	*Saccoglottis* cf. *guianensis*	1	0.18							**1**	**0.07**
HUMIRIACEAE	*Saccoglottis* sp. *(a)*	1	0.18							**1**	**0.07**
HUMIRIACEAE	*Saccoglottis* (unidentified sp.)	1	0.18							**1**	**0.07**
ICACINACEAE	*Dendrobangia* cf. *boliviana*	1	0.18							**1**	**0.07**
ICACINACEAE	*Dendrobangia multinervia*	3	0.54							**3**	**0.20**
LACISTEMATACEAE	*Lacistema aggregatum*			4	0.76					**4**	**0.27**
LACISTEMATACEAE	*Lacistema* cf. *nena*	1	0.18	2	0.38					**3**	**0.20**
LAURACEAE	*Aniba* cf. *hotsmaniana*			1	0.19					**1**	**0.07**
LAURACEAE	*Aniba* sp. *(a)*	2	0.36							**2**	**0.14**
LAURACEAE	*Aniba* sp. *(b)*			1	0.19					**1**	**0.07**
LAURACEAE	*Endlicheria* sp. *(a)*			1	0.19					**1**	**0.07**
LAURACEAE	*Mezilaurus* sp. *(a)*	1	0.18							**1**	**0.07**
LAURACEAE	*Ocotea argyrophylla*	1	0.18							**1**	**0.07**
LAURACEAE	*Ocotea* cf. *marmellensis*	1	0.18							**1**	**0.07**
LAURACEAE	*Ocotea oblonga*	1	0.18							**1**	**0.07**
LAURACEAE	*Ocotea* sp. *(a)*	1	0.18							**1**	**0.07**
LAURACEAE	*Ocotea* sp. *(b)*			2	0.38					**2**	**0.14**
LAURACEAE	*Ocotea* sp. *(c)*			1	0.19					**1**	**0.07**
LAURACEAE	Unidentified Lauraceae (1 or 2 spp.)	2	0.36							**2**	**0.14**
LECYTHIDACEAE	*Allantoma lineata*	1	0.18							**1**	**0.07**
LECYTHIDACEAE	*Couratari oligantha*			7	1.33			8	2.80	**15**	**1.02**
LECYTHIDACEAE	*Eschweilera albiflora*			34	6.44					**34**	**2.32**
LECYTHIDACEAE	*Eschweilera* cf. *parvifolia*			11	2.08					**11**	**0.75**
LECYTHIDACEAE	*Eschweilera coriacea*	34	6.09							**34**	**2.32**
LECYTHIDACEAE	*Eschweilera tessmanni*	16	2.87							**16**	**1.09**
LECYTHIDACEAE	*Eschweilera* sp. *(a)*	1	0.18							**1**	**0.07**
LECYTHIDACEAE	*Eschweilera* sp. *(b)*	1	0.18							**1**	**0.07**
LECYTHIDACEAE	*Eschweilera* sp. *(c)*	1	0.18							**1**	**0.07**
LECYTHIDACEAE	*Eschweilera* sp. *(d)*	1	0.18	2	0.38					**3**	**0.20**
LECYTHIDACEAE	*Eschweilera (unidentified* sp.*)*	1	0.18							**1**	**0.07**
LECYTHIDACEAE	*Gustavia augusta*			3	0.57			1	0.35	**4**	**0.27**

LECYTHIDACEAE	*Gustavia longifolia*			1	0.19					**1**	**0.07**
LECYTHIDACEAE	*Lecythis* sp. *(a)*	1	0.18							**1**	**0.07**
LEPIDOBOTRIACEAE	*Ruptiliocarpon caracolito*	1	0.18							**1**	**0.07**
LINACEAE	*Hebepetalum humirifolium*	1	0.18							**1**	**0.07**
MALPIGHIACEAE	*Byrsonima arthropoda*			2	0.38					**2**	**0.14**
MALPIGHIACEAE	*Byrsonima* sp. *(a)*			1	0.19					**1**	**0.07**
MELASTOMATACEAE	*Miconia amnicola*			1	0.19					**1**	**0.07**
MELASTOMATACEAE	*Miconia* cf. *klugii*	2	0.36							**2**	**0.14**
MELASTOMATACEAE	*Miconia* sp. *(a)*			1	0.19					**1**	**0.07**
MELASTOMATACEAE	*Miconia* sp. *(b)*			1	0.19					**1**	**0.07**
MELASTOMATACEAE	*Miconia* sp. *(c)*			1	0.19					**1**	**0.07**
MELASTOMATACEAE	*Miconia* sp. *(d)*	1	0.18							**1**	**0.07**
MELASTOMATACEAE	*Miconia* (unidentified spp.)	2	0.36							**2**	**0.14**
MELIACEAE	*Carapa* cf. *guianensis*	1	0.18							**1**	**0.07**
MELIACEAE	*Guarea macrophylla*	4	0.72	1	0.19					**5**	**0.34**
MELIACEAE	*Trichilia septentrionalis*	6	1.08							**6**	**0.41**
MELIACEAE	*Trichilia* sp. *(a)*	3	0.54							**3**	**0.20**
MELIACEAE	*Trichilia* (unidentified sp.)	2	0.36							**2**	**0.14**
MEMECYLACEAE	*Mouriri* cf. *acutifolia*			2	0.38					**2**	**0.14**
MEMECYLACEAE	*Mouriri* cf. *vernicosa*	3	0.54	2	0.38					**5**	**0.34**
MORACEAE	*Brosimum guianense*	1	0.18	6	1.14					**7**	**0.48**
MORACEAE	*Brosimum lactescens*	1	0.18	9	1.70					**10**	**0.68**
MORACEAE	*Ficus* cf. *guianensis*			2	0.38			1	0.35	**3**	**0.20**
MORACEAE	*Ficus* cf. *mathewsii*			1	0.19					**1**	**0.07**
MORACEAE	*Ficus pertusa*							1	0.35	**1**	**0.07**
MORACEAE	*Ficus* sp. *(a)*							1	0.35	**1**	**0.07**
MORACEAE	*Helicostylis elegans*	1	0.18							**1**	**0.07**
MORACEAE	*Helicostylis tomentosa*	7	1.25							**7**	**0.48**
MORACEAE	*Naucleopsis concinna*	1	0.18							**1**	**0.07**
MORACEAE	*Naucleopsis oblongifolia*	1	0.18							**1**	**0.07**
MORACEAE	*Naucleopsis* cf. *ternstroemiiflora*	2	0.36							**2**	**0.14**
MORACEAE	*Naucleopsis ulei* ssp. *amara*	7	1.25							**7**	**0.48**
MORACEAE	*Perebea tessmannii*	1	0.18							**1**	**0.07**
MORACEAE	*Pseudolmedia laevigata*	3	0.54	12	2.27					**15**	**1.02**
MORACEAE	*Trymatococcus amazonicus*	5	0.90							**5**	**0.34**
MYRISTICACEAE	*Compsoneura capitellata*	3	0.54							**3**	**0.20**
MYRISTICACEAE	*Iryanthera elliptica*	5	0.90							**5**	**0.34**
MYRISTICACEAE	*Iryanthera juruensis*	3	0.54			1	1.09			**4**	**0.27**
MYRISTICACEAE	*Iryanthera lancifolia*	3	0.54			3	3.26			**6**	**0.41**
MYRISTICACEAE	*Iryanthera macrophylla*	2	0.36							**2**	**0.14**
MYRISTICACEAE	*Iryanthera paraensis*	1	0.18			1	1.09			**2**	**0.14**
MYRISTICACEAE	*Iryanthera polyneura*	1	0.18							**1**	**0.07**
MYRISTICACEAE	*Iryanthera tessmannii*			4	0.76					**4**	**0.27**
MYRISTICACEAE	*Iryanthera tricornis*	13	2.33							**13**	**0.89**
MYRISTICACEAE	*Osteophloeum platyspermum*	8	1.43							**8**	**0.55**
MYRISTICACEAE	*Virola caducifolia*	1	0.18							**1**	**0.07**
MYRISTICACEAE	*Virola calophylla*	9	1.61	12	2.27					**21**	**1.43**
MYRISTICACEAE	*Virola* cf. *elongata*	8	1.43	1	0.19					**9**	**0.61**
MYRISTICACEAE	*Virola mollissima*	1	0.18							**1**	**0.07**
MYRISTICACEAE	*Virola* cf. *multinervia*	1	0.18							**1**	**0.07**
MYRISTICACEAE	*Virola pavonis*	4	0.72							**4**	**0.27**
MYRISTICACEAE	*Virola* cf. *peruviana*			23	4.36			1	0.35	**24**	**1.64**
MYRISTICACEAE	*Virola sebifera*	9	1.61							**9**	**0.61**
MYRISTICACEAE	*Virola surinamensis*			6	1.14	6	6.52	26	9.09	**38**	**2.60**
MYRISTICACEAE	*Virola* sp. *(a)*	1	0.18							**1**	**0.07**
MYRISTICACEAE	*Virola* (unidentified sp.)	1	0.18							**1**	**0.07**
MYRTACEAE	*Calyptranthes* cf. *maxima*			1	0.19					**1**	**0.07**
MYRTACEAE	*Calyptranthes pulchella*			1	0.19					**1**	**0.07**
MYRTACEAE	*Calyptranthes* cf. *tessmannii*			2	0.38					**2**	**0.14**
MYRTACEAE	*Myrciaria floribunda*			2	0.38					**2**	**0.14**
MYRTACEAE	Unidentified Myrtaceae sp. (a)			10	1.89					**10**	**0.68**
MYRTACEAE	Unidentified Myrtaceae sp. (b)			6	1.14					**6**	**0.41**
MYRTACEAE	Unidentified Myrtaceae sp. (c)			1	0.19					**1**	**0.07**
MYRTACEAE	Unidentified Myrtaceae sp. (d)			1	0.19					**1**	**0.07**
MYRTACEAE	Unidentified Myrtaceae sp. (e)			1	0.19			1	0.35	**2**	**0.14**
MYRTACEAE	Unidentified Myrtaceae sp. (f)			1	0.19					**1**	**0.07**
MYRTACEAE	Unidentified Myrtaceae sp. (g)			1	0.19					**1**	**0.07**
MYRTACEAE	Unidentified Myrtaceae sp. (h)			1	0.19					**1**	**0.07**
MYRTACEAE	Unidentified Myrtaceae sp. (i)	1	0.18							**1**	**0.07**
MYRTACEAE	Unidentified Myrtaceae sp. (j)					1	1.09			**1**	**0.07**
MYRTACEAE	Unidentified Myrtaceae sp. (k)			1	0.19					**1**	**0.07**
MYRTACEAE	Unidentified Myrtaceae sp. (l)			1	0.19					**1**	**0.07**
MYRTACEAE	Unidentified Myrtaceae sp. (m)			3	0.57					**3**	**0.20**
MYRTACEAE	Unidentified Myrtaceae sp. (n)			1	0.19					**1**	**0.07**
NYCTAGINACEAE	*Neea* cf. *divaricata*	2	0.36	2	0.38					**4**	**0.27**
NYCTAGINACEAE	*Neea spruceana*	2	0.36							**2**	**0.14**

OCHNACEAE	*Cespedesia spathulata*	1	0.18			1	1.09			2	0.14
OCHNACEAE	*Ouartea* cf. *pendula*	2	0.36	1	0.19					3	0.20
OLACACEAE	*Aptandra tubicina*	1	0.18							1	0.07
OLACACEAE	*Heisteria duckei*	2	0.36							2	0.14
OLEACEAE	*Chionanthus* cf. *caribea*	1	0.18							1	0.07
POLYGONIACEAE	*Coccoloba densifrons*			2	0.38					2	0.14
POLYGONIACEAE	*Triplaris cumingiana*			2	0.38			1	0.35	3	0.20
RUBIACEAE	*Alibertia stenantha*	1	0.18							1	0.07
RUBIACEAE	*Alibertia* sp. *(a)*	1	0.18							1	0.07
RUBIACEAE	*Amaioua guianensis*	1	0.18							1	0.07
RUBIACEAE	*Duroia paraensis*			4	0.76					4	0.27
RUBIACEAE	*Ferdinandusa* cf. *clorantha*	1	0.18							1	0.07
RUBIACEAE	*Ladenbergia amazonensis* or *L. magnifolia*	5	0.90							5	0.34
RUBIACEAE	*Posoqueria latifolia*	1	0.18							1	0.07
RUBIACEAE	*Psichotrya* cf. *flaviflora*							1	0.35	1	0.07
RUBIACEAE	*Simira rubescens*			2	0.38					2	0.14
RUBIACEAE	*Tocoyena williansii*	1	0.18							1	0.07
SABIACEAE	*Ophiocaryon heterophyllum*	1	0.18							1	0.07
SAPINDACEAE	*Allophyllus* cf. *dodsonii*	1	0.18							1	0.07
SAPINDACEAE	*Matayba* sp. *(a)*			1	0.19					1	0.07
SAPINDACEAE	*Matayba* sp. *(b)*	1	0.18							1	0.07
SAPOTACEAE	*Chrysophyllum sanguinolentum*	1	0.18							1	0.07
SAPOTACEAE	*Chrysophyllum* sp. *(a)*	3	0.54							3	0.20
SAPOTACEAE	*Ecclinusa lanceolata*	1	0.18			6	6.52	1	0.35	8	0.55
SAPOTACEAE	*Manilkara bidentata*			1	0.19					1	0.07
SAPOTACEAE	*Micropholis* cf. *egensis*	1	0.18	1	0.19					2	0.14
SAPOTACEAE	*Micropholis guyanensis*	3	0.54							3	0.20
SAPOTACEAE	*Micropholis venulosa*	1	0.18					1	0.35	2	0.14
SAPOTACEAE	*Micropholis* (unidentified sp.)	1	0.18							1	0.07
SAPOTACEAE	*Pouteria cuspidata*	1	0.18	2	0.38					3	0.20
SAPOTACEAE	*Pouteria gomphiifolia*			14	2.65					14	0.96
SAPOTACEAE	*Pouteria* cf. *guianensis*	5	0.90							5	0.34
SAPOTACEAE	*Pouteria platyphylla*	2	0.36							2	0.14
SAPOTACEAE	*Pouteria plicata*			2	0.38					2	0.14
SAPOTACEAE	*Pouteria rostrata*	1	0.18	4	0.76					5	0.34
SAPOTACEAE	*Pouteria* sp. *(a)*	1	0.18							1	0.07
SAPOTACEAE	*Pouteria* sp. *(b)*	2	0.36							2	0.14
SAPOTACEAE	*Pouteria* sp. *(c)*			1	0.19					1	0.07
SAPOTACEAE	*Pouteria* sp. *(d)*	1	0.18							1	0.07
SAPOTACEAE	*Pouteria* sp. *(e)*			2	0.38			1	0.35	3	0.20
SAPOTACEAE	*Pouteria* sp. *(f)*			2	0.38			1	0.35	3	0.20
SAPOTACEAE	*Pouteria* sp. *(g)*			1	0.19					1	0.07
SAPOTACEAE	*Pouteria* sp. *(h)*	1	0.18							1	0.07
SAPOTACEAE	*Pouteria* sp. *(i)*			1	0.19					1	0.07
SAPOTACEAE	*Pouteria* (unidentified spp)	4	0.72							4	0.27
SAPOTACEAE	*Pradosia* sp. *(a)*			1	0.19					1	0.07
SIMAROUBACEAE	*Simaba polyphylla*			2	0.38					2	0.14
SIMAROUBACEAE	*Simarouba amara*	3	0.54							3	0.20
SIPARUNACEAE	*Siparuna* cf. *cristata*	2	0.36							2	0.14
SIPARUNACEAE	*Siparuna cuspidata*	1	0.18							1	0.07
SIPARUNACEAE	*Siparuna* sp. *(a)*	1	0.18							1	0.07
STERCULIACEAE	*Sterculia killipiana*	1	0.18							1	0.07
STERCULIACEAE	*Sterculia* sp. *(a)*							3	1.05	3	0.20
STERCULIACEAE	*Sterculia* sp. *(b)*	1	0.18							1	0.07
STERCULIACEAE	*Sterculia* sp. *(c)*	1	0.18							1	0.07
STERCULIACEAE	*Theobroma grandiflorum*	1	0.18							1	0.07
STERCULIACEAE	*Theobroma subincanum*	2	0.36			2	2.17			4	0.27
VIOLACEAE	*Casearia pitumba*	1	0.18							1	0.07
VIOLACEAE	*Leonia crassa*			1	0.19					1	0.07
VIOLACEAE	*Leonia glycycarpa*			2	0.38					2	0.14
VIOLACEAE	*Paypayrola grandiflora*	1	0.18							1	0.07
VIOLACEAE	*Rinorea racemosa*	3	0.54							3	0.20
VIOLACEAE	*Rinorea* (unidentified sp.)	1	0.18							1	0.07
VOCHYSIACEAE	*Qualea cuminata*	1	0.18			1	1.09			2	0.14
VOCHYSIACEAE	*Vochysia lomatophylla*			1	0.19					1	0.07
VOCHYSIACEAE	*Vochysia venulosa*	2	0.36							2	0.14
Family unidentified	Family unidentified	10	1.79	25	4.73	2	2.17	4	1.40	41	2.80
TOTAL TREES		558		528		92		286		1464	