

.....

The Ecology, Biogeography and Conservation of the Uakaris, *Cacajao* (Pitheciinae)

Adrian Ashton Barnett, Douglas Brandon-Jones

Department of Psychology, University of Reading, UK

Key Words

Amazonia · *Cacajao* · Colobinae · Diet · Glacial refugia · Habitat selection · Metachromism · Seasonal migration

Abstract

With the sakis (*Pithecia*) and the bearded sakis (*Chiropotes*), the uakaris (*Cacajao*) constitute the cebid subfamily, Pitheciinae. The most recent revision recognized six *Cacajao* subspecies in two species, confined to the Amazon basin. Before 1970 most field information derived from 19th century travellers. Studies still lag behind those of other cebid genera. This paper summarises the known ecology of *Cacajao*, and identifies future research and conservation priorities. The relevance of Pleistocene refugia and metachromism in analysing its biogeography is discussed. Range size remains obscure but, with the exception of *C. c. calvus*, may be extensive, as all other subspecies appear to migrate in the dry season from flooded riverine forest to terra firme. Observed group size ranges from 5 to 50, indicating the operation of a fission-fusion society. Social organization appears to be multi-male and non-hierarchical. This accords with the minimal sexual dimorphism. The highly developed canines function primarily as fruit openers. *Cacajao* is a dietary specialist on hard-shelled fruit, and appears unique among Amazonian cebids in its dependence (at least seasonally) on riverine forests. Hunting may be a problem locally, but local taboos sometimes offer protection. They appear vulnerable to habitat disturbance. On the Rio Negro, the range of *C. m. melanocephalus* appears to have greatly diminished. To ensure protection of viable populations, the inferred dietary dependence on seasonal migration may require accommodation. Research priorities include the status, habitat preference, diet and social ecology of all taxa except *C. c. calvus*. A more complete knowledge of the biogeography of the genus would be valuable.

KARGER

© 1997 S. Karger AG, Basel
0015-5713/97/0685-0223\$12.00/0

E-Mail karger@karger.ch
Fax +41 61 306 12 34
<http://www.karger.ch>

Douglas Brandon-Jones
11 York Road
Battersea
London SW11 3PX (UK)

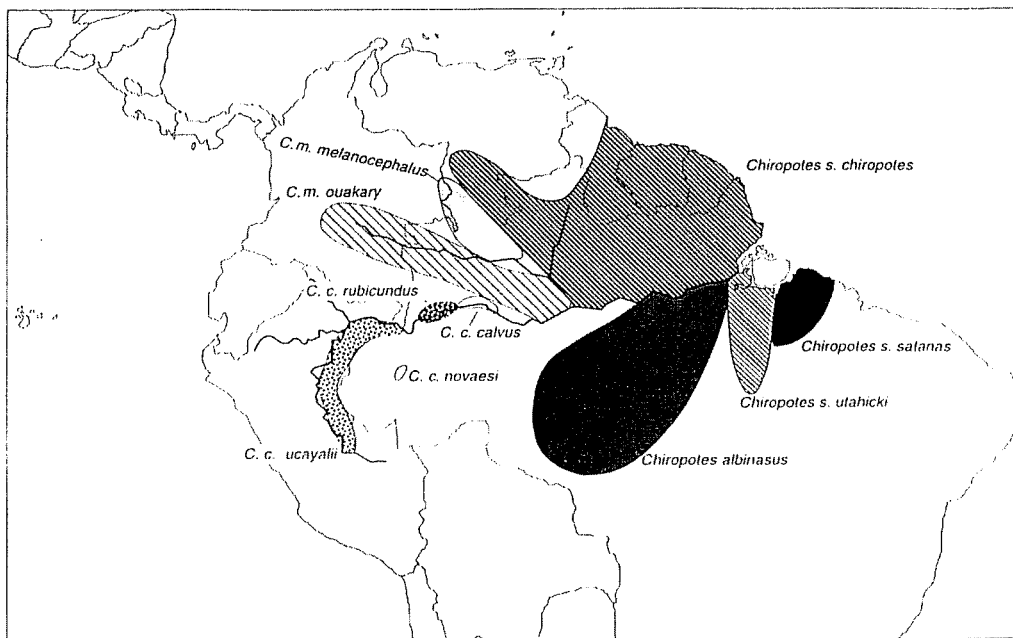


Fig. 1. Geographic distribution of the genera *Cacajao* and *Chiropotes*. Locality data from Hershkovitz [4, 74] and Boubli [28].

Introduction

The genus *Cacajao* is one of the least known of Neotropical primate genera. Uakari biology has been reviewed by Fontaine [1] and Whitehead [2], and extensive bibliographies provided by Ayres [3] and Hershkovitz [4]. Barnett is preparing an updated review. This paper stresses the relevance of past, as well as existing factors, to the full understanding of the ecology, biogeography and conservation of this neglected, but fascinating genus (appendix). Priorities for further study are identified.

The most recent revision of the genus [4] recognized two species, *Cacajao calvus* with four subspecies (*calvus*, *rubicundus*, *ucayalii*, *novaesi*), and *Cacajao melanocephalus* with two (*melanocephalus*, *ouakary*). The distribution of these six forms is given in figure 1. Uniquely among New World primates, uakaris possess a tail less than one-third of the head and body length [4]. This abnormal character for an arboreal mammal led early Western scientists to assume the tail was docked or self-mutilated [5]. Uakaris are the largest members of the subfamily Pitheciinae and are the largest non-prehensile-tailed South American primates. Adult males weigh some 3 to 4 kg, females being slightly smaller. There is little gross or dental sexual dimorphism [6], though the head of male *C. calvus* appears larger, because the temporal muscles bulge more above the skull [7]. The pronounced fleshy, globular, occipital swellings present in male *Chiropotes* are absent in *Cacajao*, as is pelage sexual dichromatism, which occurs in *Pithecia*. Hill [8], however, indicates that there may be skin sexual dichromatism in *C. c. rubicundus*, with the female face being more pink than the scarlet face of the male.

Habitat

Uakari ecology appears to be strongly influenced by riverine forest variation in its Amazon Basin habitat. Amazonian rivers fall into three categories: white-water, black-water and clear-water. White-water rivers originate on the eastern slopes of the Andes, and derive their café-au-lait colour from the erosion of a geologically young formation. Black-water rivers flow over the more ancient Guyana Shield, where the rocks are now poor in soluble or erodable materials [9]. A hydrologist has even described the contents of the Rio Negro as 'slightly contaminated distilled water' [10]. Such rivers are coloured dark brown by their high humus content, and are quite acid (due to humic acids), but the lack of suspended silt denies them the complex system of creeks, islands and levees that border white-water rivers [3, 11]. These are replaced by a gentle slope to higher ground. Clear-water rivers drain savannas rather than forest, and are effectively less acid black-water rivers without the leaf litter and hence the tannins [10].

Amazonian river levels may vary annually by as much as 11 m. High-ground forests are never inundated and are called terra firme. Lowland forests are subject to flooding for up to nine months. Those bordering black-water rivers are termed igapó [12], those along white-water rivers, várzea [13]. These seasonally flooded forests are unique in that fish are the principal agents of fruit dispersal and predation [10]. Consequently, most of their trees fruit during the flood season [10, 12, 14]. The wide floodplain of várzea is a much more heterogeneous and diverse habitat than are the thin ribbons of igapó [3, 13].

There are some indications of a habitat divergence between the two *Cacajao* species. *C. melanocephalus* appears exclusive to black-water river areas, and its avoidance of várzea is quite marked. Rylands [pers. commun. to A.A.B., 1989] reported that the species was absent from the Rio Padauari, a small white-water tributary on the north bank of the Rio Negro, but that it was present on the neighbouring Rio Preto, a black-water river. Ayres [3] working on Lake Mamirauá, a predominantly white-water area, saw *C. melanocephalus* there, but noted that all records were in the vicinity of neighbouring black-water lakes [11]. Most *C. calvus* subspecies seem restricted to várzea and adjacent inter-fluvial terra firme. Putative records of *C. calvus* from nominally black-water rivers, usually have a hydrological explanation. For example, the Rio Jacurapá, a small black-water tributary of the Rio Içá where Mittermeier and Coimbra-Filho [15] observed *C. c. rubicundus* in igapó forest, may fluctuate between black- and white-water, depending on the season and relative flow rates of its feeder streams. Most, if not all, records of *C. c. ucayalii*, however, have been in terra firme forest [16, 17] or in *Mauritia flexuosa* swamps [17]. Sightings reported by Heymann [18] were also in terra firme forest [E.W. Heymann, pers. commun.]. *C. c. ucayalii* populations between the Tahuayo and Yavarí Mirim rivers in northeastern Peru probably do not inhabit flooded forest which is absent there except on the banks of the Tahuayo [E.W. Heymann, pers. commun.].

Figure 2 shows recorded localities for the subspecies of *Cacajao*. *Cacajao c. rubicundus* is absent from the margins of the lower Juruá in Brazil [19]. *C. c. ucayalii* rarely occurs in riverside vegetation on the Rio Ucayali, Peru [17, 20]. *C. melanocephalus* is restricted to the tributaries of the Rio Negro [21, 22]. These accounts corroborate Mittermeier and Coimbra-Filho's [15, p. 144] conclusion that 'all uakaris appear to avoid the margins of larger rivers'. Cunha and Barnett [23, 24] and Barnett

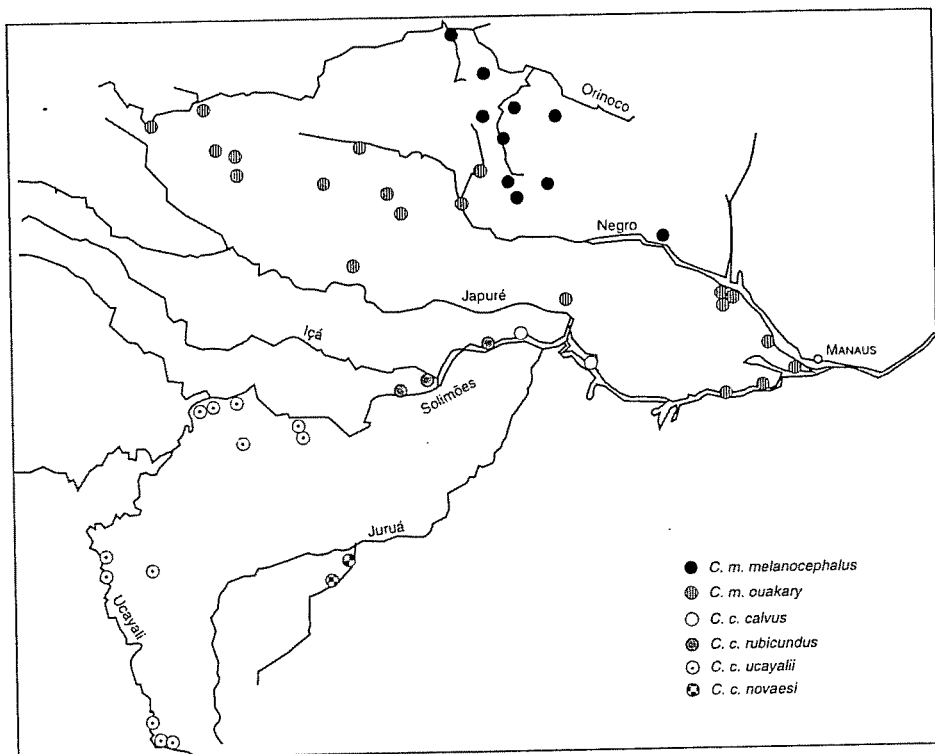


Fig. 2. Geographic distribution of recorded localities for the subspecies of the genus *Cacajao*. Data from Hershkovitz [4] and Boubli [28].

and Cunha [25], however, found *C. m. ouakary* alongside the lower Uaupés where the river is at least 1,500 m wide. Maps in Rylands [26] indicate that this species has also been recorded from the mainstream Rio Negro in the Barcelos region. Local informants told Fontaine [1] that red uakaris tend to avoid river banks in the dry season, when they move to aguajal (swamp forest dominated by the palm *M. flexuosa*). Cunha and Barnett [23] failed to find *C. melanocephalus* in the igapó forests of small black-water rivers and 'lakes', but did find it in the taller igapó along the side of large rivers.

Seasonal Migration

Though frequently regarded as an inhabitant of riparian and flooded forest, evidence is accumulating that *Cacajao* is, at least regionally, a seasonal migrant to terra firme forest. Such movements follow patterns of food availability in flooded and terra firme forest.

In Colombia, Defler [27] noted that, while other species of primate were attracted to, but not dependent on, the wet-season abundance of fruit in the igapó, this resource appeared crucial for *Cacajao*. *C. m. ouakary* 'was almost constantly over the water of

the igapó at the early stages of the annual flooding cycle in June and July, when a strong flux of fruit is available'. As 'the foods in the igapó become exhausted, *Cacajao* begin to forage farther inland. By December and January, they are making wide foraging loops away from the igapó; I have seen them up to 1.5 km inland from the edge of the igapó' [27, p. 53]. In Brazil, 9 of 12 interviewees informed Cunha and Barnett [23] that *C. m. ouakary* occurred in igapó only during the winter months when rain is heaviest and waters at their highest. At other times it was said to move either to terra firme forest or to unknown or unspecified areas. Mittermeier and Coimbra-Filho [15] received similar intelligence. Boubli [28] observed *C. m. melanocephalus* away from riversides. Fontaine [29] firmly believed and Heymann [30, pers. commun.] strongly suspects that seasonal or periodic movements by *C. c. ucayalii* also occur. *C. c. calvus* cannot seasonally migrate between seasonally flooded and permanently dry forest types, as it is restricted to a huge fluvial island.

Several studies [31–33] have shown seasonal changes in ranging behaviour and diet for primate species of the Amazonian terra firme forests. Four such species seasonally migrated between várzea and terra firme on the Tapajós river, and Branch [34] attributed it to shifts in food availability. Seasonal migrations between habitats have been recorded in Africa [35] and Asia [36]. Jolly [37] believed Allen's swamp monkey (*Allenopithecus nigroviridis*) to be the Old World *Cacajao* analogue. The Zairian swamp forests which it inhabits are permanently inundated and the species has not been recorded undergoing any form of seasonal migration [38, 39].

Diet

Preliminary data indicate a uniformity of diet in all uakaris. Like bearded sakis, they are now regarded as hard-fruit dietary specialists [11, 40–42]. Morphologically, this is indicated by their exceptionally robust and divergent canines.

Over an 18-month period, the staple 13% of nearly 100 plant species in the diet of *C. c. calvus* was found to be the hard-shelled fruit of *Eschweilera turbinata* [3]. Seeds of immature fruit from trees and lianas totalled some 67% of feeding observations, with 43.8% of the diet being from one liana and four tree species. Almost half the feeding records were from plants with large (10–100 g) fruits. Most of these had hard or thick shells, and 82% were selected for young seeds. Seventy percent of small (1–10 g) fruits were selected for their mature pulp. The biochemical constituents varied. Ayres [11] concluded that *C. c. calvus* adopts a mixed-feeding strategy to maximise nutrient intake and minimise handling times. He inferred that *Cacajao* is a frugivore specialising on immature seeds.

Over a twelve-month period, Aquino [17] recorded *Cacajao c. ucayalii* feeding on the fruits of some 50 tree species, of which the most important were *Couma macrocarpa* (Apocynaceae), *Schistostemon* spp. (Humiraceae), *Eschweilera* spp. (Lechythidaceae), *M. flexuosa*, *Pouteria* spp. (Sapotaceae), *Rhigospira quadrangularis* (Apocynaceae) and *Parahancornia peruviana* (Apocynaceae). The majority of these have hard-shelled fruits. Seeds constituted 51% of the diet, fruit mesocarps 26%. The ripeness of the fruit was unrecorded. In Peru, the thick-shelled fruits of four tree species were eaten [16]. The seeds were ingested of three (*Micrandra spruceana*: Euphorbiaceae, *Parkia oppositifolia*: Mimosaceae and an unidentified species), of the seven plant species the fruits of which Heymann [30] recorded in its diet. Local

inhabitants informed Fontaine [29] that *C. c. ucayalii* fed on species of *Inga* (Mimosaceae) and various Rubiaceae, including *Bothriospora corymbosa*, *Duroia longifolia* and *Warszewiczia coccinia*. The plant parts eaten were not specified.

In Venezuela, Lehman and Robertson [21, 22] observed *C. m. melanocephalus* eating the 'heavily armoured fruit' of *Manilkara bidentata* or *M. zapota* (Sapotaceae) and of *Mauritia flexuosa* (Palmae). The former have shell thicknesses of 7 mm, the latter of 10 mm. In Brazil, Boubli [43] observed *C. m. melanocephalus* eating seeds of unripe fruits of *Cunaria* sp. (Euphorbiaceae). Defler [27] has reported *C. m. ouakary* feeding on immature *Eschweilera* sp. in Colombia. In each case, the animals broke open the fruits to eat the seeds.

Cunha and Barnett [23, 24] recorded three dietary items for *Cacajao m. ouakary* in Brazil. The fruit of one (*Gomphiluma gomphifolium*), is small and soft, while that of another, also a Sapotaceae (either *Labatia macrocarpa* or *Pseudolabatia penicillata*) is the size and shape of a tennis ball, with a hard shell up to 4 mm thick. The walls of the fruit of *Swartzia polyphylla* (Papilionaceae) are up to 10 mm thick, but are spongy [24, 25]. Local Tucano indians told them that these monkeys also fed on unripe fruits of *Aldinia latifolia* (Caesalpiniaceae), and the ripe fruits of *Manilkara surinamensis* and *Hevea* sp. (Euphorbiaceae, probably *H. spruceana*). Though an *Eschweilera* species (*E. tenuifolia*) was quite common at their Uaupés river study site, Barnett and Cunha [25] observed no uakaris feeding on it, nor evidence of attributable seed predation. Local informants reported that this species was not eaten by *C. m. ouakary*.

Gut proportions indicate that *C. melanocephalus* may be more folivorous than *C. calvus* [44, 45]. Despite the success of this method in predicting diet, Cunha and Barnett [23] countered that the low-crowned molars with nearly obsolete cusps of *Cacajao* seem ill-adapted to masticate the small, thick and tough leaves of igapó trees. Leaves, important to most *Pithecia* [46], are a minor item in the diet of both *Chiropotes satanas* [47] and *C. albinasus* [48]. The food passage rate in *Pithecia* is unusually slow for a pitheciine [46]. Those for *Cacajao* and *Chiropotes* [49] are both typical for frugivores. Perhaps the gut modifications are to facilitate the digestion of seeds or unripe fruit.

In the dry season, Ayres [3] observed *C. c. calvus* eating caterpillars and taking nectar. Ayres [11] found large numbers of noctuid caterpillars in the stomachs of *C. c. calvus* and *C. m. melanocephalus*. Captive *C. c. rubicundus* eat invertebrates [50, 51]. Similar behaviour has been reported in wild *Chiropotes* [52, 53], and in captive wild-caught *Pithecia* [54, 55]. Insectivory in *Chiropotes* is most common in the dry season [56]. *C. c. calvus* plucked seeds and seedlings from the seasonally exposed floor of várzea forest [11], and Aquino [17] reported *C. c. ucayalii* feeding on epiphytes (including bromeliads) at this time. *Pithecia albicans* increases the proportion of leaves in its diet during the seasonal scarcity of fruit [56, 57].

The dry season folivory adopted by *P. albicans*, and the extensive dry season insectivory practised by *Chiropotes* and *C. calvus* may not be an option for *C. melanocephalus*. Compared to those of terra firme or várzea, leaves of igapó forest trees are smaller, heavier, and have a lower nutrient concentration [58]. As the white sand soils on which igapó grows are exceptionally nutrient-poor [13], their foliage may be predicted to contain high levels of secondary compounds deterrent to folivores [59]. This might render not only the leaves, but also folivorous insects ingesting plant-derived toxins, inedible to an occasional or facultative folivore and/or insectivore.

Terra firme forests are botanically more diverse than igapó [60], and in central Amazonia have a dry season peak in availability of immature fruits [14, 31]. Cunha and Barnett [23] suggested this might induce dry season migration from the adjacent igapó by a fruit- and seed-eating specialist like *C. melanocephalus*. Among the alternative sources of food exposed in the igapó during this period, are the eggs from the nesting beaches of river turtles (*Podocnemis* spp.) which *C. melanocephalus* has been seen raiding [Clare and Clare, pers. commun. to A.A.B., 1991]. The significance of this resource in its annual diet is unknown.

There are strong similarities between the diets of *Chiropotes* and *Cacajao* in, for example, the high proportion of unripe seeds in their diet and the importance of members of the Lecythidaceae [11, 61–63]. This, and their allopatry (fig. 1) were factors which led Ayres [11] to propose that the two taxa are fluvial/terra firme sister taxa, occupying the same ecological niche in their respective forest types. Electrophoretic analysis of blood proteins led Schneider et al. [64] to propose that the two formed a clade within the subfamily Pitheciinae, with *Pithecia* more distantly related.

Social Organization

Ayres [3] reported multi-male groups for *C. c. calvus*. From the high degree of tolerance shown by same-sex adults in captivity (such as minimal food competition), Fontaine [50] speculated that free-living *C. c. ucayalii* live in age-graded or multi-male groups with many or all of equal rank. Cunha and Barnett [23] presented preliminary data which indicate a similar social organization in *C. m. ouakary*. The absence of an inter-male dominance hierarchy accords with the data of Kay et al. [6] who reviewed the correlation between social structure and canine sexual dimorphism in platyrrhine monkeys. Cunha and Barnett [23] found that some male *C. m. ouakary* made threat displays (pilo-erection and vocalizations) while the rest of the troop withdrew. This indication of some inter-sexual behavioural variation parallels the distraction displays in *Pithecia* recorded by Johns [45].

Group Size

Uakaris have been recorded in both small and large groups. *C. melanocephalus* occurs in groups of from 4 to 100 individuals. Most groups number about 50 [15, 23, 25, 27]. *C. c. calvus* [3], *C. c. rubicundus* [65] and *C. c. ucayalii* [16, 17] have similar group sizes, with a maximum of 120 in *C. c. ucayalii* [17]. Both *C. c. calvus* troops [3] and *C. c. ucayalii* troops [16, 30] frequently subdivide to forage. Smaller groups are probably subdivisions of larger ones. Large groups may be temporary aggregations of more than one group [27].

Mixed-Species Associations

Associations have been reported between *C. melanocephalus* and *Saimiri sciureus* and/or *Cebus apella*, or with *Cebus albifrons* [15]. *C. c. ucayalii* has frequently been seen with *S. sciureus* and *Lagothrix lagothricha*, and occasionally with *Pithecia*

monachus, *C. apella* and *C. albifrons* [17, 20, 30]. Ayres [3] reported mixed groups of *C. c. calvus* and *C. c. rubicundus*. The lack of interspecific associations in *C. m. ouakary* noticed by Cunha and Barnett [23], however, was not contradicted by direct questioning of local informants.

Biogeography

From his studies of South American mammals, especially primates, Hershkovitz [4, 66, 67] coined the term 'metachromism' for trends in pelage and skin colouration. He believed they represented a non-adaptive long-term evolutionary process, commencing with agouti colour (which he regarded as primitive), and terminating with complete bleaching to albinotic. Brandon-Jones' initial resistance to this concept gave way to qualified acceptance when his systematic revision of the Asian Colobinae confirmed that they were subject to comparable chromatic successions [68–71]. The Asian colobines, however, display a more limited colour sequence which can be expressed simplistically as black to grey to brown and, sometimes, onwards to red and albinotic.

In the simple-nosed Asian Colobinae, the predominantly black-pelaged populations in such sequences inhabit areas identifiable as glacial refugia by an abundance of endemic species, and the presence of others whose closest relatives are geographically remote. The areas occupied by brown, red and albinotic morphs cannot be so categorized. It is inferred that black pelage is an ancestral rather than a primitive character, and that the black-pelaged populations were the sole survivors of a species whose pre-glacial distribution was fragmented by the cold dry climate accompanying the glaciations. The implication is not that mammals are relentlessly evolving towards an albino future, but that albinism is the end-product of the relatively short-term period of recolonization as the rainforest and its inhabitants reclaim the areas vacated during the glaciation. Integumental colour variation in the Asian colobines indicates that the blackish colour may be irretrievable in populations which have acquired the red or albinistic condition, but that some of the brownish species, notably *Semnopithecus* (*Trachypithecus*) *obscurus*, appear to be reverting to the pre-glacial colour. The integumental colour dilution appears to be an unstable process associated with rapid dispersal into post-glacially regenerating habitat.

Cacajao inhabits a region thought to have been deforested by the cold dry periods of the glaciations, and which includes several presumed glacial refugia [72]. Applying conclusions drawn from the Asian colobines, may, therefore, assist in investigating the biogeography of the genus. Although their geographic distribution (fig. 2) is irregular, the six *Cacajao* taxa recognized by Hershkovitz [4] can be arranged into a chromatic succession. The predominantly black *C. m. melanocephalus* represents the most saturated form, and *C. c. calvus* the most dilute. *C. m. melanocephalus* is restricted to a small area of southern Venezuela and adjacent Brazil [28]. It apparently intergrades with *C. m. ouakary* whose distribution extends south-westwards to the Río Japurá, westwards into Colombia, and south-eastwards to the Rio Negro-Rio Solimões confluence. The slight dilution in pelage colour on the upper part of the back in *C. m. melanocephalus*, intensifies in *C. m. ouakary* to a reddish yellow, with a reddish suffusion throughout most of the black of the rest of the body. In *C. c. rubicundus*, which has a small distribution on either side of the mouth of the Río Japurá, the black is almost completely supplanted by red, and the reddish colour on the upper part of the

back by yellow. This dorsal colour substitution is more uniform in *C. c. ucayalii*, which occurs along the east bank of the Río Ucayali and below the Río Amazonas near Iquitos. The orange-buff pelage colour of *C. c. novaesi* (not personally examined), from near the mouth of Río Tarauacá tributary of the Río Juruá, culminates in the almost complete albinism of *C. c. calvus*, which is distributed on the Amazon between *C. c. rubicundus* and *C. m. ouakary*.

It is conceivable that *Cacajao* has dispersed along the pathway suggested by the above chromatic succession. The distribution of *C. m. melanocephalus* coincides with that of previously identified refugial populations [72]. The disproportionately larger distribution of *C. m. ouakary* perhaps represents the comparatively pronounced first stage of population expansion. The next stage, *C. c. rubicundus*, however, represents an anomalous constriction in the dispersal from *C. m. ouakary* to *C. c. ucayalii*. The reality of this constriction remains to be confirmed by an intensive survey of primate distribution on the Río Içá and Río Putumayo. Available evidence suggests the genus then re-expands in distribution as *C. c. ucayalii*. The tiny reported distribution of *C. c. novaesi* is probably an artefact of inadequate surveying, and it would be very instructive to learn whether there are populations further downstream on the Río Juruá, and whether these are intermediate with *C. c. calvus*.

The near circular dispersal route implied by this interpretation appears less paradoxical when it is appreciated that the location of inferred glacial refugia indicates the presence of a dry zone in central south Amazonas during the Pleistocene glaciations. Rainforest regeneration would have been correlated with the gradual post-glacial recession of this dry zone. A population to the west of it would predictably skirt round it in the manner displayed by *C. c. ucayalii*. As the climate moistened, rainforest would have concentrically encroached further, thus accounting for the location of the palest populations. Doubtless this interpretation is over-simplified, and the reddish pelage colour of the golden snub-nosed monkey, *Pygathrix roxellana*, for example, demonstrates that presumed glacial refugial primates can display such colour [71]. It and one or more populations of *C. calvus* may be analogous in having originally evolved as the product of a chromatic succession as described above, and having subsequently become isolated by encirclement by a cold dry climatic zone inimical to their habitat requirement. The remission of such climatic barriers could explain why *C. calvus* populations are more morphologically discrete from each other than a conventional clinal subspecific distribution would predict, with troops containing both red and white individuals reported in the contact zone between their geographic ranges [3].

C. m. melanocephalus with its diluted dorsal pelage area, is an unsatisfactory candidate as the principal glacial relic population of the genus. This begs the question of relationships with other genera. The most closely related extant genus is *Chiropotes*, a genus which is distinguished only by its smaller skull and longer tail. Such differences have been considered inadequate to separate, for example, the Asian colobines, *Nasalis* and *Simias* at more than subgeneric level [73]. The relative insignificance of tail length is highlighted by its observed variation in *Chiropotes satanas chiropotes*. Two Natural History Museum, London specimens (ZD.1910.5.4.3 and 1910.9.29.5, with undoubtedly intact tails, but regrettably without field measurements) from the River Supinaam, Guyana, have tail lengths measured along the bone in the study skins of about 290 mm, while that of a third specimen (ZD.1910.9.29.4) from the same locality is the more typical 350 mm. These Guyana skins also seem to have a consistently paler dorsal pelage colour than NHM skins of the same subspecies from Brazil,

and less-pronounced temporal hair clumps. This opens the possibility that the melanic *Chiropotes s. satanas* or *C. albinasus* (whose geographic distributions are shown in fig. 1) is the earliest glacial relic population of *Cacajao* and *Chiropotes*, and that these taxa are congeneric, if not consubgeneric. Modern Asian primate distribution was moulded by at least two dry glacial periods [68, 70, 71], the first more severe than the second. The subordinate status to *C. s. satanas* and/or *C. albinasus* of *C. m. melanocephalus* as a glacial relic, might result from it existing as such during only the second dry period.

Conservation

Uakaris are listed as Indeterminate/Vulnerable by the IUCN [75] and are in Appendix I of CITES. Over much of their range their status is unknown. Typical densities vary from 2.5 [76] to 47 [77] individuals per square kilometre, but can be much lower [20, 29]. This variation results partly from differences in productivity between various habitat types [9, 59, 78], but human impacts are important [17, 20, 29].

The uakari's riparian habitat makes it especially vulnerable to hunting [21, 22, 27]. It may be preferentially hunted [20–22, 27, 79] or taken only when other species are unavailable [25]. In some places, local hunting taboos protect *Cacajao* and high densities are achieved [77]. Elsewhere, it has been almost extirpated by hunting [17, 18, 29, 80, 81].

Uakaris are captured and used for live bait by hunters of big cats on the lower Rio Negro [15]. The former pet trade in uakaris has now largely ceased as a commercial enterprise [15, 21, 82, 83], although it still affects some *C. c. ucayalii* populations in Peru [18]. Uakaris fare poorly in close confinement, and are therefore not favoured as laboratory animals [84].

C. melanocephalus declines in areas of degraded igapó [79]. The effects of habitat disturbance such as logging and oil exploration, have not been objectively examined in *Cacajao*, but neither *Chiropotes* nor *Pithecia* thrive in such disturbance [85]. *C. c. ucayalii* is threatened by logging and other non-sustainable forms of forest resource exploitation which threaten uakari populations through both habitat disturbance and through removal of important food sources (notably *Mauritia flexuosa* and *Couma macrocarpa*) [17, 20, 29]. Red uakaris have bred in captivity [86], but *Cacajao* is poorly represented in zoological collections. No captive breeding programmes exist, so conservation efforts will have to be restricted to the wild. Currently, only the future of *C. c. calvus* seems assured, as its population is protected by the special status and high profile of the Mamirauá Ecological Station [87]. Other national parks within the range of *Cacajao* taxa, such as Pico de Neblina, are far from secure [21, 22, 28].

Acknowledgements

We are greatly indebted to Christine Brandon-Jones for transcribing, formatting and assisting in the editing of the manuscript, and for preparing the maps. We also thank her, David Chivers, Eckhard Heymann, Anthony Rylands and Becca Shapley for useful comments on drafts of the paper. The Natural History Museum, London, provided access to specimens and reference material.

Appendix: Research Priorities

Ecology

- The reality of seasonal migration. (All taxa, except *C. c. calvus*.)
- Habitat influences on group density. (All taxa.)
- Seasonal variation in group size. (All taxa, except *C. c. calvus*.)
- Further data on diet and its selection. Dietary influences on social structure. (All taxa, except *C. c. calvus*. Priority investigation of *C. c. novaesi*.)
- The validity of the black-water/white-water habitat divergence. Priority investigation of the area between the Japura and Negro.
- Reproductive season, inter-birth intervals and age at sexual maturity.

Biogeography

- The distributional limits, especially the eastern and western ones for *C. m. melanocephalus* and *C. m. ouakary*. The validity of the Rio Negro as the southern barrier for *C. m. melanocephalus*.
- To confirm or refute reports of an all-black uakari on the Rio Curicuriari.
- To confirm or refute reports of *C. c. calvus* south of the Rio Solimões.
- The reality or the restricted known distribution of *C. c. novaesi*.

Status and Conservation

- Population estimates. (All taxa.)
- Estimates of sensitivity to hunting, logging, eco-tourism. (All taxa.)
- Recent extinctions: Comparison of current distributions with those derived from museum specimens.

References

- 1 Fontaine R: Survey of the Red Uakari (*Cacajao calvus rubicundus*) in Eastern Peru. Unpublished report to the New York Zoological Society, 1979.
- 2 Whitehead M: Howler monkeys (*Alouatta* spp.) and uakaris (*Cacajao* spp.) in captivity and in the field; in: Management of Prosimians and Neotropical Monkeys. Proceedings of Symposium 8 of the Association of British Wild Animal Keepers. 1984, pp 5–21.
- 3 Ayres JM: The White Uakaris and the Amazonian Flooded Forests; unpubl PhD diss, Cambridge University, 1986.
- 4 Hershkovitz P: Uacaries. New World monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): A preliminary taxonomic review with a description of a new subspecies. *Am J Primatol* 1987;12:1–53.
- 5 Wood JG: The Illustrated Natural History: Mammalia. London, George Routledge & Sons, 1865.
- 6 Kay RF, Plavcan JM, Glander KE, Wright PC: Sexual selection and canine dimorphism in New World monkeys. *Am J Phys Anthropol* 1988;77:385–397.
- 7 Duplaix N, Simon N: World Guide to Mammals. New York, Greenwich House, 1983.
- 8 Hill CA: Maintenance of facial colouration in the red uakari (*Cacajao rubicundus*). *Int Zool Yb* 1965;5:140–141.
- 9 Meggers BJ: Amazonia: Man and Culture in a Counterfeit Paradise. Chicago, Aldine-Atherton, 1971.
- 10 Goulding M, Carvalho ML, Ferreira EG: Rio Negro: Rich Life in Poor Water. The Hague, SPB Academic Publishing, 1988.
- 11 Ayres JM: Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *J Hum Evol* 1989;18:697–716.
- 12 Kubitzki K, Ziburski A: Seed dispersal in flood plain forests of Amazonia. *Biotropica* 1994;26:30–43.
- 13 Prance GT: Notes on the vegetation of Amazonia. III. The terminology of Amazonian forest types subject to inundation. *Britonia* 1979;31:26–38.
- 14 Revilla J: Aspectos Florísticos e Fitosocioecológicos da Floresta Inundável (igapó). Praia Grande, Rio Negro, Amazônia. Brasil; unpubl master's thesis, Universidad de Amazonas and INPA, Manaus, 1981.
- 15 Mittermeier RA, Coimbra-Filho AF: Primate conservation in Brazilian Amazonia; in Prince Rainier of Monaco, Bourne G (eds): Primate Conservation. New York, Academic Press, 1977, pp 117–166.
- 16 Bartecki U, Heymann EW: Sightings of the red uakaris, *Cacajao rubicundus*, at the Rio Blanco, Peruvian Amazon. *Prim Conserv* 1987;8:34–36.
- 17 Aquino R: Conservación de *Cacajao calvus ucayalii* en la Amazonía Peruana. *Neotrop Prim* 1995;3:40–42.
- 18 Heymann E: Further field notes on red uakaris, *Cacajao calvus rubicundus*, from the Quebrada Blanco, Amazonian Peru. *Prim Conserv* 1990;11:7–8.
- 19 Ranfi R, John JL: Primates of the lower Rio Jurua in Brazil. *Prim Conserv* 1983;3:18–19.

- 20 Aquino R: Preliminary survey on the population densities of *Cacajao calvus ucayalii*. Prim Conserv 1988;9: 24–26.
- 21 Lehman SM, Robertson KL: Survey of Humboldt's uakari in south Amazonas, Venezuela. Am J Primatol 1994;33:223.
- 22 Lehman SM, Robertson KL: Preliminary survey of *Cacajao melanocephalus melanocephalus* in southern Venezuela. Int J Primatol 1994;15:927–934.
- 23 Cunha da AC, Barnett AA: Project Uakari: First Report: The Preliminary Survey. Part 1. Zoology. Unpublished Report to WWF-Netherlands, Pronatura (Brazil) and RGS (UK). 1989.
- 24 Cunha da AC, Barnett AA: Sightings of the golden-backed uakari, *Cacajao melanocephalus ouakary*, on the Upper Rio Negro, Amazonas, Brazil. Prim Conserv 1990;11:8–11.
- 25 Barnett AA, da Cunha AC: The golden-backed uakari on the upper Rio Negro, Brazil. Oryx 1991;25:80–88.
- 26 Rylands AB: The Distribution of Primates on the Upper Rio Negro. Unpublished report to the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus. 1976.
- 27 Defler TR: The status and some ecology of primates in the Colombian Amazon. Prim Conserv 1989;10: 51–56.
- 28 Boubli JP: Southern expansion of the geographical distribution of *Cacajao melanocephalus melanocephalus*. Int J Primatol 1993;14:933–937.
- 29 Fontaine R: Reconocimiento y censo del huapo colorado (*Cacajao calvus rubicundus*) en el oriente Peru- viano; in La Primatología en el Peru: Investigaciones Primatológicas (1973–1985). Proyecto Peruano de Pri- matología 'Manuel More Sommo', Lima. 1990. pp 96–103.
- 30 Heymann EW: The red uakari (*Cacajao calvus ucayalii*): Some field observations and speculations on a lit- tle-known species. Primate Eye 1992;47:6–7.
- 31 Peres CA: Primate responses to phenological changes in an Amazonian terra firme forest. Biotropica 1994;26: 98–112.
- 32 Garber PA: Seasonal patterns of diet and ranging in two species of tamarin monkeys: Stability versus vari- ability. Int J Primatol 1993;14:145–166.
- 33 Garber PA, Preutz JD, Isaacson J: Patterns of range use, range defense and intergroup spacing in moustached tamarin monkeys. Primates 1993;34:11–25.
- 34 Branch LC: Seasonal and habitat differences in the abundance of primates in the Amazon (Tapajos) National Park, Brazil. Primates 1983;24:424–431.
- 35 Struhsaker TT: Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. Ecology 1967;48:891–904.
- 36 Tan B: The status of primates in China. Prim Conserv 1985;5:63–61.
- 37 Jolly A: The Evolution of Primate Behavior. New York, MacMillan. 1972.
- 38 Thornback J, Jenkins M: Mammalian Red Data Book. Part 1. Threatened Mammal Taxa of the Americas and Australasian Zoogeographic Regions (excluding Cetacea). Gland, IUCN. 1982.
- 39 Zeeve SR: Swamp monkeys of the Lomako Forest, central Zaire. Prim Conserv 1985;5:32–33.
- 40 Kinzey WG: Dietary and dental adaptations in the Pitheciinae. Am J Phys Anthropol 1992;88:499–514.
- 41 Kinzey WG, Norconk MA: Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chi- ropotes* in Surinam and Venezuela. Int J Primatol 1993;14:207–227.
- 42 Setz E: Feeding ecology of golden-faced sakis. Neotrop Prim 1994;2:13–14.
- 43 Boubli JP: The black uakari monkey in the Pico de Neblina National Park. Neotrop Prim 1994;2:11–12.
- 44 Chivers DJ: The anatomy of feeding behaviour in primates; in Harrison RJ, Navaratnan RJ, Navaratnan V (eds): Progress in Anatomy. Cambridge, Cambridge University Press. 1982, vol 2, pp 99–135.
- 45 MacLarnon AM, Chivers DJ, Martin RD: Gastro-intestinal allometry in primates and other mammals includ- ing new species; in Else JG, Lee PC (eds): Primate Ecology and Conservation. Cambridge, Cambridge Uni- versity Press. 1984, pp 75–86.
- 46 Johns A: Notes on the ecology and current status of the buffy saki, *Pithecia albicans*. Prim Conserv 1986;7: 26–29.
- 47 Roosemalen van MGM, Mittermeier RA, Milton K: The bearded sakis, genus *Chiropotes*; in Coimbra-Filho AF, Mittermeier RA (eds): Ecology and Behavior of Neotropical Primates. Rio de Janeiro, Academia Brasi- leira de Ciências. 1981, vol 1, pp 419–441.
- 48 Ayres JM: Observações sobre a ecologia e o comportamento dos cuxiús (*Chiropotes albinasus* e *Chiropotes satanas*); unpubl master's thesis, Universidad de Amazónas and INPA, Manaus. 1981.
- 49 Milton K: The role of food processing factors in primate food choice; in Rodman PS, Cant JGH (eds): Adap- tations for Foraging in Non-Human Primates. New York, Colombia University Press. 1984, pp 249–279.
- 50 Fontaine R, DuMond FV: The red ouakari in a seminatural environment: potentials for propagation and study; in Prince Rainier of Monaco, Bourne GH (eds): Primate Conservation. New York, Academic Press, 1977, pp 167–226.
- 51 Fontaine R: The uakaris, genus *Cacajao*; in Coimbra-Filho AF, Mittermeier RA (eds): Ecology and Behavior of Neotropical Primates. Rio de Janeiro, Academia Brasileira de Ciências. 1981, vol 1, pp 443–493.
- 52 Ayres JM, Nessimian JL: Evidence for insectivory in *Chiropotes satanas*. Primates 1982;23:458–459.
- 53 Frazao E: Insectivory in free-ranging bearded saki (*Chiropotes satanas chiropotes*). Primates 1991;32:243–245.
- 54 Bartecki U, Heymann EW: Observations on predatory behaviour of a young saki monkey, *Pithecia hirsuta* (Platyrrhini: Cebidae). Primate Report 1988;20:29–33.

- 55 Heymann EW, Bartecki U: A young saki monkey, *Pithecia hirsuta* feeding on ants, *Cephalotus atratus*. *Folia Primatol* 1990;55:181-184.
- 56 Rylands AB: Primate communities in Amazonian forests: Their habitats and food resources. *Experientia* 1987;43:265-279.
- 57 Peres CA: Notes on the ecology of buffy saki monkeys (*Pithecia albicans*, Gray 1860): A canopy seed-predator. *Am J Primatol* 1993;31:129-140.
- 58 Klinge H, Furch K, Harms E, Revilla J: Foliar nutrient levels of native tree species from central Amazonia. I. Inundation forests. *Amazoniana* 1983;8:19-45.
- 59 Janzen DH: Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica* 1974;6:69-103.
- 60 Keel SHK, Prance GT: Studies of the vegetation of a white-sand black-water igapó (Rio Negro, Brazil). *Acta Amazon* 1979;9:645-655.
- 61 Johns A: Current status of the southern bearded saki (*Chiropotes satanas satanas*). *Prim Conserv* 1985;5:28.
- 62 Roosemalen MGM, Mittermeier RA, Fleagle JG: Diet of northern bearded saki (*Chiropotes satanas chiropotes*): A Neotropical seed predator. *Am J Primatol* 1988;14:11-35.
- 63 Kinzey WG: Corellates of seed processing and dental morphology in *Chiropotes*. *Int J Primatol* 1988;8:434.
- 64 Schneider MPC, Schneider H, Sampaio MIC, Carvalho-Filho NM, Encarnacion F, Montoya E, Salzano FM: Biochemical diversity and genetic distances in the Pitheciinae subfamily (Primates, Platyrrhini). *Primates* 1995;36:129-134.
- 65 Abordo EJ, Mittermeier RA, Lee J, Mason P: Social grooming between squirrel monkeys and uakaris in a semi-natural environment. *Primates* 1975;16:217-221.
- 66 Hershkovitz P: Metachromism or the principle of evolutionary change in mammalian tegumentary colors. *Evolution* 1968;22:556-575.
- 67 Hershkovitz P: *Living New World Monkeys (Platyrrhini)* with an introduction to Primates. Chicago, University of Chicago Press, 1977, vol 1.
- 68 Brandon-Jones D: The taxonomic affinities of the Mentawai Islands sureli, *Presbytis potenziani* (Bonaparte, 1856) (Mammalia: Primates: Cercopithecidae). *Raffles Bull Zool* 1993;41:331-357.
- 69 Brandon-Jones D: A revision of the Asian pied leaf monkeys (Mammalia: Cercopithecidae: superspecies *Semnopithecus auratus*), with a description of a new subspecies. *Raffles Bull Zool* 1995;43:3-43.
- 70 Brandon-Jones D: *Presbytis* species sympatry in Borneo versus allopatry in Sumatra: An interpretation; in Edwards DS, Booth WE, Choy SC (eds): *Tropical Rainforest Research: Current Issues, Monographiae Biologicae*. Dordrecht, Kluwer, 1996, pp 71-76.
- 71 Brandon-Jones D: The Asian Colobinae (Mammalia: Cercopithecidae) as indicators of Quaternary climatic change. *Biol J Linn Soc*, 1996;59:327-354.
- 72 Haffer J: Avian species richness in tropical South America. *Stud Neotrop Fauna Envir* 1990;25:157-183.
- 73 Groves CP: The forgotten leaf-eaters, and the phylogeny of the Colobinae; in Napier JR, Napier PH (eds): *Old World Monkeys: Evolution, Systematics and Behavior*. New York, Academic Press, 1970, pp 555-587.
- 74 Hershkovitz P: A preliminary taxonomic review of the South American bearded saki monkeys genus *Chiropotes* (Cebidae, Platyrrhini), with a description of a new subspecies. *Fieldiana Zool* 1985;New Ser.27:1-46.
- 75 IUCN: IUCN Red List of Threatened Animals. Cambridge, World Conservation Monitoring Centre Gland, IUCN, 1994.
- 76 Puertas P, Bodmer RE: Conservation of a high diversity primate assemblage. *Biodivers and Conserv* 1993;2:586-593.
- 77 Peres CA: Effects of hunting on western Amazonian primate communities. *Biol Conserv* 1990;54:47-59.
- 78 Sioli H (ed): *The Amazon: Limnology and Landscape of a Mighty Tropical River and Its Basin*. Dordrecht, Junk, 1984.
- 79 Hernandez-Camacho J, Cooper RW: The non-human primates of Colombia; in Thorington RW, Heltn PG (eds): *Neotropical Primates: Field Studies and Conservation*. Cambridge, Cambridge University Press, 1976, pp 35-69.
- 80 Grimwood IR: Notes on the Distribution of Some Peruvian Mammals. Special Publications to the American Committee on International Wildlife Protection 1969, vol 21, pp 1-86.
- 81 Soini P: Primate conservation in Peruvian Amazonia. *Int Zool Yb* 1982;22:37-47.
- 82 Aquino R: La fauna primatólogica en área de Janero Herrera. *Proyecto de Asento Rural Integrable Janero Herrera. Boletim Técnico* 1978, vol 1, pp 1-20.
- 83 Kavannah M, Bennett E: A synopsis of legislation and primate trade in habitat and user countries; in Mack D, Mittermeier RA (eds): *The International Primate Trade*. Washington, TRAFFIC (USA)-WWF (US), 1984, vol 1.
- 84 Mack D, Eudley A: A review of the US primate trade; in Mack D, Mittermeier RA (eds): *The International Primate Trade*. Washington, TRAFFIC (USA)-WWF (US), 1984, vol 1.
- 85 Johns A, Skorupa JP: Responses of rainforest primates to habitat disturbance: A review. *Int J Primatol* 1987;8:157-191.
- 86 Fontaine R, Hendon M: Breeding New World monkeys at Miami's Monkey Jungle. *Int Zool Yb* 1982;22:77-84.
- 87 Ayres JM: *As Matas de Várzea do Mamirauá: Medio Rio Solimões, Tefe: MCT-CNPq-Programa do Tropicó Umido*, 1993.