Peruvian Red Uakaris (Cacajao calvus ucayalii) Are Not Flooded-Forest Specialists

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Abstract In the literature, particularly in primatological books, the Peruvian red uakari (Cacajao calvus ucayalii) is generally considered as a species that is specialized on living in flooded forest, despite existing evidence to the contrary. Here we review all available information on habitats where Cacajao calvus ucayalii have been observed. Most sightings are from terra firme, including palm swamps, or from mixed habitats, including terra firme and flooded forest. Therefore, we conclude that the species is not a flooded-forest specialist, but is flexible in its habitat requirements and generally uses terra firme forests or a mixture of habitats. Proper recognition of habitat requirements is important for understanding the ecoethological adaptations of a species and for appropriate conservation measures.

Keywords bald-headed uakaris • ecology • habitat

Introduction

Throughout their tropical and subtropical range of distribution, primates occupy a wide variety of different habitats (Fleagle 1999). Few primate species seem to be confined to a single habitat type, e.g., Theropithecus gelada to montane grasslands (Kawai 1979). Some others may require the presence of a specific habitat type in at least part of their home range, e.g., bamboo forest in Callimico goeldii (Porter and Garber 2004). However, supposed habitat specialization may actually be the result of limited knowledge of a species that can be specified once additional information...
becomes available (Defler 1994), and may also be the result of incorrect inference and ignorance of relevant literature.

Uakaris (Cacajao), and particularly the Peruvian red uakari (Cacajao calvus ucayalii, previously included within Cacajao calvus rubicundus: Hershkovitz 1987), represent an example of the latter case. In a survey in the Rio Tapiche area in eastern Peru, Fontaine (1978, 1990) encountered Cacajao calvus ucayalii on 3 occasions: 1) in swamp forest or aguajal (swamps dominated by the aguaje palm Mauritia flexuosa); 2) on a restinga (strip of high-ground forest within a low-ground matrix) from where the uakaris fled into an aguajal; and 3) on the edge of an aguajal. Based on these observations only, Fontaine (1981, p. 446), in the first review of Cacajao, claimed that “uakaris prefer and may even be restricted to flooded forests.” This perception of Cacajao calvus ucayalii and of uakaris in general dominates in the primatological literature, despite accumulating evidence to the contrary. In many primatological textbooks and overview articles, uakaris in general are referred to as “flooded-forest specialists” (Table I), with very few exceptions (Sussman 2000). The fact that the first detailed field study on any uakari species reported the closely related white uakari (Cacajao calvus calvus) to be confined to várzea (forest seasonally flooded by white-water rivers; Ayres 1986, 1989; cf. Peres 1997) may have contributed to cementing this incorrect perception of red uakaris as a flooded-forest specialist. Published evidence for the occurrence of Cacajao calvus ucayalii in nonflooded forests seems to be largely ignored. To correct this bias, we reviewed the available information, both published and unpublished, about habitats where Cacajao calvus calvus has been observed. We hope that this review will correct

Table I Examples for statements on Cacajao calvus ucayalii (or Cacajao in general) as flooded-forest specialists

| Statement                                                                 | Source                                      |
|--------------------------------------------------------------------------|---------------------------------------------|
| “Specialized to flooded whitewater and blackwater forests”               | Robinson et al. 1987, p. 47                 |
| “Uakaris are restricted to seasonally flooded forests of the Amazon Basin.” | Kinzey 1997, p. 209                         |
| “Uakaris are found in flooded forest.”                                   | Fleagle 1999, p. 140                        |
| “Uakaris appear to be restricted to the Amazonian inundation forest.”    | Preston-Matham and Preston-Matham 1999, p. 60|
| “They live in seasonally flooded forests in the Amazon.”                 | Falk 2000, p. 161                           |
| “The red uakari occurs nearly always in blackwater flooded forest, while the white subspecies prefers whitewater flooded forest.” | Janson 2001, p. 325                         |
| “Found in the flooded forests of the white-water rivers of the upper Amazon.” | Dunbar and Barrett 2000, p. 164             |
| “Uakaris ... sind spezialisiert auf das Leben in saisonal überschwemmten Wäldern” [“uakaris ... are specialized to live in seasonally flooded forests.”] | Geissmann 2003, p. 162                     |
| “White and red uakaris (Cacajao calvus) being associated with white-water forests (várzeas)” | Ferrari 2004, p. 109                        |
| “They inhabit flooded forests.”                                          | Nystrom and Ashmore 2008, p. 57             |
the perception of this taxon as a flooded-forest specialist. Such a correction is necessary both for scientific reasons, e.g., for the interpretation of its morphological and behavioral adaptations, and for the sake of appropriate considerations on the conservation of Peruvian red uakaris.

Methods

We studied the available literature and unpublished reports, and compiled personal observations or personal communications on the habitat of *Cacajao calvus ucayalii*. For each area, we extracted information on the habitats where *Cacajao calvus ucayalii* had been observed and categorized these as 1) terra firme forest, 2) flooded forest, and 3) *aguajales*. We also compiled the available data on population densities and encounter rates to determine whether habitat influences these variables.

Results

The majority of sites where *Cacajao calvus ucayalii* has been recorded represent terra firme forest (Table II). This holds true even if 1) Quebrada Blanco and the Estación Biológica Quebrada Blanco, which are located on opposite banks of the same river only about 2 km apart, and the nearby sites at Quebradas Cuchara, Palmichal, Tahuaillo, Tangarana, and Tunchí; and 2) Agua Negra and Lago Preto on the Río Yavarí are considered as nonindependent counts, perhaps harboring the same populations of *Cacajao calvus ucayalii*.

The highest encounter rates for *Cacajao calvus ucayalii* stem from the Sierras de Contamana (Table II), a site that is not only a terra firme forest, but also has a much higher altitude (600–700 m a.s.l.) than any of the other sites.

Discussion

We here provide clear evidence that *Cacajao calvus ucayalii* occurs not only in flooded forests, but also in terra firme forests and in areas with a mixture of forest types. The terra firme forests (or *bosques de altura* in the terminology of Encarnación 1985) include a variety of vegetation types like high terrace forest (*bosque de terraza*), low hill forest (*bosque de colina baja*), high hill forest (*bosque de colina alta*), premontane forest, and *aguajales de altura* (see also Malleux 1982, for terminology of Peruvian forests) that are all nonflooded. Therefore, one cannot consider *Cacajao calvus ucayalii* as a flooded-forest specialist, as is commonly reported in the literature. The highest encounter rate and thus probably the highest population density is found at a relatively high altitude (Sierras de Contamana), untypical for the major part of the Amazon lowlands, suggesting that this habitat might be favorable to *Cacajao calvus ucayalii*. However, because the Sierras de Contamana is an area with very little human disturbance (Aquino *et al*. 2005), we cannot distinguish whether this factor or favorable habitat accounts for the high encounter rate.
| Locality coordinates | Habitat | Altitude [m a.s.l.] | Population density or encounter ratea | Source |
|----------------------|---------|---------------------|--------------------------------------|--------|
| Río Tapiche          | *Aguajal* | n.a. | n.a. | Fontaine 1978, 1990 |
| Río Tapiche 5°39′S 74°00′W | Terra firme, flooded forest, *Aguajal* | 110 | 1) 0.47 grp/km², 7.4 ind/km² 2) 0.78 grp/km², 25.8 ind/km² | Bennett *et al.* 2001 |
| Alto Tapiche         | Flooded forest | n.a. | 0.23 grp/km² | Aquino 1988, 1990 |
| Jenaro Herrera       | Terra firme | n.a. | 0.07 grp/km² | Aquino 1978, 1988, 1990 |
| Quebrada Blanco      | Terra firme, *aguajal* | 120 | n.a. | Ramirez 1989; Bodmer and Fang 1987 |
| Estación Biológica Quebrada Blanco (EBQB), 4°21′S 73°09′W | Terra firme | 120 | n.a. | Bartecki and Heymann 1987d; Siegel 1987; Heymann 1989d, 1990; Castro Coronado 1991; Heymann *et al.* unpubl. data |
| Headwaters of Quebrada Blanco | Terra firme | n.a. | n.a. | Bodmer and Fang 1987 |
| Quebrada Cuchara 4°24′S 73°10′W | Terra firme, *aguajal* | n.a. | n.a. | Leonard and Bennett 1995, 1996; Aquino 1998 |
| Quebrada Tunchio     | Terra firme, *aguajal* | n.a. | n.a. | Aquino 1998 |
| Quebrada Palmichal   | Terra firme, *aguajal* | n.a. | n.a. | Aquino 1998 |
| Quebrada Tangarana 4°24′S 73°17′W | Terra firme, *aguajal* | n.a. | n.a. | Ward and Chism 2003 |
| Quebrada Tahuaillo 4°33′S 73°19′W | *Aguajal* | n.a. | n.a. | Ward and Chism 2003 |
| Rio Tahuayo area     | n.a. | 0.4 grp/km² 2.5 ind/km² | Bodmer *et al.* 1988; Puertas and Bodmer 1993 |
| Rio Orosa            | Terra firme | n.a. | 0.4 grp/km² | Aquino 1988, 1990 |
## Table II (continued)

| Locality                              | Habitat, 
aguajal | Altitude (m a.s.l.) | Population density or encounter rate\(^a\) | Source |
|---------------------------------------|-------------|---------------------------------------------|-----------------|
| Sierras de Contamana                  | Terra firme, 
aguajal | >600                                        | 6.1 grp/100 km, 479 ind/100 km | Aquino et al. 2005 |
| Agua Negra—Carolina 4°30'S 71°43'W    | Terra firme, flooded forest, 
aguajal | n.a.                                        | n.a.             | Aquino 1997, 1998; Aquino and Encarnación 1999 |
| Lago Preto (Agua Negra), Río Yavarí   | Terra firme, Flooded forest, 
aguajal | 90                                          | n.a.             | Puertas and Bodmer 1993; Bowler 2007; Bowler and Bodmer 2009 |
| 4°28'S 71°46'W                        |             |                                             |                 |
| Upper Río Yavarí                      | Terra firme | 90–190                                      | 14.8 ind/100 km | Pitman et al. 2003 |
| Lower Río Yavarí Mirí                 | Terra firme, flooded forest | n.a.                                        | 4.9 ind/km\(^2\) | Pitman et al. 2003 |
|                                       |             |                                             | 47.3 ind/100 km |                 |
| Upper Río Yavarí Mirí                 | n.a.        | n.a.                                        | 6.1 ind/100 km  | Pitman et al. 2003 |
| Ojo de Contaya (Sierra del Divisor)   | Terra firme | n.a.                                        | n.a.            | Vriesendorp et al. 2006 |
| Tapiche                               | Aguajal     | n.a.                                        | n.a.            | Vriesendorp et al. 2006 |
| Yanayacu-Pucate 4°56'S 74°08'W        | Flooded forest | n.a.                                       | n.a.            | Bowler et al. 2009 |

\(^a\) Population density is given as per survey area (individuals: ind/km\(^2\), groups: grp/km\(^2\)), encounter rates as per transect length (individuals: ind/100 km, groups: grp/100 km)

\(^b\) n.a.: no data available

\(^c\) These sources quote the site as Río Blanco or Blanco Stream; to avoid confusion with the proper Río Blanco, a major affluent of the Río Tapiche, the river was renamed Quebrada Blanco

\(^d\) These sources also quote Río Blanco, but actually refer to the Estación Biológica Quebrada Blanco; see previous footnote

\(^e\) The habitats where Cacajao calvus calvus were sighted are not mentioned by the authors, but the census area includes terra firme forest and aguajales, but not flooded forest
Cacajao calvus ucayalii have large daily ranging distances (>6 km: Bowler 2007; 7.3 km: Leonard and Bennett 1996) and they may migrate seasonally between different habitats, including flooded forests (Bowler 2007). In the Quebrada Blanco area, the nearest seasonally flooded forest is ca. 8–10 km away along the Río Tahuayo and the lower parts of Quebrada Blanco. Given the daily ranging distances quoted above, this forest is in the reach of Cacajao calvus ucayalii. Nevertheless, neither researchers and their field assistants nor local settlers have ever seen these animals in flooded forest along the Río Tahuayo and lower Quebrada Blanco in the last 25 yr.

Aguajales, swamps dominated by aguaje palms (Mauritia flexuosa), occur both in forests subject to inundation and in areas of terra firme (where they are called aguajales de altura; Encarnación 1985). Though Mauritia flexuosa may represent an important food resource for Cacajao calvus ucayalii in some areas (Aquino and Encarnación 1999; Bowler 2007), it is probably not essential for the existence of these uakaris, as indicated by their rarity in the Sierras de Contamana (Aquino et al. 2005).

Altogether, we can reasonably conclude that Cacajao calvus ucayalii is not a habitat specialist restricted to flooded forests. Together with the report by Peres (1997) of Cacajao calvus calvus at a terra firme site, this indicates that habitat requirements and utilization in bald-headed uakaris are much more variable than previously appreciated.

Incorrect perceptions of or misconceptions on aspects of the biology of a primate taxon may have several implications. First, they may lead to erroneous interpretations of the behavioural, ecological, morphological, and physiological adaptations and the evolution of these adaptations. Second, they may lead to bad conservation strategies, particularly when habitat preferences are concerned. Though the first implication is mainly academic, the second one is of strong practical relevance. In a world, where primate habitats are constantly shrinking and an increasing number of primate taxa is getting closer to extinction, accurate knowledge of habitat requirements are amongst the most basic information needed for conservation efforts.

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E. W. Heymann dedicates this paper to his wife Ursula Bartecki, who in 1985/86 made the first systematic effort to study red uakaris in the Quebrada Blanco area.

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