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Cacajao melanocephalus.

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Cacajao Lesson, 1840

Simia Humboldt, 1811:316, 1812:359, plate 29. Type species *Simia melanocephala*.

Pithecia E. Geoffroy Saint-Hilaire 1812:117. New name for *Simia* Humboldt, 1811.

Brachyurus: Spix, 1823:12. Part, not *Brachyurus* Fischer, 1813: 24 (a rodent).

Cacajao Lesson, 1840:181. Replacement name for *Brachyurus* Spix, 1823.

Cercoptochus Gloger, 1842:41. New name for *Brachyurus ouakary* Spix, 1823.

Ouakaria Gray, 1849:9. Type species *Ouakaria spixii* Gray, 1849.

Uacaria Flower and Lydekker, 1891:712. Emendation of *Ouakaria* Gray.

Cothurus: Palmer, 1899:493. New name for *Brachyurus* Spix, 1823; not *Cothurus* Champion, 1891 (a coleopteran).

Neocothurus Palmer, 1903:873. Replacement name for *Cothurus* Palmer, 1899.

CONTEXT AND CONTENT. Order Primates, family Cebidae, subfamily Pitheciinae. *Cacajao* includes 2 living species, *C. calvus* and *C. melanocephalus* (Hershkovitz 1987). *C. c. rubicundus* is not a separate species (contra Cruz Lima 1944; Hill 1960; Napier and Napier 1967). Lesson (1840) lists *Cebus melanocephalus* Fischer (1813) as a synonym. This is in error, because Fischer never mentions this species.

Cacajao melanocephalus (Humboldt, 1811)

Black-headed Uacari

Simia melanocephala Humboldt, 1811:316, 1812:359, plate 29. Type locality "San Francisco Solano Mission, Río Casíquiare, Venezuela," Amazonas State, Venezuela.

Pithecia melanocephala: E. Geoffroy Saint-Hilaire, 1812:117. Name combination.

Brachyurus ouakary Spix, 1823:12. Type locality "Carvœira, Rio Negro, opposite mouth of Rio Branco, Marabitanas, Rio Negro," Amazônas State, Brazil.

Cacajao melanocephalus: Lesson, 1840:182. Name combination.

Ouakaria spixii Gray, 1849:9. No type locality specified.

Uakaria melanocephala: Flower and Lydekker, 1891:712. Name combination and gender change.

Cothurus melanocephalus: Palmer, 1899:493. Name combination.

Neocothurus melanocephalus: Palmer, 1903:873. Name combination.

CONTEXT AND CONTENT. Context as above. Holotype of *C. melanocephalus* is not preserved. Original description was made from a living infant purchased by Alexander von Humboldt at San Francisco Solano Mission on the Río Casiquiare, Amazonas, Venezuela, and illustrated after the animal's death (Humboldt 1812: 359, plate 29). Two subspecies of *C. melanocephalus* (Fig. 1) are recognized (Hershkovitz 1987): *C. m. melanocephalus* (black-backed uacari) and *C. m. ouakary* (golden-backed uacari). Holotype of former is not preserved; holotype of latter is a mounted specimen in Zoologischen Staatssammlung, Munich, Germany (Kraft 1983). Although originally described as separate species, the 2 subspecies of *C. melanocephalus* have long been conflated. This started with Wagner (1833), who regarded Spix's animal (i.e., the animal now considered to be the holotype of *C. m. ouakary*) as a juvenile of the species described by Humboldt (although Humboldt's animal is, in fact, itself a juvenile, and Spix's animal is an adult male). Lesson (1840) and subsequent authors followed his opinion. Elevation of the 2 forms to subspecies was proposed by Hernández-Camacho and Cooper (1976) and formalized by Hershkovitz (1987).

C. m. melanocephalus (Humboldt, 1811:316), see above.

C. m. ouakary (Spix, 1823:12), see above; *spixii* is a synonym.

DIAGNOSIS. *Cacajao melanocephalus* is distinguished from the congeneric *C. calvus* by a fully haired head, which contrasts with the very lightly haired to bald cranium of *C. calvus*. In addition, *C. melanocephalus* has strongly pigmented black facial skin, whereas the almost completely depigmented facial and cranial skin of *C. calvus* appears red from subcutaneous blood vessels. The 2 species also are distinguished by pelage; *C. melanocephalus* has cinnamon flanks, tail, and upper limbs and black lower limbs and hands, whereas in *C. calvus* all these areas are a single color.

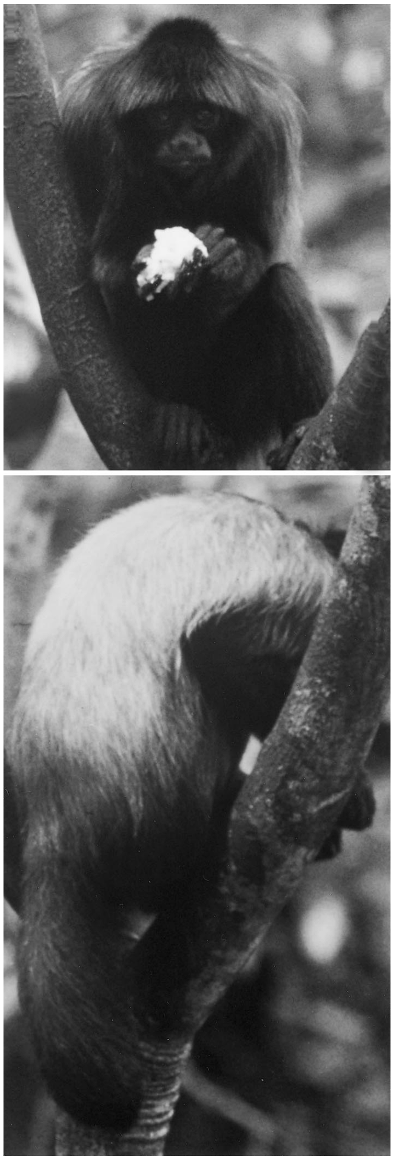

FIG. 1. Frontal and dorsal views of an adult *Cacajao melanocephalus ouakary* in semicaptivity, Amazonian Brazil. Photographs provided by Ralph Smith.

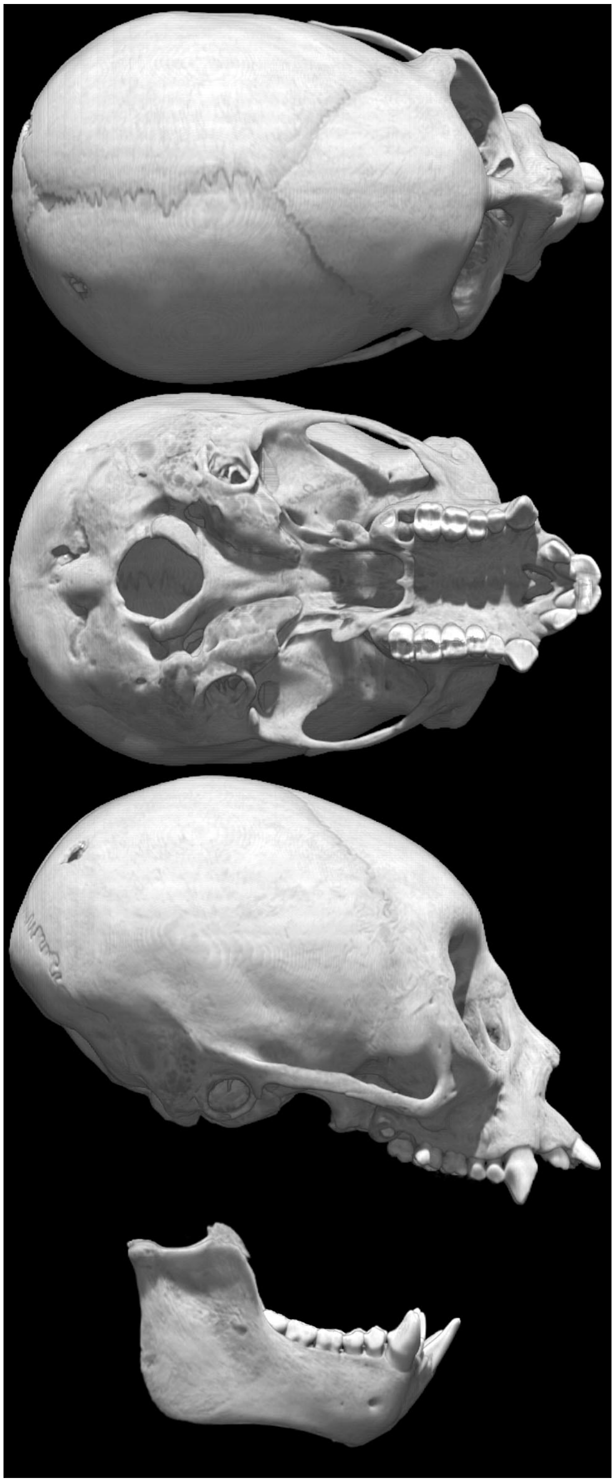

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Cacajao m. melanocephalus* (USNM 406427). Greatest length of skull is 82.8 mm. Specimen scanned at the High-Resolution X-ray CT Facility at the University of Texas at Austin for Dr. James Rossie of the Carnegie Museum of Natural History. Images courtesy of Dr. Rossie and DigiMorph.

GENERAL CHARACTERS. Both subspecies are same size. They are separated by pelage characters of nape and midback, which are black in *C. m. melanocephalus* and golden yellow in *C. m. ouakary*. Face is naked and pigmented black. Head has black fur. Flanks, tail, and upper limbs are uniform deep cinnamon red. Lower limbs and hands are black. Soles of hands and feet are black. Fur is long (to 10 cm on flanks), obscuring a nearly naked belly. Sexual dichromatism is limited.

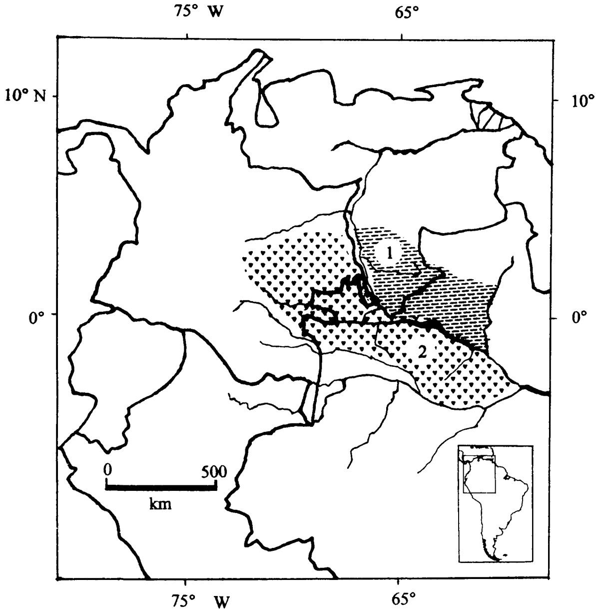

FIG. 3. Distribution of *Cacajao melanocephalus* modified from Barnett and Brandon-Jones (1997), Boubli (1994), and Hershkovitz (1987): 1, *C. m. melanocephalus*; 2, *C. m. ouakary*.

Adult females are 84–91% of length of adult male head and body. External measurements (in mm) of 16 males and 21 females, respectively, are: length of head and body, 435–485, 365–445; length of tail, 155–185, 150–165. Mass is 2.5–3.7 kg, with adult females rarely exceeding 3 kg (Hershkovitz 1987). Tail is markedly short (less than one-half the length of head and body) and not prehensile.

Dentition is highly specialized (Fig. 2). Incisors are narrowly elongate, styliform, bear a mesiolingual cusp, lack a distinct lingual heel, and are markedly procumbent with crowns pressed closely together; canines are enlarged, powerful, angular, procumbent, and laterally splayed; molars are low-crowned, the cusps nearly obsolete. A wide diastema separates lower canines from lower lateral incisors (see Hershkovitz 1987).

DISTRIBUTION. Black-headed uacaris occur in the Rio Negro basin and its tributaries in Amazon region of South America (Fig. 3). *C. m. melanocephalus* is restricted to Amazonas State, Venezuela, and adjacent areas of Brazil north and east of the Rio Negro (Boubli 1993, 1994). *C. m. ouakary* occurs south and west of Rio Negro of Brazil and into the Río Vaupés river system of Colombia (Hershkovitz 1987). In Brazil, *C. m. ouakary* does not occur south of the Japurá-Solimões or east of its confluence with Rio Negro. Although still common in Colombia (Defler et al. 2003), *C. m. ouakary* now occurs only patchily on the upper (Barnett and Cunha 1991; Cunha and Barnett 1990) and lower (Barnett et al. 2000, 2002) Rio Negro in Brazil. Boundaries between the 2 subspecies are unclear (Barnett and Brandon-Jones 1997; Cunha and Barnett 1989b). No fossils are known.

FORM AND FUNCTION. Cranium, mandible, and teeth of *C. melanocephalus* reflect a diet of hard fruits (Anapol and Lee 1994; Kinzey 1992). Frontal bones are modified to form a slightly prognathous snout, nasal bones are correspondingly enlarged, and palate is narrow and U-shaped. Comparatively, the area for insertion of masseter muscle is large. Zygomatic arch is moved relatively forward so that anterior origin of masseter lies above M1. Anterior root of zygoma is thickened, with a bony flange (M. Plavcan, pers. comm.). Sagittal crest is absent. *C. melanocephalus* has large temporal and masseter muscles (Cachel 1979) and a large condylar area (Smith et al. 1983). Mandible of *C. melanocephalus* is robust, with a very thick deep and robust symphysis region; the front is widened to create jaws with parallel sides (Kinzey 1974; Smith 1983).

Dental formula is i 2/2, c 1/1, p 3/3, m 3/3, total 36. Incisors are markedly procumbent with adpressed crowns and a scooplike form (Kay 1990), which forms an efficient nipping, cropping, or gouging device (Kinzey 1992). This is related to a diet that requires incisal preparation to separate husk from the pulp and seed (Eaglen 1984).

Reaching up to 14 mm, canines of *C. melanocephalus* are large (Smith 1981) and represent dietary specializations, not adaptations to sexual display (Greenfield 1992; Greenfield and Washburn 1991; Smith 1981). In line with low male–male competition (Kay et al. 1988), canine size has little sexual dimorphism (Leutenegger 1982). Each lower canine bears a strong flange on inner surface. Chisellike, this flange occludes with mesial surface of corresponding upper canine (Kay 1990). A lower buccal cingulum is present, a feature related to shearing of each upper canine tooth against corresponding lower anterior premolar (canine honing—Kinzey 1974). Premolars and molars are relatively small and square, with low-relief cusps. Wear facets and cusp cavitation indicate the use of molars as grinders with little puncture-crushing (Hagura 1994). Molars do not have thick enamel, but are strengthened with densely packed enamel prisms (Martin et al. 1994). Molars exhibit strong horizontal decussation, and so are more mechanically resistant to crack propagation than abrasion (Kinzey 1992, 1997a). Wear is resisted by low occlusal relief (Rosenberger and Kinzey 1976). *C. melanocephalus* molars triturate mechanically protected seeds; tooth-wear patterns shows these seeds are often tough, but elastic and resilient rather than hard and brittle (Kinzey 1992; 1997a). Molars have surface crenulations that contain deformation in seeds during trituration (Kinzey 1992, 1997a).

Quadrupedal walking and running are the most frequently observed locomotional modes (Boubli 1997). Leaping occurs predominantly when traveling, with gaps to 10 m wide being covered (Boubli 1997; Cunha and Barnett 1989b). Leaping by *C. melanocephalus* usually occurs between horizontal surfaces, primarily in forest where a broken and irregular canopy makes travel difficult. Mean ± *SE* intermembral index (a ratio of hindlimb and forelimb length) is 81.85 ± 1.6 ($n = 7$—Boubli 1997; Fleagle and Meldrum 1988).

Thumb is nonopposable. Small objects are grasped by pressure contact at the interphalangeal joint or thenar pad. Hands of *C. melanocephalus* are schizodactylus; thumb and index finger move in tandem and oppose the remaining 3 digits. Schizodactyly facilitates grasping branches, but precludes fine manipulation (Candland and Bush 1995). *C. melanocephalus* mostly uses the 2nd and 3rd digits when grasping branches (Erikson 1957). Dermatoglyphics of *C. melanocephalus* have a low density of whorls and loops (total pattern index $\leq$2.20) and a high palm–sole index (291—Newell-Morris and Nieijrer 1989).

In *C. melanocephalus*, the carpal tunnel is comparatively shallow, reflecting the arboreal quadruped and leaper mode of locomotion of *C. melanocephalus*, a method infrequently requiring hooked hands. Functional analysis of limb bones of *C. melanocephalus* (D. Gebo, pers. comm.) shows hypermobility at hip, elbow, knee, and upper ankle joint; high femoral neck and head angle; very large capitulum; and very dished surface for radial head. Vertebral formula is 7 C, 13 T, 6 L, 3–4 S, 17–20 Ca, total 46–50. Black-headed uacaris have a short, or bobbed, tail less than one-third length of head and body. Tail vertebrae are much reduced in size, with the most distal often very small and ankylosed.

Caecum comprises 60–70% of the digestive tract's total volume. Stomach comprises 5–8% of total gut volume (Ayres 1989). Based on passage times, *C. melanocephalus* eats fruits and seeds (Milton 1984).

Scrotum is sessile and parapenial; baculum is absent; penis, which is large for body size, is complex (Hershkovitz 1993). Distal surface of shaft is convex longitudinally, concave ventrally, subtriangular in cross section. A terminal lappet projects beyond the meatus. Penile shaft is pigmented, tapers to tip, curves upward with a sideways twist of >30°; and has hypertrophied recurved spines for nearly its entire length. Spines up to 1 mm long are formed of overlapping scales of keratinized epidermis, and directed at a variety of angles from the shaft. Penes of juveniles and subadults lack spines. Penile spines have a grappling function and during intromission break apart copulatory plugs (Hershkovitz 1993).

ONTOGENY AND REPRODUCTION. Litter size of *C. melanocephalus* is 1. Infants have only been recorded in March and April. In Pico de Neblina National Park, Brazil, adult female *C. m. melanocephalus* with very small infants occurred in March, the beginning of the rainy season and the period of peak fruit availability (Boubli 1997), and in nearby Venezuela, lactating females occurred in March and April (C. Handley, pers. comm.). On the upper Rio Negro, births occurred around April and babies were carried dorsally in July, the season of highest water and of flooding in the igapó (Cunha and Barnett 1989b). Lower on the Rio Negro, infant *C. m. ouakary* occurred in March (Rylands 1992). In both locations, birthing coincides with the onset of the fruiting season in the igapó. *C. melanocephalus* has not bred in captivity.

ECOLOGY. Both subspecies are known only from margins and interfluvial basins of Amazonian black-water rivers. Here they have been most commonly recorded in the igapó (Barnett and Brandon-Jones 1997), a seasonally inundated forest on the margins of black-water rivers (Prance 1979). Sightings are most frequent during the forest's annual inundation (Barnett and Brandon-Jones 1997; Defler 2001), when fruit availability is highest (Goulding et al. 1988). Although *C. m. melanocephalus* lives in igapó (Lehman and Robertson 1994), *C. m. melanocephalus* from Pico de Neblina National Park, Brazil, lived throughout the year in uninundated *Eperua*- and *Micranda*-dominated caatinga forest (Boubli 1997, 1998).

Cacajao melanocephalus is sparsely or patchily distributed (Barnett and Cunha 1990; Lehman and Robertson 1994; Mittermeier and Coimbra-Filho 1977). Based on 34 days of encounters over a 16-month period, average daily distance traveled was 2,300 m and minimum home range was estimated at 1,053 ha (Boubli 1997). Although ca. 600 *C. m. ouakary* live in the 14,450 ha surrounding Taraira Lake, lower Río Apaporis, Colombia (a density of 4.15 animals/km^2), dispersion of appropriate habitat means effective ecological density is 12 animals/km^2 (Defler 2001).

Cacajao melanocephalus is a sclerocarpic forager (Kinzey and Norconk 1990) and is primarily a predator of hard, unripe seeds of trees (Kinzey 1997a, 1997c). When feeding, *C. melanocephalus* generally shatters hard husks, then extracts and eats the seeds (Kinzey 1992). Black-headed uacaris are seed predators, not seed dispersers (Aquino and Encarnacion 1999).

Fruits of 95 species of tree and 25 liana species occur in the diet of *C. m. melanocephalus* (Boubli 1997, 1998, 1999). Of these, 23% were defined as having soft fruits and 67% were eaten when unripe (Boubli 1999). All have large seeds, protected by dry hard husks, even when ripe. The most frequently eaten species were *Hevea braziliensis* and *Micrandra spruceana* (both Euphorbiaceae) and *Eperua leucantha* (Fabaceae: Caesalpinoidea). Euphorbiaceae and Fabaceae with heavily armored fruits are foraged on in proportion to their frequency in the environment (Boubli 1999). Fruits of lianas are frequent in the diet of *C. melanocephalus* only early in the dry season, when overall fruit availability is low (Boubli 1999). The dry season is also the peak time for consumption of ripe fruits and arils (Boubli 1999). *C. m. melanocephalus* eat young leaves, bromeliad leaf bases, petioles, whole flowers, stamens, and nectar (Boubli 1997). Seeds of *Eschweilera* (Lecythidaceae) are seasonally dominant food items for *C. m. ouakary* (Barnett et al. 2000, 2002; Defler 1989, 1999). These are enclosed in a tough pyxidum with walls up to 4 mm thick. However, of 64 food plants of *C. m. ouakary*, 22 (34%) were either small, thin skinned, or both (Barnett and de Castilho 2000). In the dry season, *C. m. ouakary* may eat large quantities of leaves of *Buchenavia oxicarpa* (Combretaceae), *Eschweilera tenuifolia* (Lecythidaceae), and *Mabea taquari* (Euphorbiaceae—Barnett and de Castilho 2000). Leaf consumption occurs when very little fruit is available.

On the lower Rio Negro, *C. melanocephalus* associates with *Cebus albifrons*, *C. apella*, and *Saimiri sciureus* (Barnett and de Castilho 2000; Mittermeier and Coimbra-Filho 1977), but surveys and observations on the upper Rio Negro suggest *C. melanocephalus* does not associate with other primates (Boubli 1997; Cunha and Barnett 1989b).

Black-headed uacaris have little competition for food. All soft fruit in the diet of *C. m. ouakary* is from abundant species (Barnett and de Castilho 2000). No other sympatric primate eats such hard fruits (Robinson et al. 1987). Although *Chiropotes* has a very similar diet to that of *Cacajao* (Kinzey 1992), the 2 are generally separated by habitat preferences (Ayres 1989) and geographic range (Kinzey 1992, 1997a). Sakis (*Pithecia pithecia*) overlap geographically with *Cacajao*, but are smaller, rarely enter igapó (Peres 1993), use the forests' middle and lower stories, are less specialized for eating sclerocarpic fruits, and include more leaves and soft fruit in their diet than does *Cacajao* (Garber and Kinzey 1992; Kinzey 1997c). *C. m. melanocephalus* and *Chiropotes* overlap in Pico de Neblina National Park (Boubli 2002). Competition occurs between black-headed uacaris and large avian specialist seed-predators, such as macaws (*Ara*—Kinzey 1992; Norconk et al. 1998).

In addition to plant material, animal foods also occur in the diet of *C. melanocephalus*. Active insectivory occurs in *C. m. melanocephalus*, with individuals rummaging for insects in arboreal detritus and in leaf bases of bromeliads (Boubli 1997, 1999). Ingested insects include Formicidae and acridid and tettiginiid Orthoptera. Active insectivory peaked during months of lowest fruit availability. Passive insectivory occurs by ingestion of fruit-eating insects in diet fruits, including pyxidia of *Eschweilera* (Lecythidaceae) and the seeds of *Sloania* (Eleocarpaceae) and pods of *Parkia* (Fabaceae—A. Barnett, pers. comm.; Barnett et al. 2000, 2002). On the upper Rio Negro, *C. melanocephalus* raids the riverbank nests of river turtles (*Podocnemis*) and extracts and eats eggs (Partridge Films 1992).

No nonhuman predators of *C. melanocephalus* are known. Black-backed uacaris are extremely aware of aerial predators, even giving alarm calls to low-flying toucans and vultures (Boubli 1997, 1999). *C. melanocephalus* is little hunted by humans. Although Yanomami Amerindians will hunt black-backed uacaris, they are reluctant to use hard-to-come-by cartridges on black-headed uacaris because they present very difficult targets (Boubli 1997). Tucano Amerindian hunters on the upper Rio Negro have similar preferences (Barnett and Cunha 1990). On Brazo Casíquare, *C. m. melanocephalus* is the most sought-after primate because it often forages close to river banks, making it an easy target for hunters with blow-guns and darts in canoes (Lehman and Robertson 1994). Nonindigenous communities from lower Rio Negro use flesh of golden-backed uacaris in traps for fish, turtle, and forest cats (Mittermeier and Coimbra-Filho 1977). *C. melanocephalus* is sometimes kept as a pet by local people (Cunha and Barnett 1989a).

BEHAVIOR. *Cacajao melanocephalus* lives in mixed-sex, multiple-male, multiple-female groups (Dixson 1987; Kinzey and Cunningham 1994). Group size is relatively large, with reported maxima ranging from 20 to 30 (Ayres 1986; Barnett et al. 2000; Boubli 1999; Fontaine 1981) to 120 (Defler 1989), but small groups of 3–10 also occur (Barnett and Brandon-Jones 1997; Barnett et al. 2002). Black-backed uacaris travel in well-dispersed aggregations, coordinating their movements through constant calling (Boubli 1999). Group spread is generally 200–300 m (Barnett et al. 2000; Boubli 1997). They feed independently on thinly spread resources, only coming together when feeding patches are large and clumped and to rest and sleep (Boubli 1999). No aggressive interactions were observed during a 16-month study of *C. m. melanocephalus* (Boubli 1997).

Tail wagging often accompanies piloerection threat displays and alarm calls that occur on 1st field contact between humans and a group of *C. m. ouakary* (Cunha and Barnett 1989b; Fernandes 1993). In *C. m. melanocephalus*, tail-wagging is a constant aspect of group behavior and accompanies contact calls in foraging groups (Boubli 1997; Fernandes 1993). *C. melanocephalus* gives a 2 syllabled "bi-koh" alarm call, which gives the species its local name over much of Amazonia, and a birdlike twittering contact call of "keeks" and "chicks" (A. Barnett, in litt.; Boubli 1997). Playing juveniles give a "hissing" vocalization (Boubli 1997).

When drinking, *C. m. melanocephalus* immerses a hand in an epiphytic bromeliad or in a water-filled tree hole, then drinks from the cupped hand and wet forearms (Boubli 1997).

GENETICS. In *C. melanocephalus* 2n = 45 for males and 46 for females, with 12 acrocentric pairs, 9 biarmed pairs, 1 heteromorphic pair, a submetacentric X chromosome, and a Y chromosome that has translocated to an acrocentric autosome (Koiffman and Saldanha 1981). Robertsonian translocations have occurred during evolution; *C. calvus* and *C. melanocephalus* have acquired 1 translocation since their divergence (Veigas-Péquignot et al. 1985).

Mitochondrial DNA indicates that *Cacajao* and *Chiropotes* lineages split ca. 9 million years ago and gives a date of 5 million years for the split into *C. calvus* and *C. melanocephalus* (Boubli and Ditchfield 2000).

CONSERVATION STATUS. Numbers of *C. melanocephalus* decline in degraded igapó (Hernández-Camacho and Cooper 1976). No captive breeding programs exist and *C. melanocephalus* is poorly represented in zoos. Formerly listed as Intermediate/Vulnerable by the International Union for the Conservation of Nature and Natural Resources (IUCN), *C. melanocephalus* is now listed as a species of Lower Risk: Least Concern (Rylands et al. 1995). In the long term, its specialized diet and habitat requirements may make it vulnerable to ecosystem disturbance and it may become endangered (Harcourt et al. 2002; Wright and Jernvall 1999). A concentrated seasonal use of flooded forest may have created a false impression that this species is common (Defler 2001).

REMARKS. *Cacajao m. melanocephalus* is widely believed to be closest to the ancestral form of *Cacajao* (Barnett and Brandon-Jones 1997; Boubli 1997; Boubli and Ditchfield 2000; Hershkovitz 1987). The pitheciine monkey stock that gave rise to *Cacajao* had a proposed geographical range within the present range of extant *C. melanocephalus*, with *Cacajao* 1st appearing either in a caatinga (white-sand forest)–chascaval (swamp forest)–terre firme (never-flooded) forest mosaic (Boubli 1997) or in terre firme and montane forests (Boubli and Ditchfield 2000) of western Guyana Shield and secondarily adapted to the igapó and varzéa floodplain forests (Boubli 1997; Boubli and Ditchfield 2000).

Based on morphological (Barnett and Brandon-Jones 1997) and DNA evidence (Goodman et al. 1998), the distinctions separating *Chiropotes* and *Cacajao* are insufficient to distinguish these taxa at more than subgeneric level. If this were implemented, priority would make *Cacajao* a subgenus of *Chiropotes* (Barnett and Brandon-Jones 1997). *Cacajao roosveltii* described by Allen (1914) is a misidentification of *Chiropotes albinasus* (Cruz Lima 1944; Napier and Napier 1967). Reports of *melanocephalus*-type uacaris in the Río Yarapa region of Peru are of the monk saki (*Pithecia monachus*—N. Ward, pers. comm.).

Cacajao is from Baré, a now-extinct Amerindian language from the Rio Uaupes region of northwestern Amazonia. Its meaning is unknown, but may relate to the "kah-kah" long-distance contact calls of *C. melanocephalus* (A. Aikhenvald, pers. comm.). *Uacari* is derived from a Tupí word of uncertain meaning. Regional names for the black-headed uacari include mono-feo ("ugly monkey," Venezuelan–Colombian border region), bicó (onomatopoeic from alarm call, central-western Brazilian Amazonia), rabico ("short-tail"), and macaco mal acabado ("unfinished monkey," both northwestern Brazilian Amazonia). Indigenous names include pîko-tuúru ("short-tail," Tucano), honsho-honshome ("ugly monkey," Yanomami), and tchitchi (onomatopoeic from close quarter contact call, Baniwa—A. Aikhenvald, G. G. Gomez, V. Golla, and D. Moore, pers. comm.; Auricchio and Grantsau 1995; Stradelli 1929).

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