

Paraguayan Primatology: Past, Present and Future

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Abstract: With just five species, the Paraguayan primate fauna is less diverse than its neighbours and, perhaps as a result of this, few biologists have chosen the country for their primate studies. Consequently, the ecological data available for three of the five species that occur in the country is scant, and most of what we know about the other two is based on studies carried out in other countries. This paper collates specimen and literature data about this group to serve as a basis to encourage future research and to correct persistent errors and contradictions. Primate specimens in all the major Paraguayan collections and all significant specimens in international collections were examined. Specimen data were collated and supplemented with literature and photographic data. Distribution data is provided according to a hierarchy of record reliability of examined specimens, specimens that we have not examined, literature records, photographic records and reliable sightings in the wild. Five species have been confirmed to be present in Paraguay, with an additional species (*Callithrix jacchus*) that is feral/introduced, and four species cited in the literature in error. Relevant discussion and distribution maps are provided for each species. The vast majority of primate specimens were collected at least 35 years ago, and the specimen record may no longer represent current distributions given the rapidly changing landscape in the country. We conclude that the available data on the distributions of Paraguayan primates are highly biased towards two species (*Alouatta caraya* and *Sapajus cay*), yet even these are poorly known, and despite most primatological studies to date being focused on the Chaco region (where diversity is greatest), we still lack basic occurrence data or an understanding of the ecological requirements and seasonal movements of most species. However, primatological research in Paraguay has experienced a renaissance in the past five years, and a brief rundown of projects that are currently underway is provided.

Key words: *Alouatta caraya*, *Aotus azarae*, *Mico melanurus*, *Plecturocebus pallescens*, *Sapajus cay*, distributions, taxonomy

Introduction

The primate fauna of Paraguay is relatively poor in diversity with just five species in five families (Fig. 1), considerably less than neighboring Bolivia and Brazil, but the same as Argentina. All Paraguayan monkeys are categorized as Least Concern on the IUCN Red List and are listed in CITES Appendix II (Saldívar *et al.* 2017; Cartes *et al.* 2018), although global conservation reassessments of most species are well overdue.

The distribution, specimen record and bibliographical history of the Paraguayan primates have yet to be properly clarified. We here review the specimens, literature and reliable recent field records with a view to consolidating the available data on the distribution and status of the

Paraguayan primates. We also provide information on current primatological work being carried out in the country.

History of Paraguayan Primatology

The first reports of Paraguayan primates were by Sanchez Labrador (1770) who observed the “dumb and ugly” Carayáa (*Alouatta caraya*) and the “small” Caí (*Sapajus cay*). Azara (1802) then provided detailed natural history information and descriptions for three species: Carayá and Caí as before, and the Miriquiná (*Aotus azarae*), with a fourth species, the Tití (*Callithrix jacchus*) specifically excluded from the Paraguayan fauna. The same three species were also described by Rengger (1830). The remaining two species were documented in the 20th Century.

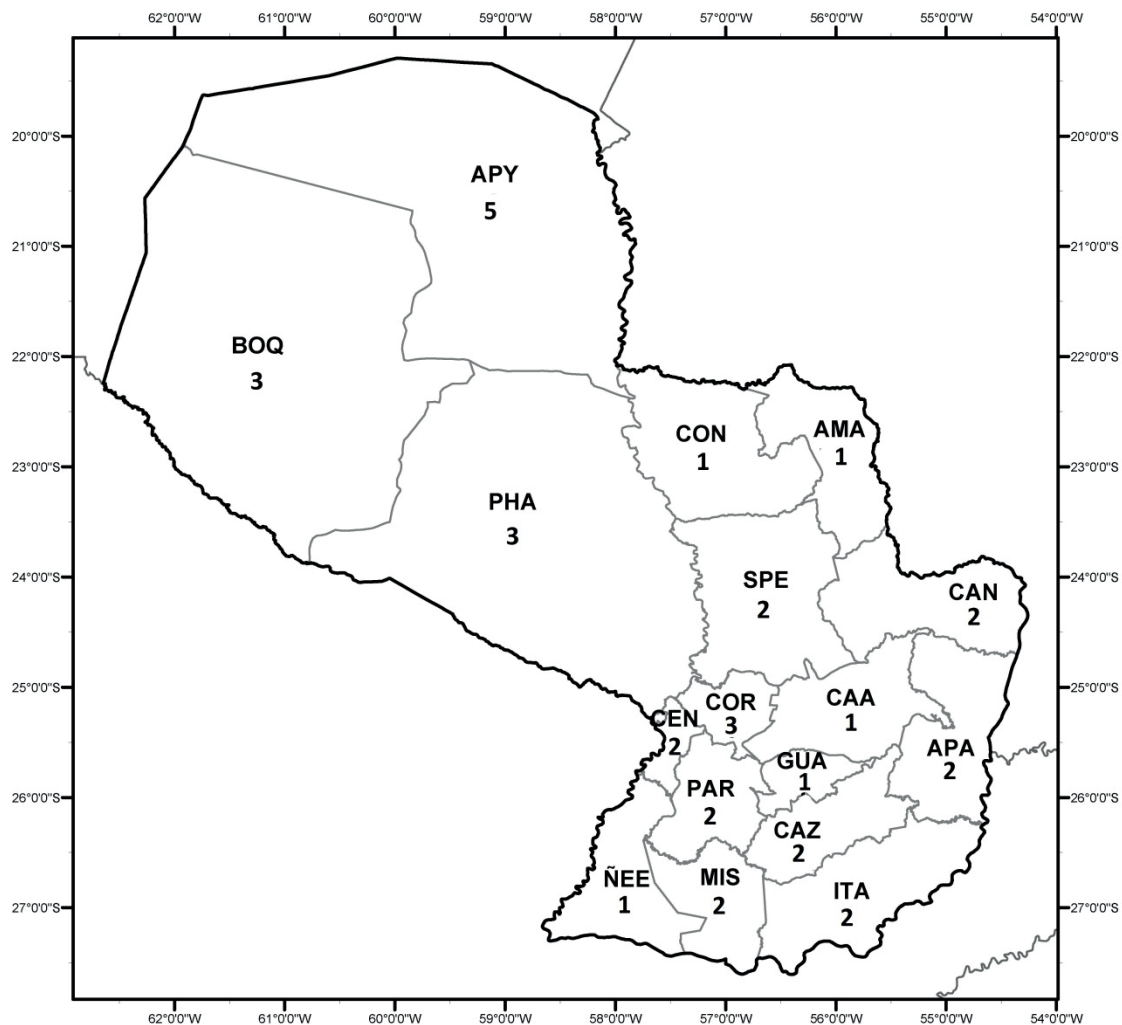


Figure 1. Map showing the political departments of Paraguay and the number of species of primates recorded in each. Departments as follows: Chaco region – Alto Paraguay (APY), Boquerón (BOQ), Presidente Hayes (PHA); Oriental region – Amambay (AMA), Alto Paraná (APA), Caaguazú (CAA), Canindeyú (CAN), Caazapá (CAZ), Central (CEN), Concepción (CON), Cordillera (COR), Guairá (GUA), Itapúa (ITA), Misiones (MIS), Ñeembucú (ÑEE), Paraguari (PAR), San Pedro (SPE).

Callicebus pallescens Thomas, 1907, was newly described from Paraguayan specimens and the first record of the black-tailed marmoset *Mico melanurus* was documented by Stallings and Mittermeier (1983).

Paraguayan primates were largely ignored by researchers until the work of Jody Stallings in the 1980s (Stallings 1983, 1984, 1985; Stallings *et al.* 1989). He provided the first modern assessment of primate distributions in the country, and in the 1980s and 1990s Patricia Wright compared the behavior of Paraguayan and Peruvian night monkeys (Wright 1983, 1989, 1994). Beyond this point, Paraguayan primate publications have consisted largely of occasional natural history notes (Clark 1983; Roguin 1986; Brooks *et al.* 1993; Brooks 1996; Ávila 2004, 2015; Campos *et al.* 2004; Giordano and Ballard 2010; Cabral *et al.* 2017), papers with a biomedical focus (Rosner *et al.* 1984, 1988; Moreno and Rosner 1999; Samudio *et al.* 1999; Diaz *et al.* 2007; Acosta *et al.* 2016), a genetic focus (Mayatoshi *et al.* 1986, 1987;

Mudry and Slavutsky 1987; Schneider *et al.* 1988; Sampaio *et al.* 1991; Martinez *et al.* 2004; Casado *et al.* 2010), and an ethnographical focus (Hill *et al.* 1999, 2003; Cartes 2007; Centrón *et al.* 2007), besides general reviews based on previously published data (Rumiz and Stallings 1989; Gamarra de Fox and Martin 1996; Villalba and Yanosky 2000; Esquivel 2001; Fariña and Hostettler 2003; Yahnke *et al.* 2003; Vinke and Vinke 2008; Horton 2008, 2010; Porter *et al.* 2013; Velázquez and Ramírez Pinto 2014). Lacking are longer-term field studies of wild populations, but a notable exception is the behavioral studies on wild *Sapajus cay* and urban *Alouatta caraya* led by Rebecca Smith (Smith and Briggs 2015; Smith 2017a, 2017b; Smith and Payne 2017; Smith *et al.* 2018; Kane and Smith 2020; Smith *et al.* 2020; Wellian and Smith in press; Duffy *et al.* in press), which have contributed to the global knowledge of these species. The national conservation status of Paraguayan primates was recently reviewed by Cartes *et al.* (2017, 2018).

Materials and Methods

Specimens of primates from the major zoological collections in Paraguay were reviewed during 2017 to 2019. Identifications were confirmed by inspection of the specimens, and locality data was collated from museum databases and specimen labels. Specimens at national park collections are also included, though these collections are uncatalogued, unregistered and specimens are not labelled. Data for these specimens were obtained, when possible by personal communication with the collectors and curators. The location of specimens in foreign museums was gleaned from the literature and from Vert Net (which returned 164 results for “Paraguay Primates”). Specimens considered to represent significant geographical range extensions were reviewed with the assistance of museum curators when feasible. Those that did not present noteworthy distributions were assumed to be correct and not examined. Maps were made using Simplemappr (<https://www.simplemappr.net/>).

Collection acronyms for museums housing Paraguayan primate specimens are as follows: AMNH American Museum of Natural History, New York; BMNH British Museum of Natural History, London; BZM Berliner Zoologisches Museums, Berlin; CBMI Colección Biológica Museo de Itaipú, Hernandarias, Paraguay; CLO Macaulay Library. Macaulay Library Audio and Video Collection; CONN University of Connecticut Museum of Natural History, Storrs, CT; CZPLT Colección Zoológica Para La Tierra, Pilar, Paraguay; DEL Delaware Natural History Museum, Wilmington, DE; MACN Museo Argentino de Ciencia Naturales “Bernardino Rivadavia, Buenos Aires, Argentina; MCNM Museo de Ciencias Naturales de Madrid, Spain; MLP Museo de La Plata, Argentina; MHNG Musée d’histoire Naturelle de Geneve, Switzerland; MNHNP Museo Nacional de Historia Natural del Paraguay, San Lorenzo, Paraguay; PRC Pro Cosara museum based at the headquarters of the NGO Pro Cosara, Estancia Nueva Gambach, Alto Verá, Paraguay; RBINS Royal Belgian Institute of Natural Sciences, Brussels, Belgium; SMNS Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; TTU Museum of Texas Tech University, Lubbock, TX; UMMZ University of Michigan Museum of Zoology, Ann Arbor, MI; USNM National Museum of Natural History, Smithsonian Institute, Washington, DC.

Species accounts begin with the current common name, scientific name and author, which are presented for each species in bold type following Mittermeier *et al.* (2013) and Rowe and Myers (2016). The original described name, author and type locality follow. There then follows a referenced list of the synonyms used in the Paraguayan literature with a (hopefully self-explanatory) single word descriptor of the subject of the publication, as follows: behavior, biogeography, conservation, diet, distribution, ecology, epidemiology, genetics, guide, habitat, list, mention, morphometry, parasitology, pharmacology, report, specimen/s, ssp. description, taxonomy, tracks, type description and use.

The synonymy deals only with Paraguayan literature or literature citing Paraguayan specimens and is not intended to be a complete list of synonyms for the species.

Local names: Local common names published in the Paraguayan literature are provided. We tried to reference the earliest published usage for each name.

Comments: Noteworthy or confusing themes in the Paraguayan literature.

There then follows a “hierarchical reliability” approach to the Paraguayan distribution of each species. This approach is taken so as to not unduly bias understanding by depending solely on the limited specimen record. The hierarchies are, in order of documented reliability: (1) examined specimen; (2) specimen not examined; (3) record from published literature; (4) published photographic record; and (5) reliable field observation by one of the authors or knowledgeable local observer. Records are presented with the political department in bold capitals, followed by the details of the record (in alphabetical order). (Records from the capital Asunción are included in Central department for geographic reasons, though officially it has an autonomous position.) For specimen records this involves the specimen number followed by the locality. These records are also mapped distinguishing the hierarchical categories so that readers may interpret their reliability for themselves. Published photographic records (category 4) and reliable field observations (category 5) include only localities that are not covered by any one of the previous three categories.

The criteria for inclusion of literature records was that it was published in Paraguay or specifically deals with Paraguay or in the case of international publications that it makes specific reference to Paraguayan specimens or primary records. We omit a recent reference (Sequera *et al.* 2019) dealing with primate epizootics in Paraguay as it is not entirely an original work, merely an adaptation of an existing Brazilian manual, as stated by the editors. Every effort was made to be thorough in this regard, though undoubtedly some references will have been missed.

A statement on the ecological affinities of each species in Paraguay is provided based on the ecoregions defined in Guyra Paraguay (2005) and Mereles (2013) (Fig. 2). These can be broadly defined as follows: Atlantic Forest (subtropical humid forests of eastern Paraguay); Cerrado (central South American tropical bush savanna of northern eastern Paraguay); Dry Chaco (low, arid thorn forest and scrub of the western Occidental region); Humid Chaco (palm savanna and marshlands of the Paraguay River Basin; Pantanal (gallery forests and swamps of the north-eastern Chaco); Cerrados del Chaco (an area of Cerrado in the northern Chaco contiguous with the Chiquitania of Bolivia) and Mesopotamian Grasslands (flooded grasslands of the southern Oriental region).

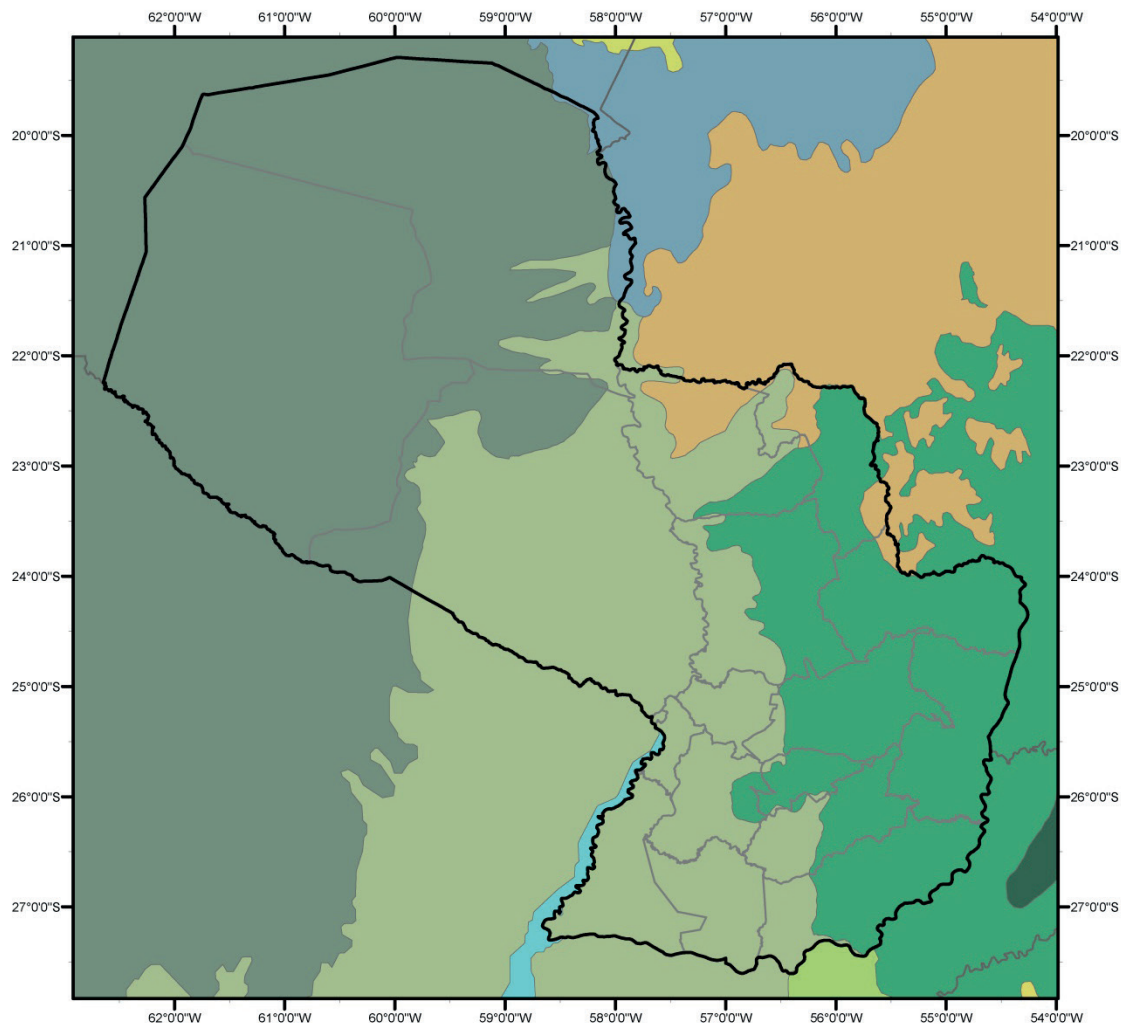


Figure 2. Map showing geographical coverage of all the localities cited in this paper on a base map of the regional ecoregions: Dark Green (Dry Chaco and Cerrados del Chaco); Light Green (Humid Chaco); Orange (Cerrado); Bright Green (Atlantic Forest).

Results

Data for five species of primates in five families are provided. One additional species is introduced/feral and four other species are considered to be erroneously cited and are thus rejected. Distributions for each of the confirmed species are mapped (Figs. 3–7) and levels of hierarchy are distinguished from each other in the map keys allowing future researchers to make their own decisions on the reliability of the records consistent with the demands of their own research.

CALLITRICHIDAE: Marmosets and Tamarins (Fig. 3)

Black-tailed Marmoset *Mico melanurus* (É. Geoffroy Saint-Hilaire, 1812)

Jacchus melanurus É. Geoffroy Saint-Hilaire, 1812: *Rec. Observ. Zool.* 1: 361. Type locality: “Brazil”, restricted to “Cuyubá, Matto Grosso” by Allen (1916).

Callithrix argentata melanura: Stallings and Mittermeier (1983: ecology, distribution); following Hershkovitz (1977; taxonomy, distribution)

Callithrix melanura: Brooks (1996: ecology)

Callithrix argentata: Stallings (1984, 1985: ecology); Stallings *et al.* (1989: ecology); Gamarra de Fox and Martin (1996: distribution, specimens); Dirección de Parques Nacionales y Vida Silvestre (1998: conservation)

Callitrix [sic] *argentata*: Morales (2007: mention)

Mico melanurus: Almeida-Noronha *et al.* (2008: distribution); Cabral *et al.* (2017: distribution); de la Sancha *et al.* (2017: checklist); attributed to *Mico* Lesson, 1840, following Rylands *et al.* (2000) (see also Groves 2004)

Mico argentata: Rumbo (2010: biogeography)

Local names: **GUARANÍ**: Cai poshy (Stallings 1985); Ka’i eléctrico (Dirección de Parques Nacionales y Vida Silvestre 1998); Ka’i pochy (Cartes 2004); Ca’i eléctrico (Morales 2007); **SPANISH**: Mono eléctrico (Dirección de Parques Nacionales y Vida Silvestre 1998); Titi de cola negra (Cartes *et al.* 2017).

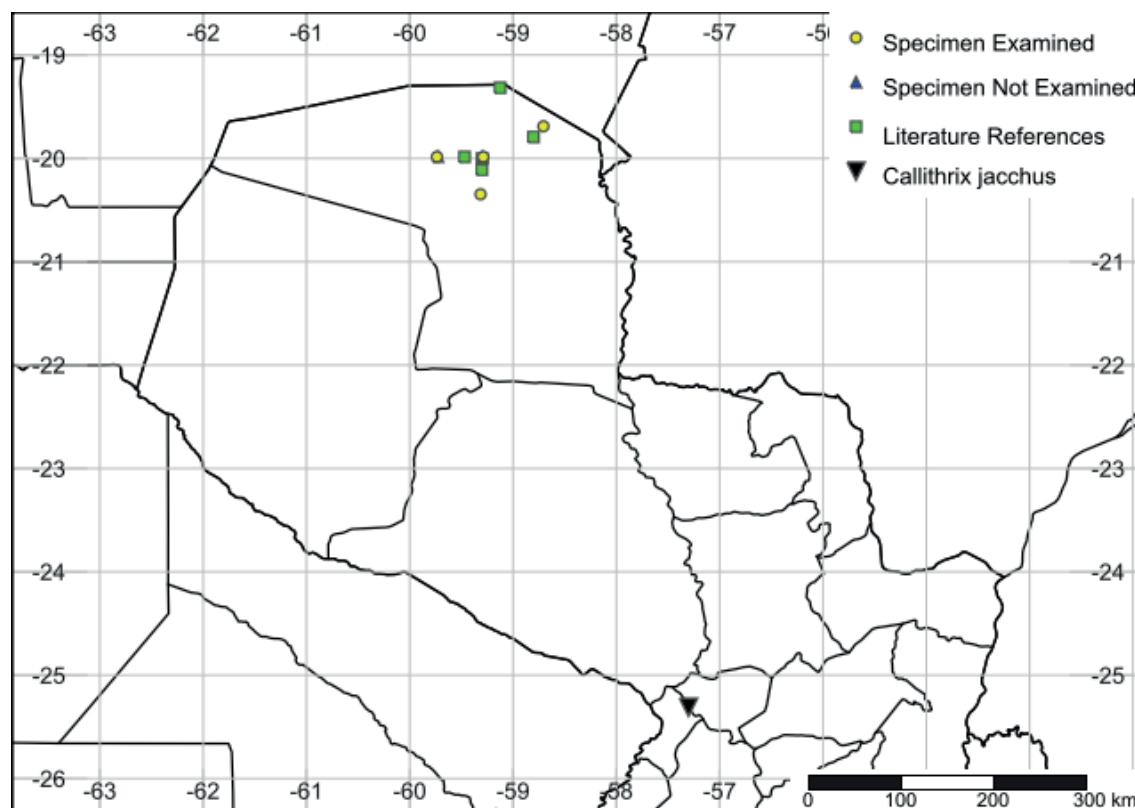


Figure 3. Distribution of *Mico melanurus* (northern Paraguay) and *Callithrix jacchus*.

Comments: The first citation for Paraguay is Stallings and Mittermeier (1983), who also provided some ecological observations. The common name provided by Stallings (1985) Cai poshy is probably intended to be Ka'i pochy, roughly “angry monkey”. A specimen (NMNH 3353) collected by Captain Page during 1852 on the “Paraguay River” lacks precise locality data and may not have been collected in Paraguay. During October 1852, Page received permission from the Paraguayan president Carlos Antonio López to explore the Upper Paraguay River as far as the limits of Paraguayan territory, and reached Bahía Negra (the northern limit) on 25 November of the same year. In defiance of the presidential instructions, however, he continued into Brazilian territory and anchored off Corumbá, state of Mato Grosso do Sul, Brazil, on 1 December (Smith and Bartlett 2009). The specimen could thus have been taken in Brazilian or Bolivian territory.

Geographical distribution: *Mico melanurus* is restricted to the northeastern part of the Chaco region, where it inhabits tall subhumid forests (Stallings 1985; Cabral *et al.* 2017) in a transitional area between the Cerrados del Chaco, Dry Chaco and Pantanal ecoregions (Mereles *et al.* 2013; Cabral *et al.* 2017). This species is considered Vulnerable in Paraguay (Cartes *et al.* 2017, 2018).

Specimens examined: **ALTO PARAGUAY:** 2 km E of Agua Dulce (MNHNP 505; Cabral *et al.* 2017); 54 km E of Agua Dulce (MNHNP 502, 504); 65 km SE of Agua

Dulce (MNHNP 503); Estancia Punto Alto (19°41'23"S, 58°42'22"W) (MNHNP 3358).

Specimens not examined: **ALTO PARAGUAY:** 3 km E of Agua Dulce, PN Defensores del Chaco (NMNH 555657); 48 km E of Agua Dulce on Linea 1 (UMMZ 158045).

Literature references: **ALTO PARAGUAY:** 20 km W of Mbarigui (19°47'38.95"S, 58°48'07.73"W) (Cabral *et al.* 2017); 30 km E of Aguadulce (Stallings and Mittermeier 1983); 48 km E of Aguadulce, 1.9 km S of Linea 1 (Stallings and Mittermeier 1983); 48 km east of Aguadulce, 14 km S of Linea 1 (Stallings and Mittermeier 1983); Choverca (Cartes *et al.* 2017).

Common Marmoset *Callithrix jacchus* (Linnaeus, 1758)

Comments: A group of approximately 10 individuals lives as a feral troop in the grounds of the Hotel del Lago, San Bernardino, department of Cordillera, with some additional individuals reported free at nearby Altos and Atyrá, in the same department. The San Bernardino troop was introduced by the owners of the hotel and is fed by them, but is free-living. The species also appears on a stamp printed in Paraguay in 1985 as part of the “Nature Protection – Animals of Paraguay” issue. We are aware of reports dating back several decades, and this species, native to Northeast Brazil, is feral/introduced in Paraguay.

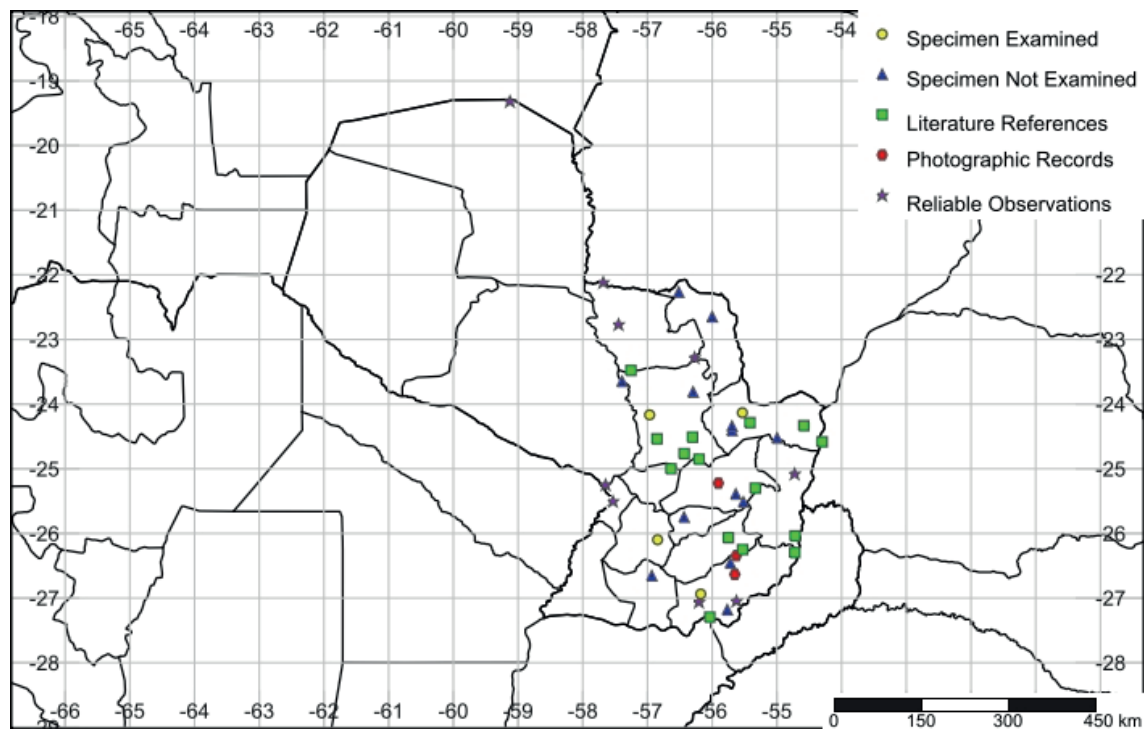


Figure 4. Distribution of *Sapajus cay* in Paraguay.

CEBIDAE: Capuchins and Squirrel Monkeys (Fig. 4)

Hooded Capuchin *Sapajus cay* (Illiger, 1815)

Callithrix Cay Illiger, 1815: *Abd. K. pr. Akad. Wiss.* p.107.

Type locality “left bank of the Río Paraguay, Paraguay.”

Cebus azarae: Rengger (1830: ecology, type description); Burmeister (1869: mention); Elliot (1913: taxonomy)

Cebus fatuellus: Bertoni (1914: list)

Cebus libidinosus: Bertoni (1914: list); Bertoni (1939: list);

Ávila (2004: morphometry, taxonomy)

Cebus fatuellus azarae: Bertoni (1939: list)

Cebus apella azarae: Pusch (1941: description)

Cebus apella morrulus: Pusch (1941: p.207, ssp. description, type locality “Santa Barbara, Central Paraguay”)

Cebus apella chacoensis: Pusch (1941: p.208, ssp. description, type locality “Chaco Paraguayo”)

Cebus apella: Servicio Forestal Nacional (1982: guide); Travi *et al.* (1982: parasitology); Stallings and Mittermeier (1983: mention); Clark (1983: report); Stallings (1984, 1985: ecology); Stallings *et al.* (1989: mention); Matayoshi *et al.* (1986: genetics); Matayoshi *et al.* (1987: genetics); Ferro *et al.* (1988: pharmacology); Rosner *et al.* (1988: parasitology); Rosner *et al.* (1988: parasitology); Ferro *et al.* (1990: pharmacology); Jara Yörg *et al.* (1990: pharmacology); Brooks *et al.* (1993: distribution); Brooks (1996: ecology); Gamarra de Fox and Martin (1996: distribution, specimens); Lowen *et al.* (1996: distribution); Hill *et al.* (1997: use); Dirección de Parques Nacionales y Vida Silvestre (1998: conservation); Szapkievich *et al.* (1998: genetics); Yahnke *et al.* (1998: distribution); Samudio *et al.* (1999: parasitology); Hill and Padwe (2000: use); Villalba and Yanosky (2000:

tracks); Esquivel (2001: guide); Cartes (2003: list); Fariña and Hostettler (2003: distribution); Hill *et al.* (2003: use); Cartes (2007: use); Morales (2007: list); Horton (2008: mention); Vera de Bilbao (2009: epidemiology); Itaipú Binacional (2010: guide); Rumbo (2010: biogeography)

Cebus apella paraguayanus: Roguin (1986: distribution); Matayoshi *et al.* (1986: genetics); Matayoshi *et al.* (1987: genetics); Mudry de Pargament and Slavutsky (1987: genetics); Schneider *et al.* (1988: genetics); Sampaio *et al.* (1991: genetics); Szapkievich *et al.* (1998: genetics); Martínez *et al.* (2004: genetics)

Cebus appella [sic] *paraguayanus*: Sampaio *et al.* (1991: genetics)

Cebus libidinosus paraguayanus: Ávila (2004: morphometry, taxonomy); Aristide *et al.* (2014: morphometry, taxonomy)

Cebus sp.: Roig *et al.* (2009: epidemiology)

Cebus (*Sapajus*) *cay*: Casado *et al.* (2010: genetics)

Cebus paraguayanus: Soria (1959: anatomy); Masi Pallarés (2011: ecology)

Cebus (*apella*) *cay*: Centrón *et al.* (2013: use)

Cebus nigrilus: Velázquez and Ramírez Pinto (2014: guide)
Sapajus cay: Ávila (2015: morphometry, taxonomy); Smith and Briggs (2015: demography); Acosta *et al.* (2016: parasitology); Cabral *et al.* (2017: mention); de la Sancha *et al.* (2017: checklist); Smith (2017a, 2017b: behavior); Smith and Payne (2017: pharmacology); Smith *et al.* (2018: behavior); Smith *et al.* (2020: behavior)

Local names: **ACHÉ**: Pua’á (Villalba and Yanosky 2000); Pua’a (Esquivel 2001); Fuakumba (Centrón *et al.* 2013); Puaa (Centrón *et al.* 2013); **GUARANÍ**: Caí

(Sanchez-Labrador 1770); Caimiri (Azara 1801); Caý (Azara 1801); Caygüazú (Azara 1801); Mihi (Rengger 1830); Kaái (Bertoni 1914); Cai comun (Stallings 1985); Ka'i Paraguay (Villalba and Yanosky 2000); Ka'i (Cartes 2003); Ca'i Paraguay (Morales 2007); **SPANISH:** Capuchino (Servicio Forestal Nacional 1982); Mono capuchino marrón (Esquivel 2001); Mono capuchino (Morales 2007); Capuchino marrón (Horton 2008); Mono caí (Velázquez and Ramírez Pinto 2014); Mono capuchino de Azara (Cartes *et al.* 2017). The local indigenous name Cay (and variations) means “resident of the forests” (Rengger 1830).

Comments: The nomenclatural history of this form is extremely complex. The “robust capuchin” genus *Sapajus* Kerr, 1792, was long considered to be part of the genus *Cebus* Erxleben, 1777, but they form two distinct, monophyletic clades (Lynch Alfaro *et al.* 2012a; Martins Jr. *et al.* 2018). Elliot (1913) split the capuchins into two groups: those with “heads without tufts on males” and those with “heads with tufts or ridges on males”. Hershkovitz (1949, 1955) agreed with this separation but argued that *Cebus apella* should be classed as a member of the tufted group. Hill (1960) reduced the 12 recognized species of tufted capuchin to one, *Cebus apella*, with 16 subspecies. Groves (2001) recognized four species (*C. apella*, *C. libidinosus*, *C. nigritus* and *C. xanthosternos*) with 13 subspecies. The tufted (*Sapajus* Kerr, 1792) and untufted (*Cebus* Erxleben, 1777) capuchins were classified as separate subgenera by Silva Jr. (2001) and as separate genera by Lynch Alfaro *et al.* (2012b) based on their morphologies. Genetic studies have since confirmed that *Sapajus* and *Cebus* diverged around the late Miocene epoch, possibly as a result of the establishment of the Amazon River (Hoorn *et al.* 2010; Halsam 2012; Lynch Alfaro *et al.* 2012a; Martins Jr. *et al.* 2014).

The correct name applicable to the species has also been much debated (Elliot 1913; Cabrera 1917, 1939, 1957; Hill 1960; Torres 1983; Mantecon *et al.* 1984; Brown and Rumiz 1985; Mudry 1990; Zunino and Mudry 1993; Ponsà *et al.* 1995; Groves 2001; Silva Jr. 2001; Martínez *et al.* 2002, 2004; Ávila 2004; Casado *et al.* 2010; Rylands *et al.* 2012; Aristide *et al.* 2014). And numerous subspecies and species have been described on the basis of Paraguayan type material (Rengger 1830; Pusch 1941).

The first citation for Paraguay is the Caý of Azara (1801: No.62 Tome 2: 182–194), who described it as “more scarce” than *Alouatta caraya* and provided a detailed description and biological data. He noted the use of two common names Caygüazú (“big monkey”) and Caimiri (“little monkey”) which he attributed to differing ages. The species was then subsequently given the name *Callithrix cay* by Illiger (1815) based on Azara’s description. Unaware of this, Rengger (1830) later described *Cebus azarae* based partly on the same description and provided additional biological details from his own observations.

Bertoni (1914, 1939) listed two species in this genus for Paraguay stating that *C. libidinosus* had a “longer tail” than *C. fatuellus* and 23 as opposed to 22 “free vertebrae.” He

noted, however, that the character was variable and “not of great value.” Both of these in fact refer to this same species.

Pusch (1941) described two subspecies from Paraguay (neither of which is currently considered valid), which he recognized in addition to the form *azarae* Rengger, 1830, and all of which he treated under the species name *Cebus apella*. One of these was a supposed Chaco subspecies *chacoensis*, but no precise locality was provided. Stallings (1985) surmised that it may have been based on a pet.

The species is the second most hunted and third most important mammal species by biomass in the diet of the Aché indigenous tribe of the Mbaracayú Reserve, Canindeyú department (Hill *et al.* 1997, 2003). It is used in local medicine to treat coughs, pain, anthrax and skin afflictions, and to increase intelligence (Cartes 2007).

Sapajus cay has long been used in the region as a species for biomedical (mainly physiology and parasitology) research in laboratories. A compilation of previous works made on the subject with Paraguayan specimens or by Paraguayan researchers was edited by Moreno Azorero and Rosner (1989) but it unfortunately failed to properly cite the original works or to mention authors. These works were identified by cross-referencing with a list of literature included at the end of the book and only the original sources are cited here. A similar case occurs with Rosner and Kawabata (1990) who edited a monograph on Chagas’ disease in Paraguay, including both unpublished and previously published works, many of them concerning Paraguayan *Sapajus*.

Geographical distribution: Distributed mainly in eastern Paraguay where it is associated with the Atlantic Forest and Cerrado eco-regions. It occurs in gallery forest, Cerradón, and Atlantic Forest and can tolerate considerable habitat modification provided it is not hunted (Smith and Briggs 2015; Smith 2017a, 2017b; Smith and Payne 2017). It extends marginally into the northern Chaco in the Cerrados del Chaco ecoregion, although the status of the species there requires confirmation, and may also extend very marginally into gallery forest in the extreme southeast of the department of Ñeembucú (Álvaro Vera pers. comm.). The distribution maps provided by Stallings (1985) and the IUCN Red List show a wide distribution throughout Ñeembucú, which is not supported by the data, and indeed the swamps of the Humid Chaco ecoregion possibly act as a barrier to its distribution.

The population in the Jardín Botánico of the capital city Asunción is of uncertain origin. In 2017, staff members at the Asunción Zoological Gardens informed author Rebecca Smith that they had been releasing their surplus animals and difficult individuals (surrendered pets) into the forested area there, making it impossible to determine whether the species occurs there naturally or if the entire population is of captive origin. The zoo has also released surplus primates in unspecified localities on the west bank of the Paraguay River close to Asunción (where the species is not known to occur naturally), and the status of these populations is unknown. At least one, extremely dark individual

resembling (from photos) the black-horned capuchin *Sapajus nigritus* was released west of the Paraguay River during one of these campaigns.

Two specimens (AMNH 139998, 139999) collected by Pedro Willim on 10 April 1941 with the vague locality of “Boquerón, Paraguay” are considered unlikely to have been collected in the department of Boquerón, and probably came from elsewhere. Willim did collect in the Chaco along the Pilcomayo during late April and early May 1941, but these specimens are two weeks earlier than the earliest specimens of other species with Pilcomayo collection data. We, therefore, consider the provenance of these specimens to be doubtful.

The populations at Rancho Laguna Blanca, San Pedro department (2013–2017), and Estancia Nueva Gambach, Itapúa department (2017 to present) are being extensively studied by Rebecca Smith and students of the Para La Tierra Centro IDEAL research center (<www.paralatierra.org>), based in Pilar (Smith and Briggs 2015; Smith 2017a, 2017b; Smith and Payne 2017; Smith *et al.* 2018; Smith *et al.* 2020).

Specimens examined: **CAAGUAZÚ:** No locality (MNHNP 1191); **CANINDEYÚ:** “Aché Tribe” (= Reserva Mbaracayú?) (MNHNP 815); Estación Biológica Reserva Mbaracayú (24°08'S, 55°32'W) (MNHNP 2035, 2036); Reserva Mbaracayú (24°7'S, 57°55'W) (MNHNP 1158, 1159, 1160); Reserva Mbaracayú (24°08'S, 56°56'W) (MNHNP 2041, 2046, 2047, 2050); Reserva Mbaracayú (24°10'S, 56°58'W) (MNHNP 2039, 2051); **ITAPÚA:** Acceso a Yatai (PRC); **PARAGUARÍ:** Parque Nacional Ybycuí (MNHNP 488).

Specimens not examined: “Paraguay” BZM 16405, 24322 (Pusch, 1941); MACN 30.190, 40.189, 47.364, 47.365 (Aristide *et al.* 2014); MCZ-BOM 6334, MHNG 1968.079, MLP 980 (Aristide *et al.* 2014); BMNH 1846.2.13.2, 1846.3.17.20, 1971.3224; RBINS 440580, 440581, 445456; SMNS 5554 (Pusch, 1941); USNM 502151, 502152, 502153, 502154, 502155, 502156, 502157, 502158, 502159, 503404, 503405, 503406, 503407, 503408, 503409, 503410, 503411, 503412, 522989, 534986, 534987, 534988, 534989, 534990, 534991, 534992, 534993, 534994, 534995, 534996, 534997, 534998, 534999, 535000, 535001, 535002, 535003, 535004, 535005, 535006, 535007, 535008, 535009, 535010, 535011; “Alto Paraná” CBMI 75; “Chaco paraguayo” BZM 38745 (type of *Cebus apella chacoensis* Pusch, 1941); **AMAMBAY:** 15 km S of Bella Vista (MHNG 1629.001, 1629.002); 28 km SW of Pedro Juan Caballero (UMMZ 125249); **CAAGUAZÚ:** 1 km ENE Colonia Sommerfeld (USNM 293143); 1 km NW Colonia Sommerfeld (USNM 293141, 293142); Río Guyraunguá (MCZ 28679); **CANINDEYÚ:** 6.3 km by road NE of Curuguaty (UMMZ 124694); 13.3 km by road N of Curuguaty (UMMZ 126129, 126130); Pozuelo (CBMI 49); **ITAPÚA:** 8 km N of San Rafael (UMMZ 126131); Capitán Meza (MACN 47.365, 47.366, Soria 1959); Hotel El Tirol, Capitán Miranda (MVZ 96); **GUAIRÁ:** Villarrica (BMNH 1973.R.350); **MISIONES:** 2.7 km by road N of San Antonio (UMMZ 124695,

124696); **SAN PEDRO:** Puerto Ybapobo (FMNH 26651, 26652); Santa Barbara Central-Paraguay (BZM 44290; type of *Cebus apella morrulus* Pusch, 1941).

Literature references: **ALTO PARANÁ:** Estancia San Antonio (Brooks *et al.* 1993); Parque Nacional Ñacunday (Stallings 1985); Reserva Nacional Kuri’y (Stallings 1985); **AMAMBAY:** Parque Nacional Cerro Corá (Stallings 1985); **CAAGUAZÚ:** Estancia Kaa’gua Rory (Lowen *et al.* 1996); Santa Catalina (Matayoshi *et al.* 1986; Matayoshi *et al.* 1987; Schneider *et al.* 1988; Sampaio *et al.* 1991; Casado *et al.* 2010); **CAAGUAZÚ/CANINDEYÚ:** Estancia La Golondrina II (Brooks *et al.* 1993); **CAAZAPÁ:** Parque Nacional Caaguazú (Stallings 1985); Reserva Ecológica Caaguazú (Lowen *et al.* 1996); Reserva Natural Tapytá (Velázquez and Ramírez Pinto 2014); **CANINDEYÚ:** Reserva Bosque Mbaracayú (Brooks *et al.* 1993; Hill *et al.* 1997; 2003); Reserva Natural Privada Itabó (Brooks *et al.* 1993; Lowen *et al.* 1996); Reserva de Patrimonio Aché de Kuetuvy (Centrón *et al.* 2013); **CORDILLERA:** Reserva Natural Privada Sombrero (Lowen *et al.* 1996); **ITAPÚA:** Encarnación (Martinez *et al.* 2004); San Rafael National Park (Horton 2008); **SAN PEDRO:** Compañía General Cáceres (Acosta *et al.* 2016); Compañía San Fernando (Acosta *et al.* 2016); Compañía Tuyango (Acosta *et al.* 2016); Itacurubí del Rosario (Rosner *et al.* 1988, 1989); Rancho Laguna Blanca (Smith and Briggs 2015; Smith 2017a, 2017b; Smith and Payne 2017); South bank of Río Ypané near Belén (Sanchez Labrador 1770); Vy’a Renda (Acosta *et al.* 2016).

Photographic records: **ALTO PARANÁ:** Tatí Yupí (SDR); **CAAZAPÁ:** Arroyo Cristal, Cordillera de Caaguazú (CLO-ML 143529); San Carlos, Cordillera de Caaguazú (CLO-ML 144233); San Rafael National Park (CLO-ML 143529); **ITAPÚA:** Estancia Nueva Gambach (Silvia Qu FPMAM 374–379PH).

Reliable observations: **ALTO PARAGUAY:** Chovoreca (Hugo Cabral); **ALTO PARANÁ:** Reserva Biológica Itabó Itaipú (PS); **AMAMBAY:** Estancia Ka’i Rague (Hugo del Castillo, Oscar Rodríguez); **CENTRAL:** Jardín Botánico de Asunción: (PS, SDR); Ruta Villeta-Alberdi (Luis Doldán); **CONCEPCIÓN:** Arroyo Tagatiyá Guasu (Hugo del Castillo); Arroyo Tagatiyá Mi (Juan Klavins); Estancia Estrella (Hugo del Castillo); **ITAPÚA:** Reserva Chopi Say’ju (Roberto Derna); Reserva Ecológica Grupo Selecta, Bella Vista Sur (PS).

AOTIDAE: Night Monkeys (Fig. 5)

Azara’s Night Monkey *Aotus azarae* (Humboldt, 1812)

Simia Azarae Humboldt, 1812: *Rec. Obs. Zool. Anat. Comp.*, p.359. Type locality “Paraguay”, restricted to “the right bank of the Río Paraguay in northeastern Argentina” by Elliot (1913).

Nyctipithecus trivirgatus: Rengger (1830: ecology); Burmeister (1869: mention); Kerr (1891: distribution)

Nyctipithecus azarae: Bertoni (1914, 1939: distribution)

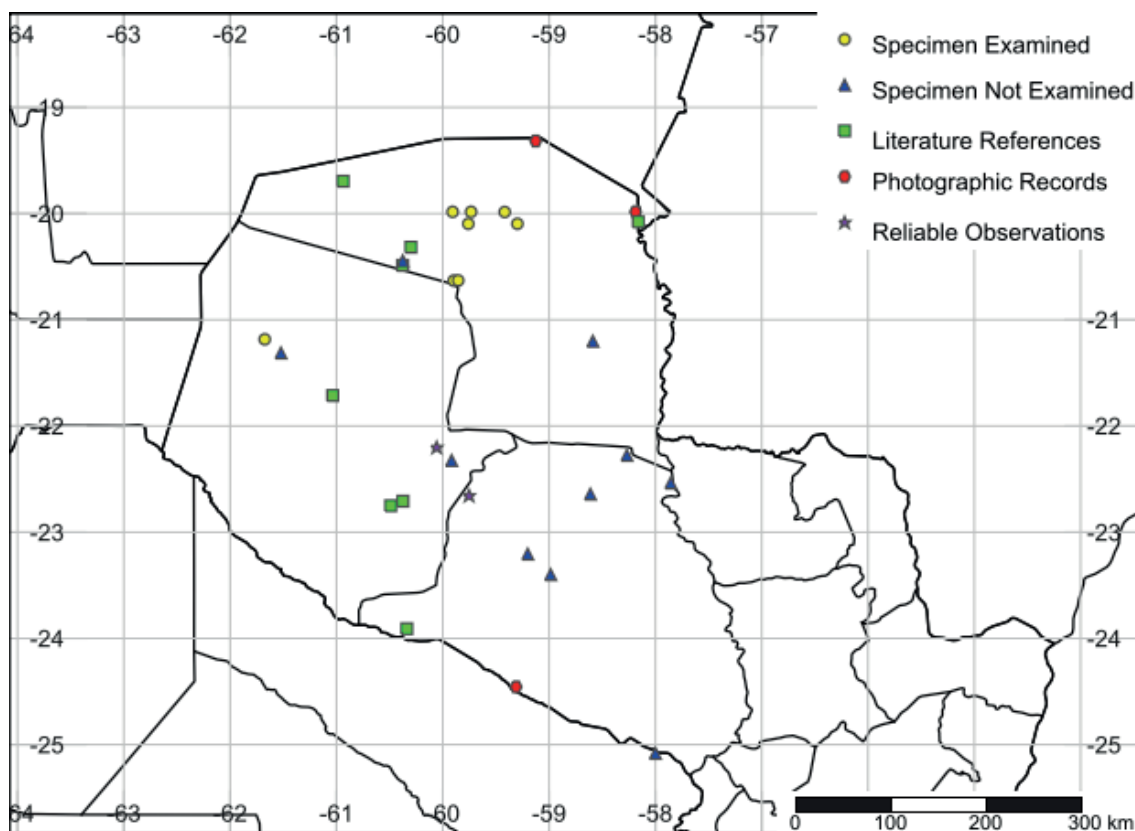


Figure 5. Distribution of *Aotus azarae* in Paraguay.

Aotus azarae: Allen (1916: specimen); Hershkovitz (1983: taxonomy, distribution); Stallings (1984, 1985: ecology); Stallings *et al.* (1989: ecology); Brooks (1996: biology); Cartes (2003: list); Itaipú Binacional (2010: guide); Masi Pallarés (2011: ecology); Cabral *et al.* (2017: mention); de la Sancha *et al.* (2017: checklist); Sánchez *et al.* (2019: ethnology); Weiler *et al.* (2019: field guide).

Aotus trivirgatus: Wright (1983: behavior); Whitaker and Abrell (1987: parasitology).

Aotus trivirgatus azarae: Cabrera (1959: mention); Wetzel and Lovett (1974: specimens); Roguin (1986: distribution)

Aotus sp.: Stallings and Mittermeier (1983: mention)

Aotus azarae: Gamarra de Fox and Martin (1996: distribution, specimens); Dirección de Parques Nacionales y Vida Silvestre (1998: conservation); Yahnke *et al.* (1998: distribution); Villalba and Yanosky (2000: tracks); Ziegler *et al.* (2002: distribution); Campos *et al.* (2004: distribution); Morales (2007: list); Vinke and Vinke (2008: guide); Rumbo (2010: biogeography).

Local names: **AYOREO:** Ñame caate (Sánchez *et al.* 2019); **GUARANÍ:** Miriquiná (Azara 1801); Mirikina (Renger 1830); Mirikiná (Bertoni 1914); Cai pyhare (Stallings 1985); Mbirikina (Stallings 1985); Ka'i pyhare (Villalba and Yanosky 2000); Mbirikiná (Villalba and Yanosky 2000); Ca'i mirikiná (Morales 2003); Mirikiña (Masi Pallarés 2011); **LENGUA-MASCOY:** Kyilineat (Stallings 1985); **MANJUI:** Laynakit (Stallings 1985); **SPANISH:** Mono nocturno (Cartes 2007); Mono de la noche (Itaipú

Binacional 2010); Mono nocturno de Azara (Cartes *et al.* 2017); Mono de noche (Weiler *et al.* 2019).

Comments: The first citation for Paraguay is the Miriquiná of Azara (1801: No. 63 Tome 2: 195–199). He states that the species is absent from the Oriental region and confined to the Chaco and provides a detailed description. This was echoed by Bertoni (1939) who stated that the species occurs in the Paraguay River basin and that he had never found it in the forests of Alto Paraná. Although Stallings (1985) mentions rumors of the species east of the Paraguay River by indigenous groups there are still no records in the Oriental Region to this day (although a feral population of released individuals is present in the Jardín Botánico de Asunción). Given what we know about the habitat requirements of this species, its natural occurrence over most of the Oriental region seems improbable. However, local reports (residents of Pilar to RS pers. comm.) from the department of Ñeembucú, an area of humid Chaco on the eastern banks of the Paraguaya River similar to the habitat in the department of Presidente Hayes, where the species is known to occur, may have substance and are worthy of investigation.

Forbes (1896) ignored Azara, providing a geographically confused distribution that the species occurs on the “right bank of the River Paraguay, in the north-east of the Argentine Republic, but not in Paraguay proper” (p.170). Elliott (1913) used the name *Aotus miriquouina* (É. Geoffroy, 1812) which was also based on Azara’s description for the species, borrowing part of Forbes (1896) distribution

in restricting the type locality to “right bank of the River Paraguay, north-eastern part of the Argentine Republic.” (p.11). Until that moment the priority of the name *Aotus miriquouina* (É. Geoffroy, 1812) over *Aotus azarae* was still assumed, as the publication date of Humboldt’s *Recueil d’Observations de Zoologie et d’Anatomie* was thought to be 1815.

Use of the masculine form of the species name *Aotus azarai* was promoted as an emendation to *A. azarae* Humboldt, 1811 by several authors (Groves 1989, 2001; Aquino *et al.* 1990; Gozalo and Montoya 1990) supposedly to comply with Article 31 of the Code of Zoological Nomenclature (Garbino and Costa 2015). However, when recognized as a Latin name, Azara (of Félix de Azara) gives *azarae* and should not be emended (Brandon-Jones *et al.* 2007; Dubois 2007).

The species is reported to be diurnal in the Argentine Chaco (Fernández-Duque and Ekert 2006) or to be most active at dawn and dusk (Fernández-Duque *et al.* 2010), but is apparently active by day and by night in the Paraguayan Chaco (Wetzel and Lovett 1974; Wright 1983). Seasonal nocturnal activity seems unlikely as animals were observed feeding close to midnight at Cerro León during mid-winter (11 August 2015) and emerging from tree roosts shortly after sunset during late spring (12 October 2017), while a troop 2 km north of Cruce Los Pioneros, Presidente Hayes, was active mid-morning on 22 September 2014 (Paul Smith). In the Argentine Chaco nocturnal activity is associated with the lunar cycle, with activity inhibited by a lack of moonlight (Fernández-Duque *et al.* 2010).

In the Paraguayan Humid Chaco, they appear to randomly select sleeping locations rather than reusing specific sleeping sites, hold home ranges about half the size of those in Peru (5 ha), and maintain a shorter daily path length (Wright 1994). Night monkeys in Paraguay are omnivorous but eat significantly more leaves in winter and insects and flowers in spring (Wright 1994). Individuals at Estancia Iparoma were seen to eat flowers of the Samu’u tree (*Ceiba chodatii*, Malvaceae).

Geographical distribution: Apparently restricted to the Paraguayan Chaco in the departments of Boquerón, Alto Paraguay and Presidente Hayes, where it is widespread in the ecoregions of Dry and Humid Chaco, Cerrados del Chaco and Pantanal. It has been observed in forested hedgerows in heavily-modified agricultural environments in the central Chaco, suggesting a tolerance for habitat modification.

Specimens examined: **ALTO PARAGUAY:** 1 km W of Madrejón Parque Nacional Defensores del Chaco (MNHNP 492); 3 km E of Agua Dulce administration Parque Nacional Defensores del Chaco (MNHNP 491); 18 km W of Agua Dulce (MNHNP 490); 35 km E of Agua Dulce on Línea 1 (MNHNP 497); 54 km E of Agua Dulce 14 km S of Línea Vieja (MNHNP 500, 501); Línea 16, 12 km S of Línea 1 Parque Nacional Defensores del Chaco (MNHNP 496); Parque Nacional Defensores del Chaco 3 km E of administration on Línea Z (MNHNP 499); **BOQUERÓN:** No

locality (MNHNP 1113); Parque Nacional Teniente Enciso, Picada Boliviana 3 km N of administration (MNHNP 498).

Specimens not examined: “Paraguay” (RBINS 448617, 448618); **ALTO PARAGUAY:** 50 km WNW of Madrejón, Misión Nuevo Tribu (UMMZ 124692, 124693, 125577); Puerto Casado, 7 km SW of Laguna General Díaz (FMNH 54331, 54332); **BOQUERÓN:** 15 km S of PN Tte Enciso, 4.5 km E of Transchaco (UF 20657); Orloff (FMNH 63864); 50 km WSW of Madrejón (AMNH 248393); **PRESIDENTE HAYES:** 30 km W of Puerto Casado on the rail road (FMNH 54333); 80 km W of Puerto Pinasco (USNM 236351); Central Chaco, 100 km N of Concepción (BMNH 1894.3.6.3, 1894.3.6.4); Estancia Apendice km 293 Ruta Transchaco (MHNG 1689.064); Left bank of Río Verde, 3 km N of line camp Juan de Salazar (DEL, CONN 16609, Wetzel and Lovett 1974); Río Negro (AMNH 36508, 36509, 36510).

Literature references: **ALTO PARAGUAY:** Cerro León (Campos *et al.* 2004); Estación Biológica Tres Gigantes (González *et al.* 2019); Estancia San José (Brooks 1996); “surroundings of 20°19’S 60°18’W” (Ziegler *et al.* 2002); **BOQUERÓN:** Neuwestland (Ziegler *et al.* 2002); “outside of Neuland” (Campos *et al.* 2004); Teniente Ochoa (Wetzel and Lovett 1974); **PRESIDENTE HAYES:** Río Pilcomayo, at mouth of Río Negro, about 100 miles west of Asunción (Kerr 1891; Allen 1916); Parque Nacional Tinfunque (Stallings 1985).

Photographic records: **ALTO PARAGUAY:** Picada Chovoreca (CLO-ML 195379); **BOQUERÓN:** Fortín Patria (José Luis Cartes); **PRESIDENTE HAYES:** Estancia La Golondrina (CLO-ML 90200, 90201, 90202, 90203, 90204, 90205, 90206).

Reliable observations: **BOQUERÓN:** Estancia Iparoma (PS); **PRESIDENTE HAYES:** 2km north of Cruce Los Pioneros (PS).

PITHECIIDAE: Titis, Sakis and Uacaris (Fig. 6)

White-coated Titi Monkey *Plecturocebus pallescens* (Thomas, 1907)

Callicebus pallescens Thomas, 1907: *Ann. Mag. Nat. Hist.*, ser. 7, 20: 161. “Chaco of Paraguay: 30 miles N of Concepción.”

Callicebus pallescens: Thomas (1907: description); Elliot (1912: taxonomy); Cartes (2003: list); Horton (2010: mention); Rumbo (2010: biogeography); Porter *et al.* (2013: conservation); Cartes (2015: ecology); Boyle (2016: conservation); Cabral *et al.* (2017: mention)

Callithrix sciurea: Bertoni (1914: list, see hypothetical sp.)

Callicebus moloch: Stallings and Mittermeier (1983: mention); Stallings (1984, 1985: ecology); Stallings *et al.* (1989: ecology); Hugot *et al.* (1994: parasitology); Brooks (1996: ecology)

Callicebus moloch donacophilus: Roguin (1986: distribution)

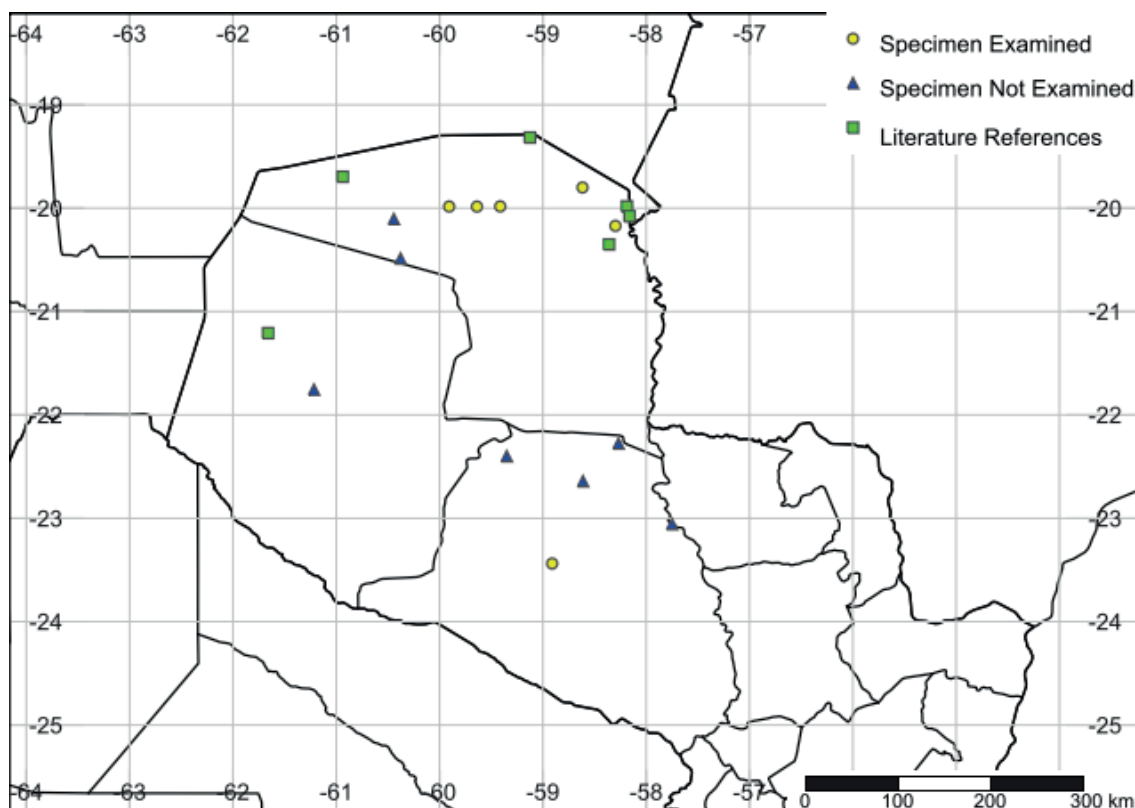


Figure 6. Distribution of *Plecturocebus pallescens* in Paraguay.

Callicebus donacophilus pallescens: Hershkovitz (1990: taxonomy, distribution)

Callicebus donacophilus: Gamarra de Fox and Martin (1996: distribution, specimens); Dirección de Parques Nacionales y Vida Silvestre (1998: conservation); Yahnke *et al.* (1998: distribution); Morales (2007: list)

Plecturocebus pallescens Byrne *et al.* (2016: taxonomy); de la Sancha *et al.* (2017: checklist); Sánchez *et al.* (2019: ethnology); Weiler *et al.* (2019: field guide).

Local names: **AYOREO:** Ñame po (Sánchez *et al.* 2019); **GUARANÍ:** Kaaí-mirí (Bertoni 1914); Cai ygau (Stallings 1985); Ka'i y'gua (Dirección de Parques Nacionales y Vida Silvestre 1998); Ka'i ygáu, Kai yguá (Cartes 2003); Ca'i ygáu (Morales 2007); Kai Ygáu (Cartes 2015); Ka'i mirí (Weiler *et al.* 2019); **LENGUA-MASCOY:** Yamkyilineat (Stallings 1985); **MANJUI:** Lawite (Stallings 1985); **SPANISH:** Tití (Azara 1801); Mono titi (Dirección de Parques Nacionales y Vida Silvestre 1998); Sahui (Cartes 2003); Mono tití blanco, Titi chaqueño (Cartes 2015); Tití del Chaco (Sánchez *et al.* 2019).

Comments: Byrne *et al.* (2016) established the genus *Plecturocebus* but retained the species in the *donacophilus* group following the traditional arrangement of previous authors (Hershkovitz 1990; Kobayashi 1995; Van Roosmalen *et al.* 2002; Groves 2001, 2005).

Geographical distribution: All modern records are from the Chaco departments of Alto Paraguay (where it appears to be widespread and common) and Boquerón and Presidente Hayes (where occurrence is more marginal and

perhaps seasonal). The species seems to be associated with Pantanal, Cerrados del Chaco and more humid areas within the Dry Chaco region (especially along water courses, even when these run dry), but may be able to expand its range further into the Dry Chaco during particularly wet years. Indeed, the Guaraní name Kai yguá means “water monkey,” potentially in reference to this association. This species is considered Near Threatened in Paraguay (Cartes *et al.* 2017, 2018).

The type locality “Chaco, 30 km N of Concepción” (BMNH 1894.3.6.1) implies that it was collected west of the Paraguay River. It is tentatively listed as in the department of Presidente Hayes here (based on the known distribution of the species), but it should be noted that, taken literally, the locality would be the only report of the species from east of the Paraguay River.

Specimens examined: **ALTO PARAGUAY:** 10 km from Colonia Tribu Nueva Bahía Negra (MNHNP 1877); 13 km E of Agua Dulce Linea 1 (MNHNP 494); 15 km W of Bahía Negra (MNHNP 817); 18 km W of Agua Dulce Linea 1 (MNHNP 493); 36 km E of Agua Dulce Linea 1 (MNHNP 495); Estancia Guyra Toro km 55 Ruta to Bahía Negra (19°48.331'S, 58°37.243'W) (MNHNP 3359); **PRESIDENTE HAYES:** 1 km E of Parador Cainn Río Verde (MNHNP 1876); Close to Río Verde (MNHNP 816).

Specimens not examined: **ALTO PARAGUAY:** Cerro León, 50 km WNW of Madrejón (UMMZ 125576; Brooks 1996); Parque Nacional Defensores del Chaco (MNHG 1636.030; Hugot *et al.* 1994; Porter *et al.* 2013); 30 km

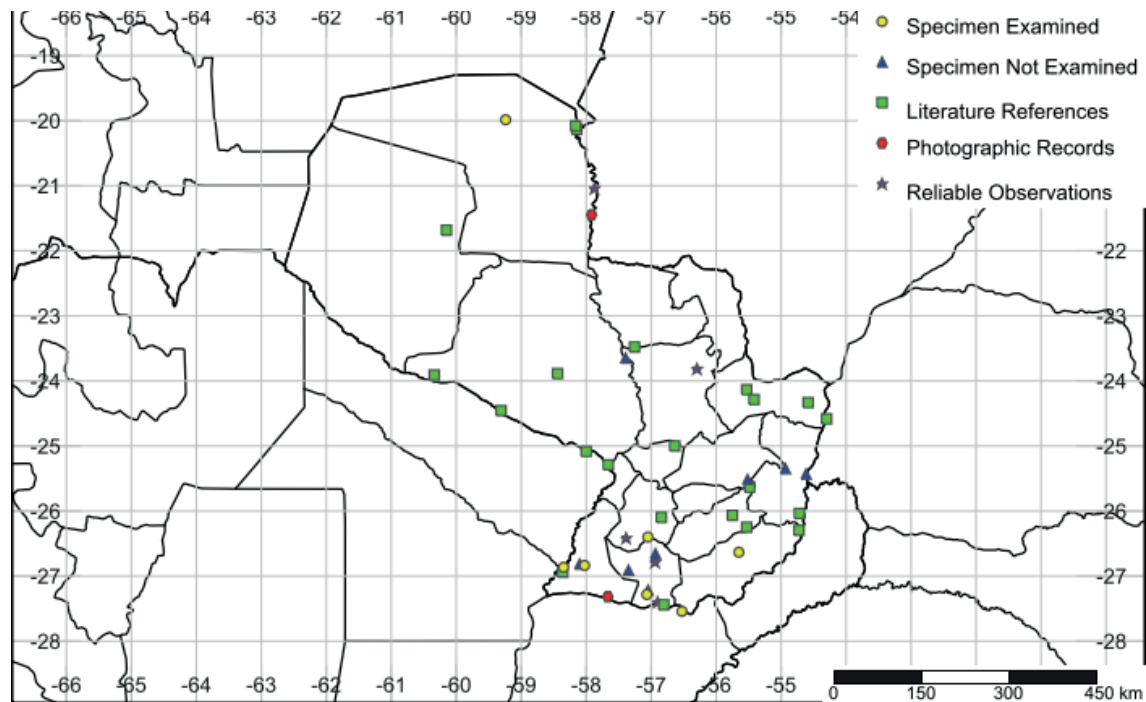


Figure 7. Distribution of *Alouatta caraya* in Paraguay.

W of Puerto Casado along the rail road (FMNH 54334); **BOQUERÓN**: 19 km WSW of Trans Chaco road km588 (UMMZ 161802); **PRESIDENTE HAYES**: Chaco, 30 miles north of Concepción (BMNH 1894.3.6.1, type specimen); Chaco opposite San Salvador (BMNH 1894.3.6.2); 80 km W of Puerto Pinasco (USNM 236352); Fort Wheeler (AMNH 42208, 42209, 42211, 42212, 42213, 42214).

Literature records: **ALTO PARAGUAY**: Cerro Chovoreca (Porter *et al.* 2013); Estación Biológica Tres Gigantes (González *et al.* 2019); Estancia San José (Brooks 1996); Finca Tobich, near Bahía Negra (Cartes 2015); Fortín Patria Lodge (Porter *et al.* 2013); Parque Nacional Río Negro (Porter *et al.* 2013); **BOQUERÓN**: Parque Nacional Teniente Enciso (Yahnke *et al.* 1998).

Photographic records: **ALTO PARAGUAY**: Picada Chovoreca (CLO ML 195381); S side of Cerro León (CLO ML 144158).

ATELIDAE: Howlers, Spider and Woolly Monkeys and Muriquis (Fig. 7)

Paraguayan Howler Monkey *Alouatta caraya* (Humboldt, 1812)

Simia Caraya Humboldt, 1812: *Rec. Obs. Zool. Anat. Comp.*, p.355. Type locality “Paraguay”.

Mycetes caraya: Rengger (1830: biology); Kerr (1891: distribution)

Mycetes caraya: Burmeister (1869: mention)

Mycetes auratus: Burmeister (1869: mention)

Alouata nigra: Bertoni (1914, 1939: distribution)

Alouatta caraya: Hill *et al.* (1999: use); Díaz *et al.* (2007: epidemiology)

Alouatta caraya: Krieg (1928: behavior, ecology); Stallings and Mittermeier (1983: mention); Stallings (1984, 1985: ecology); Mudry de Pargament and Slavutsky (1987: mention); Stallings *et al.* (1989: mention); Brooks *et al.* (1993: distribution); Brooks (1996: ecology); Gamarra de Fox and Martin (1996: distribution, specimens); Lowen *et al.* (1996: distribution); Dirección de Parques Nacionales y Vida Silvestre (1998: conservation); Szapkievich *et al.* (1998: genetics); Yahnke *et al.* (1998: distribution); Hill and Padwe (2000: use); Villalba and Yanosky (2000: tracks); Esquivel (2001: guide); Cartes (2003: list); Fariña and Hostettler (2003: distribution); Asunce *et al.* (2007: genetics); Díaz *et al.* (2007: epidemiology); Morales (2007: list); Roig *et al.* (2009: epidemiology); Giordano and Ballard (2010: distribution); Horton (2010: mention); Rumbo (2010: biogeography); Masi Pallarés (2011: ecology); Centrón *et al.* (2013: use); Cabral *et al.* (2017: mention); de la Sancha *et al.* (2017: checklist); Kowalewski *et al.* (2017: parasitology); Sánchez *et al.* (2019: ethnology).

Local names: **ACHÉ**: Krajá (Villalba and Yanosky 2000); Kraja (Esquivel 2001); Karaja (Centrón *et al.* 2013); **AYOREO**: Ojojo (Sánchez *et al.* 2019); **GUARANÍ**: Carayáa (Sánchez-Labrador 1770); Carayá (Azara 1801); Karadyá, Pohû (Bertoni 1914); Guarí, Karayá (Bertoni 1939); Caraya (Stallings 1985); Karaja (Villalba and Yanosky 2000); **GUAYCURU**: Aychega (Sanchez Labrador 1770); **LENGUA-MASCOY**: Yitsenei Kyelowai (Stallings 1985); **MBYA**: Pohu (Villalba and Yanosky 2000); **SPANISH**: Mono aullador (Esquivel 2001); Mono aullador negro

(Morales 2007); Mono carayá (Velázquez and Ramírez Pinto 2014); Mono aullador negro y dorado (Cartes *et al.* 2017); Macaco (in Ñeembucú region).

Comments: The first citation for Paraguay is the Carayá of Azara (1801: No.61 Tome 2: 169–182), meaning “chief of the forest”. He provided a detailed description and biological data, later complemented by Rengger (1830). Burmeister (1869) mentioned a specimen “very probably” from Paraguay under the name *Mycetes auratus* Gray, 1845, from “Orinoco”, adding that it is probably a synonym of the “Carayá de Azara”.

A semi-habituated troop is resident in the town plaza at Santa María de la Fe, department of Misiones, and the species is commonly encountered in urban parks of Ayolas, Misiones and in the urban area of Pilar, department of Ñeembucú, which has a substantial population of over 100 individuals (Para La Tierra, unpubl. data). The latter population is being extensively studied by Rebecca Smith and students at the Para La Tierra Centro IDEAL research centre (www.paralatierra.org), based in Pilar (Pinkowski and Smith 2018; Alesci *et al.* 2018; Kane and Smith 2019; McBride and Smith 2019; Kane and Smith 2020; Wellian and Smith in press; Duffy *et al.* in press).

A series of specimens (USNM 3354, 3355, 3357, 3359, 4619) collected during the mid-19th Century by Captain T. Page on or near the Río Paraguay lack precise data. They are omitted here because of the possibility they were collected in Argentina. Similarly, a BMNH specimen no.1911.10.27.5, reportedly from Tayru, Paraguay, is accompanied by approximate coordinates (c. 27°00'W, 58°33'S) that place it marginally into Argentina close to the mouth of the Río Bermejo. We are unable to find reference to a Paraguayan locality with that name, so it is not included below.

The species forms only a minor part of the diet of the Aché indigenous of Canindeyú department (Hill *et al.* 1999; Centrón *et al.* 2013). Researchers from Para La Tierra have been informed that howler monkeys are not uncommonly hunted for food both in and around the city of Pilar in the department of Ñeembucú, where it is very common (Alesci *et al.* 2018, submitted).

Geographical distribution: Widespread across the country. It is absent only from the most arid areas of the Dry Chaco, but is prone to wandering and may extend its distribution west during wet years. Especially common in gallery forest and palm savannas in the Paraguay River watershed. It is sympatric with *Aotus azarae* and *Plecturocebus pallefcens* in the Humid Chaco and Pantanal, *Mico melanurus* in the Pantanal and *Sapajus cay* in the Atlantic Forest and Cerrado zone (though it is much less frequently encountered in those habitats). We were unable to find any published records from the departments of Concepción, Amambay and Guairá, but the species undoubtedly occurs in all three, albeit at low densities in the Cerrado region.

Specimens examined: **ALTO PARAGUAY:** 54 km E of Agua Dulce (MNHNP 489); **ITAPÚA:** Estancia Bogado, Isla Yacyretá (MNHNP 1107, 1108, 1109); Estancia

Melgarejo, Isla Yacyretá, (MNHNP 1115, 1116); Isla Talavera (MNHNP 1101); Isla Vaí, Isla Yacyretá (MNHNP 1112); Schulz property “Área para Parque Nacional” San Rafael (PRC 003); **MISIONES:** Bosque Mbaepú, Estancia Santa Ana (MNHNP 1105); “on the main road to Encarnación” (MNHNP 1114); Reserva Yabebyry, Estancia Santa Ana (MNHNP 1163); **ÑEEMBUCÚ:** Estancia Santa Ana (CZPLT 950); Pilar (CZPLT 482, 483, 498, 491, 492, 509, 951); **PARAGUARÍ:** Banks of the Tebicuary River, opposite Hotel Centu-Cue (26°23.942'S, 57°02.756'W) (MNHNP 3360).

Specimens not examined: “Paraguay” BMNH 1930.7.31.6; **ALTO PARANÁ:** Hernandarias, Vivero Forestal de Itaipú (CBMI 90, 103); Tatí Yupí (CBMI 91); **CAAGUAZÚ:** Río Guyraunguá near Estancia Primera (MCZ 28095, 28096, 28654, 28655, 28656, 28713); **MISIONES:** 2.7 km N of San Antonio by road (UMMZ 124689, 124690); 37 km SW of San Ignacio by road (UMMZ 146506); 40 km S of San Ignacio (AMNH 234785, 234786); **ÑEEMBUCÚ:** Tacuaras (UMMZ 124691); **SAN PEDRO:** Puerto Ybapobo (FMNH 26650, 26653).

Literature references: **ALTO PARAGUAY:** Estación Biológica Tres Gigantes (González *et al.* 2019); Puerto Casado (Soria 1959); Río Negro (Horton 2010); **ALTO PARANÁ:** Parque Nacional Ñacunday (Stallings 1985); Reserva Nacional Kuri'y (Stallings 1985); **BOQUERÓN:** “130 km S of Chaco Defensores National Park (21°41.176'S, 60°09.234'W)” (Giordano and Ballard 2010); **CAAGUAZÚ/CANINDEYÚ:** Estancia La Golondrina II (Brooks *et al.* 1993); **CAAZAPÁ:** Estancia La Golondrina (= Reserva Ypeti) (Brooks *et al.* 1993); Parque Nacional Caaguazú (Stallings 1985); Reserva Natural Tapytá (Velázquez and Ramírez Pinto 2014); **CANINDEYÚ:** Estancia Itabó (Brooks *et al.* 1993); Reserva Mbaracayú (Brooks *et al.* 2013, Lowen *et al.* 1996); Reserva de Patrimonio Aché de Kuetuvy (Centrón *et al.* 2013); **CENTRAL:** Asunción (Asunce *et al.* 2007); **CORDILLERA:** Reserva Natural Privada Sombrero (Lowen *et al.* 1996); **ITAPÚA:** Isla Yacyretá (Brooks *et al.* 1993; Szapkievich *et al.* 1998; Asunce *et al.* 2007; Díaz *et al.* 2007); Monumento Nacional Bosque de Arary (Lowen *et al.* 1996); **MISIONES:** Ayolas (Szapkievich *et al.* 1998); **ÑEEMBUCÚ:** “S of Pilar” (Brooks 1996); **PARAGUARÍ:** Parque Nacional Ybycuí (Stallings 1985); **PRESIDENTE HAYES:** Banks of the Pilcomayo within 100 miles of Asunción (Kerr 1891); Río Negro affluent of the Pilcomayo (Allen 1916); Riacho Negro at 58°W, 25.5°S (Krieg 1928); Estancia La Golondrina (Stallings 1985); Parque Nacional Tinfunque (Stallings 1985); Montelindo (Brooks 1996); **SAN PEDRO:** S bank of Río Ypané near Belén (Sanchez Labrador 1770).

Photographic records: **ALTO PARAGUAY:** Estancia Cerrito, 21°26'46"S, 57°55'W, 25 km N of Carmelo Peralta (SDR); **ITAPÚA:** Reserva Chopi Sayju (Roberto Derna); **ÑEEMBUCÚ:** Cerrito (CLO ML 195463).

Reliable observations: **ALTO PARAGUAY:** Fuerte Olimpo (PS); **ITAPÚA:** Estancia Nueva Gambach (PS),

RS); **MISIONES:** Santa María de la Fe (PS, RS, SDR); **PARAGUARÍ:** Base Farmer, Caapucú (Roberto Derna); **SAN PEDRO:** Rancho Laguna Blanca (RS).

Species Cited Erroneously

Black-horned Capuchin *Sapajus nigrinus* (Spix, 1823)

Velázquez and Ramírez Pinto (2014) used the scientific name *Cebus nigrinus* for the species inhabiting the Reserva Natural Tapytá, department of Caazapá, but this is a misapplication of the nomenclature and refers to *Sapajus cay*. Bertoni (1914, 1939) listed that species as “Kaaí hũ” *Cebus vellerosus* I. Geoffroy Saint-Hilaire, 1851, for Misiones, Argentina stating clearly that the species occurs from Santa Ana to Ihuasú “but does not cross to Paraguay.”

Various other species of capuchin monkey have been listed as occurring in Paraguay in the older literature (for example, *Cebus xanthocephalus* Spix, 1823, in Gray 1870, considered a synonym of *nigrinus* by Groves [2001]), but all of these are attributable to confusion over the correct application of the nomenclature. Cabrera (1912) notes a specimen in the Museo de Ciencias Naturales de Madrid (MCNM 1465) identified as *Cebus cirrifer* É. Geoffroy St. Hilaire in Humboldt, 1812, with the collection locality “Paraguay”. The specimen was bought from a Parisian dealer who considered the specimen to be *Cebus azarae* Rengger, 1830, and Cabrera (1912) believed that the locality was assigned by the dealer based on the “erroneous identification.” Groves (2001) believed that *Cebus cirrifer* is a senior synonym of *Cebus cucullatus* Spix, 1823 that Groves placed as a subspecies of *C. nigrinus* Goldfuss, 1809. Silva Jr. (2001) believed that *cucullatus* was a junior synonym of *C. nigrinus*, but molecular genetic studies by Lynch Alfaro *et al.* (2012a) have shown that *cucullatus* (which perhaps should be named *cirrifer*) is a distinct species. We have been unable to examine this specimen but assume that if it really came from Paraguay then it would refer to *Sapajus cay*.

A single subadult individual of *Sapajus nigrinus* was photographed at Salto de Monday, Hernandarias, department of Alto Paraná during October 2019 and shared by the Club de Observadores de la Naturaleza - Paraguay (CONPY). It is unknown whether this individual was a member of a complete family group, but its unnaturally habituated behavior indicated that it may have been a released pet. It has been suggested that it may have crossed the river from the Iguassu National Park in Brazil during a drought that caused the river level to drop dramatically, but this seems unlikely.

Black-headed Night Monkey *Aotus nigriceps* Dollman, 1909

Mapped for Paraguay by Petter and Desbordes (2013) who apparently erroneously included the distributions of *A. azarae* and *A. infulatus* under this species.

Chestnut-bellied Titi *Callicebus caligatus* (Wagner, 1842)

Listed by Forbes (1896) as *Callithrix castaneiventris* Gray, 1866 (considered a junior synonym of *Callicebus caligatus* by Groves [2001]), perhaps following Gray (1870) who apparently associated the name with Azara’s Miriquiná. This species is well out of range and cited in error.

Atlantic Titi *Callicebus personatus* (É. Geoffroy in Humboldt, 1812)

Listed for the “Chaco now occupied by the Paraguayans” by Burmeister (1869), under the name “*Callitrix personata* Illig. Pr. Wied” [sic]. Although the authorship indicated by Burmeister was wrong, the name is associated with what now is considered *Callicebus personatus*, endemic to eastern Brazil. The intended species is presumably the only Titi in Paraguay, the at the time undescribed *Plecturocebus pallescens*.

Common Squirrel Monkey *Saimiri sciureus* and Black-capped Squirrel Monkey *Saimiri boliviensis*

Bertoni (1914, 1939) listed “*Callithrix sciurea* L. - Kaaí-mirí Paraguay?,” citing a specimen “obtained from the Indians of the Paraguay River” and adding that “it seems to be the same species as that which inhabits the yerba plantations of the northern interior of the country.” The common name Kaaí-mirí translates roughly as “little monkey.” This name and spelling was also mentioned by Illiger (1815).

Callithrix sciureus (Linnaeus, 1758) has been applied in the older literature to squirrel monkeys of the genus *Saimiri* Voigt, 1831 – a name which has its root in Tupi meaning “little monkey” (sai-mirim or çai-mbirín), with sai (çai) meaning monkey and mirim (mbirín) meaning “small” (Simpson 1941). However, no *Saimiri* has ever been documented to occur in Paraguay. The black-capped squirrel monkey *S. boliviensis* (d’Orbigny, 1834, cf. Groves 2001) of northern and eastern Bolivia is the species which comes geographically closest to Paraguay, but it is distributed well to the north (Wallace *et al.* 2010). Probably on the basis of Bertoni’s works, Cabrera and Yepes (1940) include Paraguay in the distribution of *Saimiri sciureus*, but they expressed doubt as to the validity of the identification. Later, Cabrera (1957) gave the distribution of *Saimiri sciureus boliviensis* as “All eastern Bolivia, reaching to the south to Paraguay” but with no additional comment regarding its supposed presence in Paraguay.

Callithrix sciureus (Schott, 1861) has also been used as a synonym of the cotton-top tamarin *Saguinus oedipus* (Linnaeus, 1758), a species that is distributed in Panama and Colombia. This represents the only usage of this name associated with the family Callitrichidae as it is currently understood. The name has never been applied as such to the only callitrichid that does occur in Paraguay, the black-tailed marmoset *Mico melanurus* (Humboldt, 1812) – the “littles monkey” in Paraguay. Bertoni’s use of the common name Kaaí mirí is however consistent with the local name still in use for white-coated titi *Plecturocebus pallescens* today and it would seem probable that this is the species intended.

Bertoni (1914, 1939) omits the name *Callicebus pallescens* Thomas, 1907, from his Catálogo, even though the type locality is “Chaco, 30 miles north of Concepción” and it is today still a common primate in the northern Paraguayan Chaco. *Callicebus* was included in *Callithrix* until Thomas (1903) clarified its usage, but the use of the genus *Chrysotrux* Kaup, 1835 for the squirrel monkeys *Saimiri* Voigt, 1831, was already widespread well before this time (Palmer 1897). Bertoni’s usage seems certain to be a misapplication of the nomenclature. Masí Pallares (2011), perhaps on the basis of this, stated erroneously that *Saimiri sciureus* “is the species found in the Chaco.”

Discussion

This paper is a first attempt to critically quantify the available data on the distribution of Paraguayan primates by highlighting gaps in our knowledge, clarifying misunderstandings and distinguishing between different types of records so that they may be assessed separately according to their level of documentation. The current representation of Paraguayan primates in museum collections is far from adequate and the age of many of the specimens provides only limited or extremely outdated information on distribution and status in a country with a rapidly changing landscape. Accurate specimen collection data is sadly lacking for a large number of specimens, and collection has been largely biased towards the Chaco, with most of the Oriental region poorly represented in collections.

Since the work of Jody Stallings in the Paraguayan Chaco in the 1980s, Paraguayan primatology has been largely dormant, but it has recently seen a rebirth, and quality publications based on extensive, long-term field observations are now at last being published again, with the focus on the two species occurring in the Oriental region—*Alouatta caraya* and *Sapajus cay*.

For the last eight years Fundación Para La Tierra (PLT) has been running Paraguay’s first-ever long-term primatological projects: The PLT Capuchin Project and the PLT Urban Howler Monkey Project. The PLT Capuchin Project began in January 2013 at Rancho Laguna Blanca, San Pedro and moved to Estancia Nueva Gambach, Itapúa in May 2017. This project studies the ecological requirements of the Paraguayan hooded capuchin in the Upper Paraná Atlantic Forest and aims to determine its adaptability to anthropogenic habitat disturbance. The PLT Urban Howler Monkey Project that began in May 2017 is based in Pilar, Ñeembucú. This project focuses on the unusual population of urban-dwelling howler monkeys in the city of Pilar. Both projects invite the participation of national and international students in carrying out research on the behavior and ecology of these monkeys. Studies so far have, for example, examined the effects of the urban environment on activity budgets (Pinkowski and Smith 2018; Overbeck *et al.* in consideration), diet, social interactions, and home range (McBride and Smith 2019; Duffy *et al.* in press.), risk awareness (Wellian *et al.*

in press) use of the vertical strata and terrestrial behavior (Henderson and Smith in prep.) and gastrointestinal parasite communities (Kane and Smith 2020), as well as the attitudes of local people towards the urban monkeys (Alesci *et al.* 2018; submitted). Results from the PLT primate projects are disseminated through several avenues at a national and international level, with presentations by students at various national and major international conferences, and multiple papers published, in press and in preparation in international peer-reviewed journals.

PLT primatology research runs in tandem with an intensive community engagement and education program. In 2018 PLT initiated the first annual Paraguayan Field Methods in Primatology course, in which international students learn participatory field methods as well as factors of relevance to primatology and conservation in Paraguay. The PLT primate team works to engage and educate the Paraguayan community in primate conservation through a series of different programs including: environmental education focusing on primate ecology and conservation in 22 rural and indigenous schools surrounding “Área para Parque Nacional” San Rafael; forest guard training courses in primatological field techniques and in delivering participatory environmental education; and, working with national zoos, a national campaign against the primate pet trade, which culminated in the publication of an illustrated children’s book (“No Soy Mascota”) (Smith and Sarvary 2017). The PLT Primate Project aims to fill the gaps in our current knowledge of Paraguayan primates and to train national and international primatologists in important techniques to encourage greater support of habitat conservation in Paraguay, using *Sapajus cay* and *Alouatta caraya* as flagship species.

In November 2019, the first Paraguayan primate society was formed during a round table meeting at the Primer Congreso Paraguayo de Zoología. It was named Ka’i Paraguay and currently has 13 members.

Acknowledgments

The authors are grateful to the locally-based research NGO Para La Tierra (www.paralatierra.org) for promoting field work with primates, offering courses in primatology, intern opportunities for students, encouraging the presentation of results at international congresses and helping bring primate education to rural Paraguayan classrooms. Isabel Gamarra de Fox (Museo Nacional de Historia Natural del Paraguay) and Brogan Pett (Colección Zoológica Para La Tierra) provided assistance in the review of primate specimens. We thank Hugo Cabral, José Luis Cartes, Hugo del Castillo, Roberto Derna, Luis Doldan, Juan Klavins, Oscar Rodríguez and Álvaro Vera for sharing their observations. Pedro, Christine and Hans Hostettler (Estancia Nueva Gambach; Hostettler S.A.) and Malvina Duarte (Laguna Blanca) are thanked for their support and encouragement of ongoing primate studies on their properties, and the support of the conservation organization Pro Cosara is also recognised.

The authors would also like to give special mention to the work of Jody Stallings, who provided the basis for the current studies. All authors are assisted by, and grateful to, the Pronii program of CONACyT Paraguay. Rebecca Smith receives assistance from the National Geographic Society (Grant Number: NGS-299-18C), the Elphinstone Scholarship (University of Aberdeen), International Primatological Society (Lawrence Jacobsen Education Development Award) and the Primate Society of Great Britain (Cyril Rosen Award).

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Received for publication: 21 May 2020
Revised: 20 January 2021