Chapter 2
Geographic Distribution of Owl Monkeys

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Abstract The owl monkeys, genus *Aotus*, are among the most widely distributed of all platyrrhine genera. The 13 currently recognized taxa are found in Argentina, Bolivia, Brazil, Colombia, Ecuador, Panama, Paraguay, Peru, and Venezuela. They

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range from lowland tropical moist and dry forests to over 3000 m.a.sl. in the cloud forests of the Andes. Owl monkeys appear to be sufficiently flexible to persist in anthropogenically altered habitats and fragmented forest patches. Here we gathered 1,703 owl monkey localities from a wide range of published and unpublished sources, making the most comprehensive database to date. These records were used to map the distributions of all owl monkey taxa based on our current understanding of the genus. Our knowledge is still limited in many areas where records are lacking, and we caution that all species IDs and maps be treated as tentative until the wide-ranging employment of genetic testing is available.

Keywords Habitat · Range · Global Biodiversity Information Facility · Mapping

2.1 Introduction

The genus *Aotus,* the owl monkeys, is among the most widely ranging platyrrhine genera covering some eight million square kilometers in Central and South America. Its range extends North to South from ~11° N in Colombia and Venezuela, and ~9.5° N in Panama, to ~27° S in Argentina, and West to East from ~41° W in Brazil to ~79° W in the Andes of Peru and ~82° W in Panama. Wild populations exist in Argentina, Bolivia, Brazil, Colombia, Ecuador, Panama, Paraguay, Peru, and Venezuela (Fig. 2.1). They occupy altitudes from sea level to >3300 m.a.s.l., and habitats including seasonally flooded and terra firme Amazonian rainforest, montane cloud forest, to seasonal dry forests (Hershkovitz 1983; Fernández-Duque et al. 2013; Méndez-Carvajal et al. 2023 this volume; Shanee 2023 this volume). They are found in primary forests with minor, if any human intervention, as well as heavily degraded ecosystems, evidencing their ability to cope with habitat degradation and adapt to anthropogenically modified areas at least in the short to medium term (Defler 2010; Fernández-Duque et al. 2013). Many studies have documented these primates utilizing disturbed and secondary forests, as well as plantations and peri-urban habitats (Castaño and Cardona 2005; Shanee 2011; García-Ayachi 2015; Shanee et al. 2015; Guzmán et al. 2016; Aquino et al. 2018; Bustamante-Manrique and Botero-Henao 2018; Henao-Isaza et al. 2020; Montilla et al. 2020; Bustamante-Manrique et al. 2021; Montilla et al. 2021).

Although the genus is widely present in humid tropical areas, owl monkeys can be found in dry forests that receive as little as 500 mm of annual rainfall in the Gran Chaco of Argentina, Bolivia, and Paraguay (Stallings et al. 1989; Campos 2004), as well as in the Marañón and Huallaga dry forests of northern Peru (Shanee et al. 2013b) and the relict dry forests of central Colombia (García-Herrera et al. 2015).

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Throughout the Amazon, they commonly live in seasonally flooded lowland forests, as well as terra firme and highland forests that do not flood. In these forests, they occupy every forest stratum from 3 to 35 m above the ground (Moynihan 1964; Wright 1978; Aquino and Encarnacion 1986; González-Hernández et al. 2020) and can use terrestrial stratum to cross natural and anthropogenic canopy gaps (Shanee and Shanee 2011; Souza-Alves et al. 2019).

Several species, at multiple sites, inhabit anthropogenically fragmented patches as small as 1 ha (Garcia and Braza 1987; Castaño et al. 2010; Shanee et al. 2013a; Shanee et al. 2015; Bustamante-Manrique et al. 2021; Montilla et al. 2021). They have also been reported moving between forest fragments (Castaño et al. 2010; Shanee and Shanee 2011; Corley and Fernández-Duque 2023 this volume; Huck and Fernández-Duque 2023 this volume; Méndez-Carvajal et al. 2023 this volume; Shanee 2023 this volume), an important behavior to allow dispersal and gene flow in anthropogenically modified habitat matrices (Juárez 2012; Juárez et al. 2017). The fact that they can inhabit forest patches smaller than the normal territory sizes of groups living in larger areas, and that they can move between such fragments, suggests a certain plasticity that may allow them to inhabit areas of seemingly inferior quality such as natural patches of shrubs or remnant forest patches in anthropogenic landscapes as well as to recolonize patches from which they may have been eliminated (de Carvalho Jr. 2003; Defler 2004; Castaño and Cardona 2005; Svensson et al. 2010; Juárez 2012; Shanee et al. 2015; Rumiz 2018; Bustamante-Manrique et al. 2021).

Over the years, there have been various reviews of the continental geographic distribution of *Aotus*. All of them were the effort of a single researcher (e.g., Wright 1981; Hershkovitz 1983; Ford 1994; Fernández-Duque 2011), or a small number of them (Fernández-Duque et al. 2013). Here, we present a comprehensive review of the genus' distribution based on the collective knowledge of researchers from six of the eight countries where owl monkeys are currently found. We present updated descriptions and distribution maps based on datasets that include both published and unpublished localities. To our knowledge, this dataset represents the most detailed review to date, based on the data available and our current understanding of owl monkey taxonomic diversity.

2.2 Methods

We mapped estimated distributions as the area of occupancy (AOO) based on existing distribution maps from the IUCN Red List (IUCN 2021), the "All The World's Primates" website (Rowe and Myers 2016), and the "Biomodelos" program of Colombia's von Humboldt Institute (Henao Díaz et al. 2020), combined with our own maps (unpublished data). We refined these maps identifying reasonable geophysical boundaries and probable natural geographical barriers based on our current knowledge of the genus' taxonomy and species' ecological and biological characteristics (e.g., rivers, mountain ranges, and ecoregions Dinerstein et al. 2017). We built a database of localities from the literature and reviewed descriptive accounts of

distributions from published sources (Aquino and Encarnación 1994a; Defler 2004; Tirira 2007; Romero-Valenzuela and Rumiz 2010; Álvarez Gonçalvez et al. 2012; Fernández-Duque et al. 2013; Wallace et al. 2013; Wilson et al. 2013; Lopez-Strauss et al. 2016; Tirira 2017). We then compiled all presence records obtained from the Global Biodiversity Information Forum (GBIF) (Anderson et al. 2016). The GBIF dataset included localities from the following collections and institutions: Administracion de Parques Nacionales – Argentina, Asociación Registros de Primates Neotropicales Convocatoria of the Asociacion Primatologica Colombiana (Henao-Díaz 2017), Conservation International, Denver Museum of Nature and Science, Field Museum of Natural History (Zoology) Mammal Collection, History Museum of Los Angeles County, Universidad Nacional de Colombia, iNaturalist Research-grade Observations (Ueda 2020), Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Louisiana Museum of Natural History, Macaulay Library Audio and Video Collection, Michigan State University, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Museo de Historia Natural de la Universidad de Caldas, Muséum d'histoire naturelle de la Ville de Genève, Museum of Comparative Zoology – Harvard University, Museum of Vertebrate Zoology, naturgucker, New York State Museum, Parques Nacionales Naturales de Colombia, Royal Belgian Institute of Natural Sciences, Servicio Forestal y de Fauna Silvestre Peru, Smithsonian National Museum of Natural History, Stichting Natuurinformatie, Texas Tech University, Universidad de Caldas, Universidad de la Amazonía Colombia, Museo de Historia Natural La Salle de Caracas, Universidad de los Andes Colombia, Universidad del Valle Colombia, Universidad Industrial de Santander Colombia, University of Michigan Museum of Zoology, University of Washington Burke Museum, and the Wildlife Conservation Society. These collections also included many localities from companies, regional governments, NGOs, individuals, and other sources (Table 2.S1). We complemented these data with additional localities from searchable online databases of museum collections and unpublished datasets that several of the authors and other researchers shared from their personal and institutional repositories (Table 2.S1). Finally, we included locality records from the published scientific literature (Text 2.S1). In all cases, only original sources that provided coordinates/georeferenced localities were included; we did not infer localities from textual descriptions or map figures. In all cases, we follow recommended guidelines regarding the inclusion of enough information for our decisions to be clear and our analyses reproducible (Borries et al. 2016).

We cleaned locality data to remove duplicate entries (e.g., between publications and the database, between publications carried out at the same sites, and when there were multiple specimens collected at the same site). We also reviewed records for species identifications which did not reflect our current understanding of owl monkey taxonomic diversity. This mainly included older records which did not consider Hershkovitz (1983) or subsequent assessments (i.e., many records were simply assigned *A. trivirgatus* or *Aotus* sp.). All localities from secondary evidence (interviews with local people or audio detection) were reassigned as *Aotus* sp. These

points were not used for estimating distributions but were included as confirmed genus level localities (Figs. 2.1, 2.2, 2.3, 2.4, 2.5, 2.6, 2.7, 2.8, 2.9, 2.10, 2.11, 2.12, 2.13, and 2.14 and Table 2.S1). We compared the geographic records gathered from all sources with databases that several authors maintain, correcting errors in coordinates and taxonomic identity when we had access to source material (e.g., have viewed the original collection records), and added our own unpublished locality records. Finally, we excluded records where we had reason to believe there could be critical errors in the coordinates given, again this was especially true for older records prior to the use of GPS, or where the original publication, or database, highlighted uncertainties in origin (as is the case of many specimens collected from hunters). We considered records as "confirmed" when they fulfilled the above criteria.

Once this dataset was complete, we overlaid locality data on the cleaned distribution maps, adding to, or removing, areas from the estimated extents as deemed necessary. We only made changes when records at new localities came from publications or collections and when they met the criteria outlined in the previous paragraph. Maps were produced showing estimated distributions for each taxon, as well as reliable localities from publications, from museum records, and other sources, overlaid on major geographical features (Figs. 2.1, 2.2, 2.3, 2.4, 2.5, 2.6, 2.7, 2.8, 2.9, 2.10, 2.11, 2.12, 2.13, and 2.14).

2.3 Results

We collected 1,703 separate localities with confirmed presence of owl monkeys. These included localities for all species and countries where the genus is present. After revision, 1,493 included identifications to species level reflecting current taxonomy; in other words, it is possible that some taxonomic identifications may be erroneous.

Aotus azarae has three recognized subspecies, *A. a. azarae*, *A. a. boliviensis*, and *A. a. infulatus*, and the widest distribution of any *Aotus* species (Fernández-Duque et al. 2013). The species is found in Argentina, Bolivia, Brazil, Paraguay, and Peru, from the Atlantic coast of northeastern Brazil at ~1°17' N to ~27°8' S in Argentina, and west to the Andes of Bolivia and southern Peru at ~7°35' W (Figs. 2.1, 2.2, 2.3, and 2.4).

A. a. azarae is found in the Gran Chaco region of Argentina, Bolivia, and Paraguay and a smaller area of the Pantanal in Brazil (Rathbun and Gache 1980; Stallings 1985; Stallings et al. 1989; Fernández-Duque et al. 2008b; Tomas et al. 2011; Álvarez Gonçalvez et al. 2012; Juárez et al. 2017; Romero-Valenzuela et al. 2020). In Argentina, it is found in the provinces of Chaco and Formosa, from just south of the Rio Bermejo near its confluence with the Rio Paraguay, to the Rio Paraná (~58°49'W, 26°48'S); from here, it extends north, along the west bank of the same river, to the border with Paraguay. It is found throughout western Paraguay in

the regions of Alto Paraguay, Boquerón, and Presidente Hayes, north to just over the Brazilian border near the confluence of the Rio Taquarí and Miranda, in the Pantanal in the states of Matto Grosso and Mato Grosso do Sul, and north into Bolivia to the Bañados do Izozog in Santa Cruz (Hershkovitz 1983; Rumiz 2013) and southwest in the departments of Chuquisaca and Tarija, south to the Rio Pilcomayo. In Bolivia, it is replaced by *A. a. boliviensis* to the north at ~16°54' S and by *A. a. infulatus* to the north in Brazil. The exact northern boundary in Bolivia is not known; in the northwest, the Rio Grande could be the limit between *A. a. azarae* and *A. a. boliviensis* (Fig. 2.2). To the west, it is known to be present to the Andes, up to an elevation of ~1,000 m.a.s.l. (Romero-Valenzuela et al. 2020).

One collection locality in Argentina places *A. azarae* cf. *azarae* ~ 100 km southwest of the known distribution, but the precise locality is not given (GBIF 2020). If this locality is confirmed, it would greatly extend the species known distribution.

A. a. boliviensis is found in Bolivia, southern Peru, and possibly Brazil (Romero-Valenzuela and Rumiz 2020). In Bolivia, it is found north of the Bañados de Izozog in the department of Santa Cruz (Hershkovitz 1983; Rumiz 2013), where it is replaced by *A. a. azarae*, and in the departments of Beni, Cochabamba, La Paz, and Pando, north to the Rio Madre de Dios (Garcia and Braza 1993; Pyritz et al. 2010; Álvarez Gonçalvez et al. 2012). To the west, it is limited by the Rio Guaporé along the border with Brazil (Fig. 2.3). In the northwest, it is present to the south of the Rios Madre de Dios and Inambari in Peru, and west to the Andes, where it may occur up to ~2,000 m.a.s.l. (Aquino and Encarnación 1994a; Romero-Valenzuela and Rumiz 2020).

The presence of *A. a. boliviensis* in Brazil is unconfirmed, but possible (Romero-Valenzuela and Rumiz 2020). If the Rio Guaporé forms the western limit of its distribution, then it is also likely to be present in the state of Mato Grosso do Sul where the river leaves the border and enters Brazilian territory. It is not known what the boundary with *A. a. infulatus* is in this area.

A. a. infulatus has a very large distribution in Brazil (Fig. 2.4) and is possibly endemic (Roberto Reis et al. 2015; Pinto et al. 2021). It is present from just north of the Amazon in Amapá state, at ~1°17' N, and Marajó and Caviana islands (Hill 1960), west through the state of Maranhão and into Piauí, just east of the Rio Parnaiba on the Atlantic coast (Pinto and Roberto 2016). Further south, it is limited to the west of the Rio Paranaiba in Maranhão State, and to the west of the Rio Tocantins in Tocantins State, then to the west of the Rio Araguaia in Mato Grosso. The southern limits are the Rios Guaporé and Corixá Grande, along the Bolivian border. To the west, *A. a. infulatus* is limited by the Rios Tapajós and Juruena in Mato Grasso and Para States (Vaz 2001; Corvelo et al. 2002; de Carvalho Jr. 2003; Pimenta and de Souza e Silva Júnior 2005; Álvarez Gonçalvez et al. 2012).

Aotus brumbacki is poorly known, possibly endemic to central eastern Colombia (Carretero et al. 2020). It is probably distributed in the lowlands of the Orinoco basin, from the eastern portions of the departments of Boyacá and Cundinamarca, and west into Arauca, Casanare, and Meta departments (Defler 2004; Wagner et al.

2009). The full altitudinal range is not known; it is present to at least 1,000 m.a.s.l. in the foothills of the eastern slopes of the Eastern Andes, where it is replaced by *A. lemurinus* (Fig. 2.5). It is present in fragments of gallery forest, lowland forest, and *Mauritia flexuosa* swamps of the "llanos" plainlands (Carretero-Pinzón and Defler 2018) as well as in the tropical rainforests of the northwestern Colombian Amazon. The species occurs north of the Rio Guaviare (Carretero et al. 2020). Further east between the Rios Guaviare and Meta, in Vichada department, *A.* cf. *brumbacki* has been collected, possibly extending its distribution to the Rio Orinoco (Defler and Bueno 2007). *A. brumbacki* has not been reported in Venezuela (Carretero et al. 2020).

Aotus griseimembra is the most northern occurring species, which is found in the lowland forests of northern and central Colombia and northwestern Venezuela (Defler 2004; Link et al. 2021b). In Colombia, it is found on both sides of the Rio Magdalena between the central and eastern cordilleras, from ~2°0' N in Huila Department, north through Tolima, Cundinamarca, Caldas, Boyacá, Antioquia, and Santander. In the higher elevations of the cordilleras, it is replaced by *A. lemurinus* (Fig. 2.6). In the northern coastal plains, it is reported west across the Rio Cauca, possibly to the Rio Sinú, in Antioquia and Córdoba. It is widely distributed in the northern lowlands and coastal plains, including the Sierra Nevada de Santa Marta, to the Caribbean Sea, in Sucre, Bolivar, Atlántico, Magdalena, and Cesar departments, as far west as the Guajira Peninsula, and reaching south along the inter-Andean valleys, especially along the upper and middle Magdalena River. It may also be found in the lowlands of the Rio Cauca valley (Fig. 2.6). In the east, along the Venezuelan border, it is located in Norte de Santander department and across the Sierra de Perijá (Hernández-Camacho and Cooper 1976; Defler 2004; Álvarez Gonçalvez et al. 2012; Fernández-Duque et al. 2013; Villanueva and Huertas 2013; Montilla et al. 2021).

In Venezuela, *A. griseimembra* is restricted to the northeastern coastal plains around Lake Maracaibo, south through the Sierra de Perijá, to the foothills of the eastern Andes, in the states of Zuila, Trujillo, Táchira, and Merida (Bodini and Pérez-Hernández 1987; Linares 1998; Álvarez Gonçalvez et al. 2012; Portillo-Quintero and Urbani 2015; Portillo-Quintero 2019; Link et al. 2021b). According to Portillo-Quintero (2019), this species may occur in larger, less disturbed forest fragments of the Lake Maracaibo basin.

The upper altitudinal limit of the species' distribution is not well known, but it appears to be replaced by *A. lemurinus* in all three Andean cordilleras above ~1,000–1,500 m.a.sl. (Defler 2004; Mantilla-Meluk and Jiménez-Ortega 2011; Link et al. 2021b; Shanee 2023 this volume).

Aotus jorgehernandezi is the least known of all species. Only one specimen has been collected (Fig. 2.7). The type locality is not known, but it is believed to be from the Los Nevados National Park in Colombia at ~2,000 m.a.s.l. (Torres et al. 1998; Defler and Bueno 2007). This locality places it on the border between Quindío and Risaralda in the central Cordillera, within the distribution of *A. lemurinus* (Fig. 2.7), and not *A. zonalis* as stated by Defler and Rodríguez (2021).

Aotus lemurinus is distributed from northern Colombia, south along the Andes, into Ecuador (Hernández-Camacho and Cooper 1976; Defler 2004; Tirira 2007; Link et al. 2021a). This species is thought to be one of two altitudinally restricted owl monkeys (Shanee 2023 this volume), ranging from ~1,000 to ~3,200 m.a.s.l. (Hernández-Camacho and Cooper 1976; Fernández-Duque et al. 2013; Link et al. 2021a). In Colombia, the species' distribution extends from the Ecuadorian border (Henao-Isaza et al. 2020) in the south, through the eastern and central cordilleras to about 7°35' N, in Nariño, Putumayo, Cauca, Huila Caquetá, Tolima, Valle del Cauca, Caldas, Risaralda, Chocó, Quindío, and Antioquia departments, and in the eastern cordillera, in Huila, Meta, Cundinamarca, Boyacá, Santander, and Norte de Santander departments, along the border, and possibly into Venezuela in the southwestern portion of the state of Táchira and the westernmost tip of the state of Apure (Castaño and Cardona 2005; Castaño et al. 2010; Fernández-Duque et al. 2013; Guzmán et al. 2016; Hirche et al. 2017; Ramirez-Chaves et al. 2020; Bustamante-Manrique et al. 2021; Link et al. 2021a; Montilla et al. 2021). In the western cordillera in Colombia, it is present to about 7°29' N. This species is thought to be replaced by *A. zonalis* in the Pacific lowlands to the west, and by *A. griseimembra* at lower elevation in the inter-Andean valleys of the Rio Magdalena and Rio Cauca (Fernández-Duque et al. 2013; Link et al. 2021a; Montilla et al. 2021). On the eastern slopes of the eastern Andes, it is replaced in areas below ~1,000 m.a.s.l. by *A. brumbacki* in the lowlands in the north and by *A. vociferans* in the south.

In Ecuador, *A. lemurinus* is present from ~1,400 to ~2,610 m.a.s.l. New evidence shows that there are no records south of the Rio Jatun Yacu (Alto Napo River) (Tirira 2021). This species occurs throughout the montane forests of the eastern Andean cordillera from the Colombian border in the north, south to the north bank of the Rio Jatun Yacu, in the provinces of Sucumbios and Napo (Tirira 2021). Previous records south of here, in the provinces of Tungurahua, Pastaza, Morona Santiago, Azuay, and Zamora Chinchipe (Rageot and Albuja V 1994; Castro-Revelo and Jaácome Rivera 1999; Castro-Revelo and Román 2000; Tirira 2001; Freile and Santander 2005; Tirira 2007; Ortiz 2008; Tirira et al. 2011; Brito and Ojala-Barbour 2016; Tirira 2017; Tirira and de la Torre 2018; Ramirez-Chaves et al. 2020), are misidentifications or unconfirmed (Tirira 2021). Lower elevation records, in the Bermejo and Sinangüé areas (Pitman et al. 2002), probably correspond to *A. vociferans*; while records of *A. vociferans*, between the rivers Chingual-Aguarico-Dué (Mena-Valenzuela 1997; Vriesendorp et al. 2009) and the slopes of Sumaco Volcano (Mena-Valenzuela 1996) probably correspond to *A. lemurinus* (Tirira 2021). In the Ecuadorian Amazon, it is replaced by *A. vociferans* (Fig. 2.8).

Aotus miconax is endemic to northern Peru, along the eastern Andean cordillera (Aquino and Encarnación 1994a; Shanee et al. 2015; Shanee and Shanee 2018). The species is one of possibly two altitudinally restricted owl monkeys (see *A. lemurinus*, above, and Shanee 2023 this volume), ranging from ~1,000, to ~3,200 meters (Thomas 1927a; Cornejo et al. 2008; Shanee et al. 2015; Campbell et al. 2019). The majority of the species' known distribution is in Amazonas, San Martín, and Huánuco Regions (Thomas a, 1927b Butchart et al. 1995a; Cornejo et al. 2008;

Shanee et al. 2015; Aquino et al. 2016b; Aquino et al. 2018) but is also probably found in La Libertad, Loreto, and Pasco (Shanee et al. 2013b; Patterson and López Wong 2014; Shanee et al. 2015; Aquino et al. 2019) (Fig. 2.9).

In Amazonas, *A. miconax* is spread as far north as the Cordillera Colán (Butchart et al. 1995a, b), further from here its distribution is limited by the lowlands of the Rio Marañón valley, and in the west and northwest, the Rio Marañón valley and the Andean highlands (Shanee et al. 2015). In San Martín, it is present in the Andean forests above 1,000 m.a.s.l. on both sides of the Rio Mayo valley, below which it is replaced by *A.* cf. *nancymaae* (Shanee et al. 2020). Further south in San Martin, it is found along the border with Amazonas and La Libertad, south to Huánuco to at least the Rio Chontayacu (Aquino et al. 2016b). At lower elevations to the east in the Rio Huallaga valley, it is replaced by *A. nigriceps* (Shanee 2016; Shanee and Shanee 2018). In La Libertad, it is probably present in Poroto (Shanee et al. 2013b). In Huánuco, its distribution extends from the border of San Martín south toward Pasco, west of the Alto Rio Huallaga (Thomas 1927b; Shanee et al. 2015) (Fig. 2.9).

The exact distributional limits for *A. miconax* are not well documented. The sympatric *L. flavicauda* is found in southwest Loreto on the border with San Martín, from where Patterson and López Wong (2014) report the presence of *Aotus* sp., and in the Inchatoshi Kametsha Conservation Concession, Junín (McHugh et al. 2019), suggesting that the species may also be present in these areas. Similarly, Aquino et al. (2016a) reported *Aotus* sp. in sympatry with *L. flavicauda* to the east of the Río Alto Huallaga in Huánuco, at 2,071 m.a.sl., which is most probably *A. miconax*. The species has not been confirmed in Pasco, but Aquino et al. (2019) reported *Aotus* sp. from surveys in the Rio Santa Cruz. Thomas (1927b) collected a specimen from hunters at Tingo Maria, ~800 m.a.s.l., which may have been caught in the highlands surrounding this city. Shanee et al. (2013b) reported the presence of *Aotus* sp. in the dry forests of the inter-Andean valley south of Bagua in Amazonas, and this area is within the distribution of *A. miconax* but far below its presumed altitudinal limit (600–800 m.a.s.l.).

Aotus nancymaae is distributed in western Brazil, south of the Rio Amazonas/Solimoes, and west as far as the northern Andean foothills in Peru below ~1,000 m.a.s.l. (Aquino and Encarnación 1988; Aquino and Encarnación 1994a; Maldonado et al. 2020; Shanee et al. 2020; Maldonado et al. 2023 this volume). In Brazil, the species is possibly distributed as far west as the Rio Jandiatuba or Jutai, ~68°50' W and ~66°57' W, respectively, in the State of Amazonas. The distribution extends as far as the Rio Jurua at about 8°10' S. The exact limit of its eastern and southern distribution in Brazil, where it is apparently replaced by *A. nigriceps*, and what limits the species, is unknown (Fig. 2.10). In central eastern Peru, *A. nancymaae* is present from ~6°40' S to north of the Rio Marañón at ~3°41' S, in the interfluve between the Rios Morona and Tigre in the region of Loreto (Aquino and Encarnación 1988; Aquino and Encarnación 1994b). Where this species is replaced by *A. vociferans* and what limits its distribution are unknown (Fig. 2.10). In its far western distribution, it reaches the Andean foothills to the west of the Rio Huallaga in San Martín, north of the Rio Huayabamba, where it is limited by the uplands of

the eastern Andean cordillera, where it is replaced by *A. miconax* at elevations above ~1,000 m.a.s.l. (Shanee et al. 2015; Shanee et al. 2020). North from here, its distribution appears to be limited to the lowlands of the Rio Marañón valley in Amazonas and Loreto (Aquino and Encarnación 1994a, b).

A small enclave population has also been reported in the Colombian department of Amazonas, just north of the Rio Amazonas, between San Juan de Atacuari and San Juan del Socó (Maldonado and Peck 2014; Maldonado et al. 2023 this volume). Whether this is a relict population or a new expansion is unknown, but it is being supplemented by the introduction of conspecifics from Peru and Brazil after their use in biomedical experiments locally (Maldonado and Peck 2014; Maldonado and Waters 2017; Maldonado et al. 2023 this volume; Shanee et al. 2023 this volume). The species was also sampled by Aquino and Encarnación (1988) northwest of the Rio Napo in northern Peru, far inside the distribution of *A. vociferans*; it is not clear whether there is sympatry of both species or a localized replacement of *A. vociferans*. Similarly, a single instance of *A. nancymaae* was reported for Ecuador, in the high elevation distribution of *A. vociferans* (Fig. 2.10). This is a captive animal, purportedly captured from the Río Nangartiza valley, Zamora Chinchipe province, on the western slopes of the Cordillera del Cóndor, near the Peruvian border (Tirira 2021). The species ID was later confirmed genetically (Shostell and Ruiz-García 2016; Tirira 2021).

Aotus nigriceps is distributed in central and western Brazil, south of the Rio Amazonas/Solimoes, and west as far as the central and southern Andean foothills in Peru (Aquino et al. 2013; Shanee et al. 2013c; Shanee et al. 2021). It ranges to ~1,000 m.a.s.l., possibly reaching to 1,500 m.a.s.l. in the southern Peruvian Andes (INRENA 2002; Shanee et al. 2013c). In Brazil, it is found from the eastern banks of the Rio Tapajos, ~55°10' W, in the State of Para (Fernández-Duque et al. 2013) through Amazonas, Mato Grosso, and Rondônia, as far south as the Rio Guaporé along the Bolivian border, ~13°48' S, and into Bolivia, in Pando department, and Peru, along the north bank of the Rio Madre de Dios (Wright 1994; Anderson 1997; Buchanan-Smith et al. 2000; Aquino et al. 2013). In Peru, it extends into the Andean foothills in the Regions of Madre de Dios and Cuzco, to at least 1,000 m.a.s.l. (Aquino et al. 2013; Gregory et al. 2014; Khimji and Donati 2014; Whitworth et al. 2016; Helenbrook et al. 2020), following this elevation north along the Andean cordillera, through Ucayali, Cerro de Pasco, and Huánuco regions, as far as central San Martín just west of the Rio Huallaga, at ~6°35' S, where it is replaced by *A. nancymaae* (Shanee et al. 2015; Shanee and Shanee 2018). In Northern Peru, the limit between *A. nigriceps* and *A. nancymaae* is suggested to be the Río Aguaytía and its tributaries, the Ríos Pintoyacu and Santa Ana, although the species has been recorded at several sites north and west of those locations. Toward the east, it crosses into Brazil to the south of the Rio Jurua in Amazonas State and north to the Rio Amazonas/Solimoes (Fig. 2.11).

Peres (1988) reported *A. nigriceps* on the western banks of the Rio Juruá at ~5°5' S, 67°10′, whereas Vidal et al. (2013) reported the presence of *A. vociferans* to the south of the Rio Amazonas in Brazil within the distribution of *A. nigriceps*, relatively near to the localities reported by Peres (1988) (Fig. 2.11). Neither *A.*

nigriceps nor *A. nancymaae* have been recorded in the area between the Rios Juruá and Jutai (Figs. 2.10 and 2.11). In Ecuador, a captive specimen, possibly trafficked internationally, was found at the Yanayacu Rescue Center, in Puyo, Pastaza province, and species ID was later confirmed genetically (Tirira 2021).

Aotus trivirgatus is poorly known. It is found in Brazil and Venezuela, and a small part of eastern Colombia (Fernández-Duque et al. 2013; Urbani et al. 2021). In Venezuela, it is documented south of the Rio Orinoco in Bolívar and Amazonas states, reaching further west into Colombia north of the Rio Negro in Guainía department (Hershkovitz 1983; Bodini and Pérez-Hernández 1987; Linares 1998; Defler 2004). In Brazil, it is reported north of the Rio Negro, where it is replaced by *A. vociferans*, and the Rio Amazonas, where it is replaced by *A. nigriceps*, as far east as the Rio Trombetas, and north to the Serra da Pacaraima in Amazonas and western Pará states (Urbani et al. 2021).

In Venezuela, the species is considered locally rare (Urbani and Portillo-Quintero 2018). Blanco Márquez and Chacares (2019) reported the remains of several individuals collected from the nest of a harpy eagle (*Harpia harpyja*) in the Imataca Forest Reserve in western Venezuela, ~7°3' N, 61°0' W, near the Guyanese border. This is far outside the known distribution of *A. trivirgatus*, or any other owl monkey species (Fig. 2.12), suggesting much more research is needed in this area.

Aotus vociferans is widely distributed in the Brazilian, Colombian, Ecuadorian, and Peruvian Amazon, north of the Rio Amazonas/Solimões, and west as far as the Andean foothills in far northern Peru, through Ecuador and southern Colombia (Aquino and Encarnación 1988; Puertas et al. 1992; Aquino and Encarnación 1994a; Defler 2004; Tirira 2007; Fernández-Duque et al. 2008a; Aquino et al. 2014b; Maldonado and Peck 2014; Bowler et al. 2017; Guzmán-Caro et al. 2021; Maldonado et al. 2023 this volume). In Brazil, the species is reported south of the Rio Negro, from ~59°54' W, east into Colombia where it is limited in the north by the Rio Guaviare and replaced by *A. brumbacki* at the head waters (Defler 2004; Guzmán-Caro et al. 2021). From there, its range extends to the Andean cordillera, as high as 1,580 m.a.s.l. (Tirira 2021), and possibly to ~2,425 m.a.s.l. (Table 2.S1), in Southern Ecuador, and south into northern Peru, to ~5°10' S, where it is replaced by *A. nancymaae* below the Rios Marañón and Amazonas (Aquino and Encarnación 1988; Puertas et al. 1992; Aquino and Encarnación 1994a; Maldonado and Peck 2014). In northern Peru, it occurs north of the Rio Marañón between the Rio Santiago and Tigre, and in the interfluve between the Morona (Loreto) and Chinchipe (Cajamarca) rivers, perhaps reaching into higher elevation pre-montane and montane areas (Aquino and Encarnación 1994a; Fernández-Duque et al. 2013; Aquino et al. 2014a).

Aquino and Encarnación (1988) reported the presence of *A. nancymaae* to the northwest of the Rio Napo, at 2°48′, within the proposed distribution of *A. vociferans*. Shostell and Ruiz-García (2016) and Tirira (2021) also reported the possible presence of *A. nancymaae* from the Nangaritza river valley, Zamora Chinchipe province (see *A. nancymaae*, above). Aquino et al. (2014a) tentatively identified *A.* cf. *vociferans* in northern Cajamarca, just south of the Ecuadorian border; similarly, Tirira (2021) recorded a possibly unidentified species in Zamora Chinchipe

Province, Ecuador, just north of the records of Aquino et al. (2014a), at elevations from 1,400 to 2,425 m.a.s.l. Vidal et al. (2013) reported the presence of *A. vociferans* to the south of the Rio Amazonas in Brazil, well within the distribution of *A. nigriceps* (Fig. 2.13). These records suggest possible niche separation and sympatry between species, or localized replacements. Similarly, in the trapezium between Brazil, Colombia, and Peru, sympatric populations of *A. vociferans* and *A. nancymaae* have been recorded on islands in the river Amazon (Pieczarka et al. 1992). As with *A. nancymaae* populations in southern Colombia, it is uncertain as to whether these are natural zones of sympatry, or the result of release of individuals into the wild after their use in biomedical experiments locally (Maldonado et al. 2023 this volume; Shanee et al. 2023 this volume).

Aotus zonalis is distributed in Panama and Colombia (Defler 2004; Méndez-Carvajal and Link 2021; Méndez-Carvajal et al. 2023 this volume), mostly at elevations below ~1,000 m.a.s.l., but may range as high as 1,600–1,800 m.a.s.l. (Méndez-Carvajal and Link 2021; Méndez-Carvajal et al. 2023 this volume). In Panama, the species is found from about 80°28' W in the provinces of Coclé and Colón (González-Hernández et al. 2020), and east through the provinces of Panamá Oeste, Panamá, Kuna (Guna) Yala, Darién, and Emberá as far as the Colombian border (Araúz et al. 2008; Svensson 2008; Méndez-Carvajal 2019; Méndez-Carvajal et al. 2023 this volume). Throughout its distribution in Panama, it is thought to occur on the Pacific and Caribbean coasts and intervening inland areas including upland areas of ~450 m.a.s.l.; in its far western range in Panama, the species distribution may not reach to the pacific coast (Méndez-Carvajal et al. this volume). There is no obvious geographical barrier which restricts the species from ranging further west; further research is needed to determine how far it extends.

In Colombia, *A. zonalis* occurs from the Panamanian border in the north in the department of Chocó, south along the Pacific coast through the departments of Valle del Cauca, Risaralda, Cauca, and Nariño, and in inland and coastal areas of the Caribbean in the departments of Antioquia and Córdoba (Defler 2004; Méndez-Carvajal et al. 2023 this volume). In the far northeast, the species' distribution is probably limited by the Rio Sinú, Córdoba, after which it is replaced by *A. grisiemembra,* although the exact limit is not known (Defler 2004; Méndez-Carvajal et al. 2023 this volume). Along the pacific coast, the species is limited by the highlands of the Andean cordillera (Méndez-Carvajal et al. 2023 this volume), where it is replaced by *A. lemurinus*. The southern distributional limit has not yet been determined. It has recently been reported just south of the Rio Mira, Nariño, bringing its distribution to within 10 km of the Ecuadorian border, but surveys in northern Ecuador have not confirmed the species presence (Méndez-Carvajal et al. 2023 this volume).

In Panama, the species has also been reported from the Isla Bastimentos, Bocas del Toro (Fig. 2.14), although surveys are needed to confirm if these records are of individuals introduced to the area or naturally occurring (Méndez-Carvajal et al. 2023 this volume).

2.4 Discussion

We reviewed the geographic distributions of all 13 owl monkey taxa occurring in Argentina, Bolivia, Brazil, Colombia, Ecuador, Panama, Paraguay, Peru, and Venezuela, following the taxonomy put forward by Hershkovitz (1983), with the addition of *A. jorgehernandezi* (Defler and Bueno 2007). There is still a need to revise the taxonomic diversity of the genus incorporating molecular data, as well as systematic sampling of areas where surveys are lacking. Similarly, the precise distributions of all *Aotus* taxa will benefit from considering a revised updated taxonomy. With rates of habitat loss increasing throughout South and Central America, it is becoming increasingly urgent to properly document the genetic and ecological diversity and adaptations of wild populations.

Owl monkeys are among the most widely distributed primate genera in the Americas (Fig. 2.1), with the fourth largest latitudinal range (after *Alouatta*, *Ateles*, and *Sapajus*), between 11° N and ~ 27° S, third largest extent of occurrence (~8,000,000 km^2, after *Alouatta* and *Sapajus*), and the second largest altitudinal variation (after *Alouatta*), from sea level to ~3500 m.a.s.l. in the Andes. This impressive geographical range is mirrored in the number of habitat types in which they are present, from hyper humid lowland seasonally flooded and terra firme Amazonian forests, arid northern dry forests, to high elevation Andean cloud forests, and highly seasonal, naturally fragmented, areas of the Gran Chaco. Unfortunately, they are also found in highly disturbed and fragmented anthropogenic landscapes, where their persistence is threatened, with a number of species now considered Threatened on the IUCN Red List of Threatened Species.

Large-scale distribution maps and niche modeling often use methods which can lead to biased assessments, including large areas where species are absent, or alternatively excluding areas of occurrence (Burgman and Fox 2003; Palminteri et al. 2011). In the best cases, correction techniques are employed to minimize these biases prior to publishing (IUCN 2013, 2019). Still, many of the maps produced through this approach are made following rivers and other geographic barriers, which often miss fine-scale detail of distributions where these barriers may be less effective, such as around headwaters of rivers, or due to highly mobile species (Haffer 2008; Palminteri et al. 2011). Although a number of studies have found evidence supporting rivers as distributional limits to Amazonian primates (Ayres and Clutton-Brock 1992; Boubli et al. 2015; Fordham et al. 2020), they are not strictly impermeable barriers. At the continental scale, mapping errors will be minimal in describing generalized species distributions. Our use of distribution maps and geographic localities allowed us to capture these cross-boundary populations in mapping and to highlight areas where information is lacking. Alternatively, distributions can be estimated through ecological niche modeling and similar techniques (Phillips et al. 2006) using occurrence data, such as the GBIF (Anderson et al. 2016) or museum specimens. These too, however, can be affected from biases, incomplete

sampling or data, and taxonomic and geographic inaccuracies, especially with older collection localities (Anderson et al. 2016).

In our review, we tried to improve accuracy through combining existing distribution maps with the most complete list of localities to date, extending coverage and removing areas from distribution maps, and reviewing these based on our own knowledge and combined field experience. Notwithstanding our efforts, there is still much uncertainty in the distributions presented here. These come from possible errors in the databases used, as well as general uncertainty regarding the taxonomic diversity of the genus (Fernández-Duque et al. 2023 this volume) and the lack of information from many large areas of potential distribution. Further research is particularly important in the areas highlighted above, and we hope that researchers concentrate efforts on resolving the taxonomy of the genus, while further surveys are carried out on the lesser-known species and areas where owl monkeys may be found.

Finally, we wish to caution readers by drawing their attention to the following concerns, caveats, and limitations in the data we used and the proposed distributions, and that these same considerations be applied when using similar data from other sources:

- All models and predictions are open to error and will never perform better than the data used to produce them.
- Geographic data prior to the use of GPS technology can be very unreliable, and even the use of GPS and GIS has not eliminated all possible errors.
- Identification of many species from visual detections in the field, especially of owl monkeys, is very unreliable. Misidentifications are common, and many identifications are made on the basis of "known distributions," in effect confirming errors. Even identifications from captured specimens can be erroneous, and changing species definitions mean that older collections may be outdated.
- Sampling is often geographically biased, leaving large areas under sampled. Distribution maps often include areas where a species has not been confirmed.
- Species and their ranges are not static, taxonomies change, and range barriers, particularly ecological ones, can be porous, changing over time.

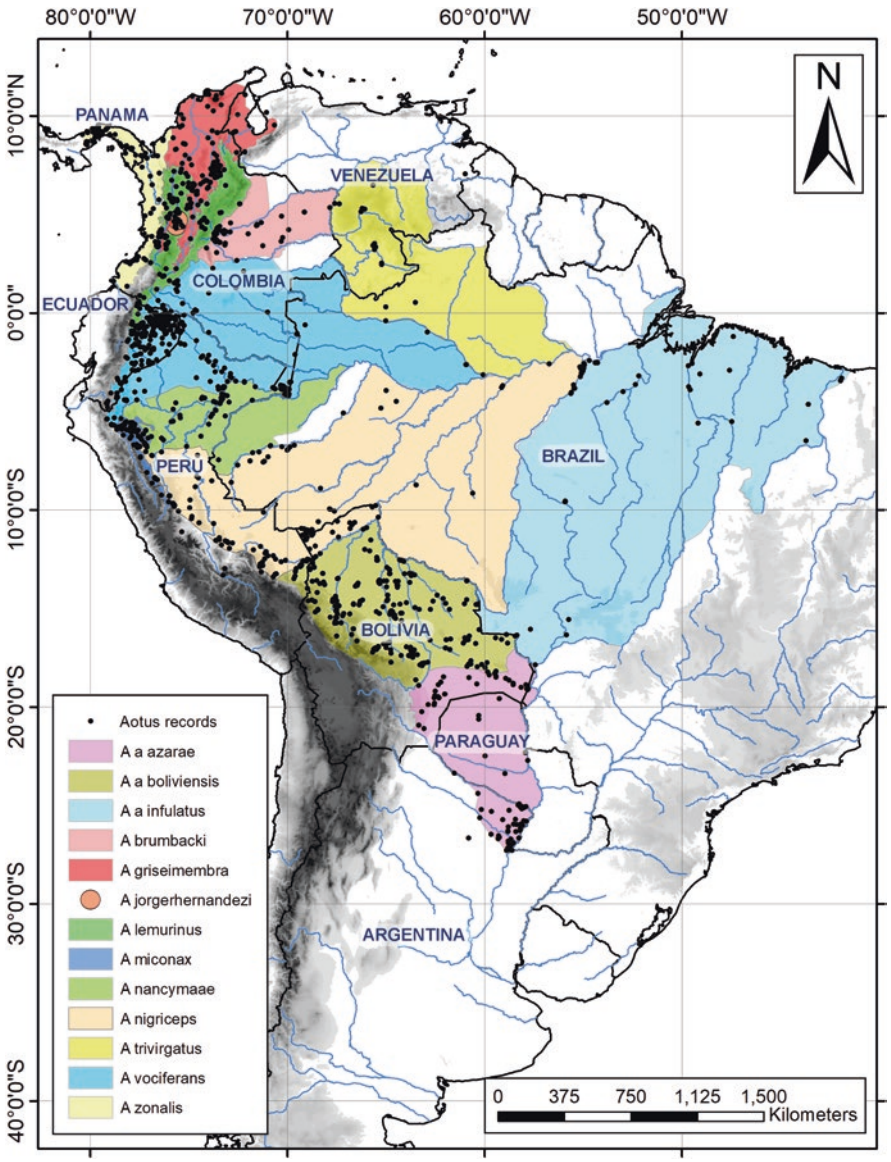

Fig. 2.1 Map of South America showing major rivers, relief, and large-scale distributions of owl monkey species. Points represent species localities used in this chapter

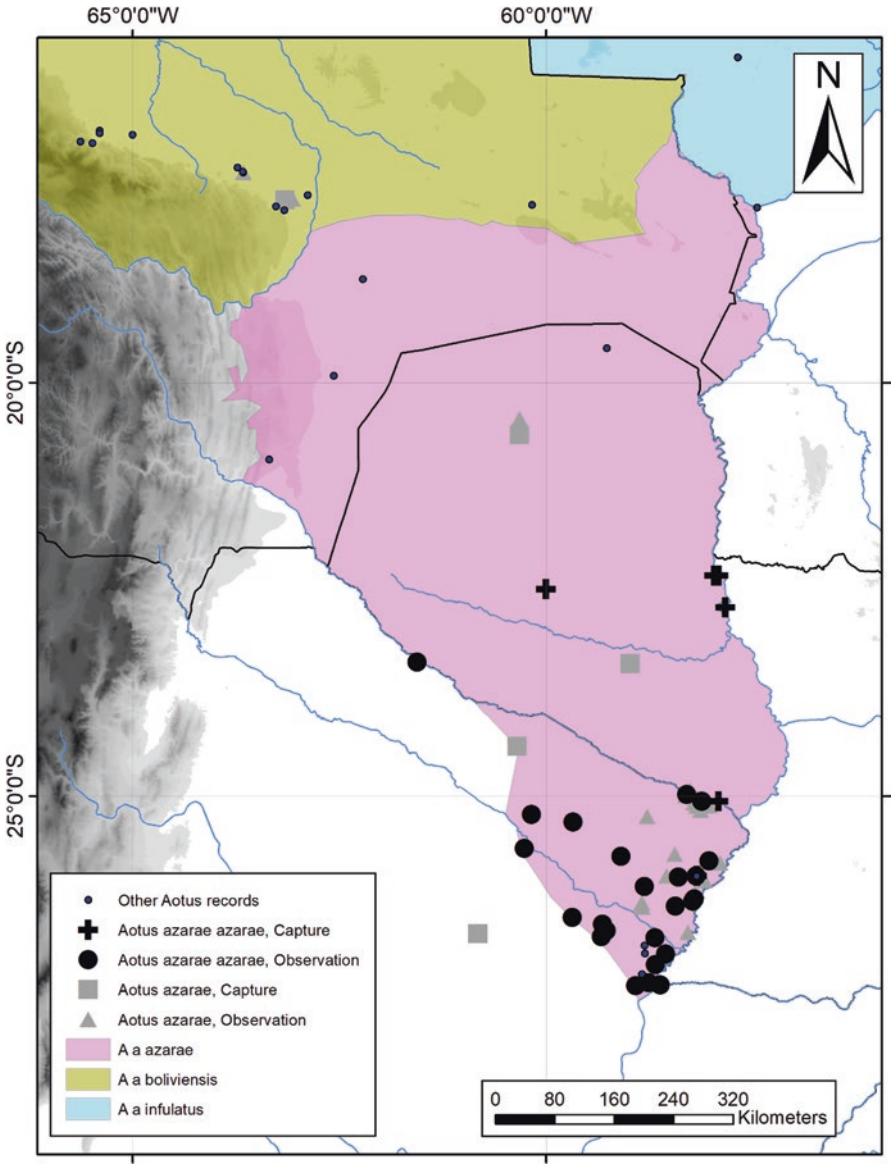

Fig. 2.2 Proposed distribution of *A. a. azarae* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

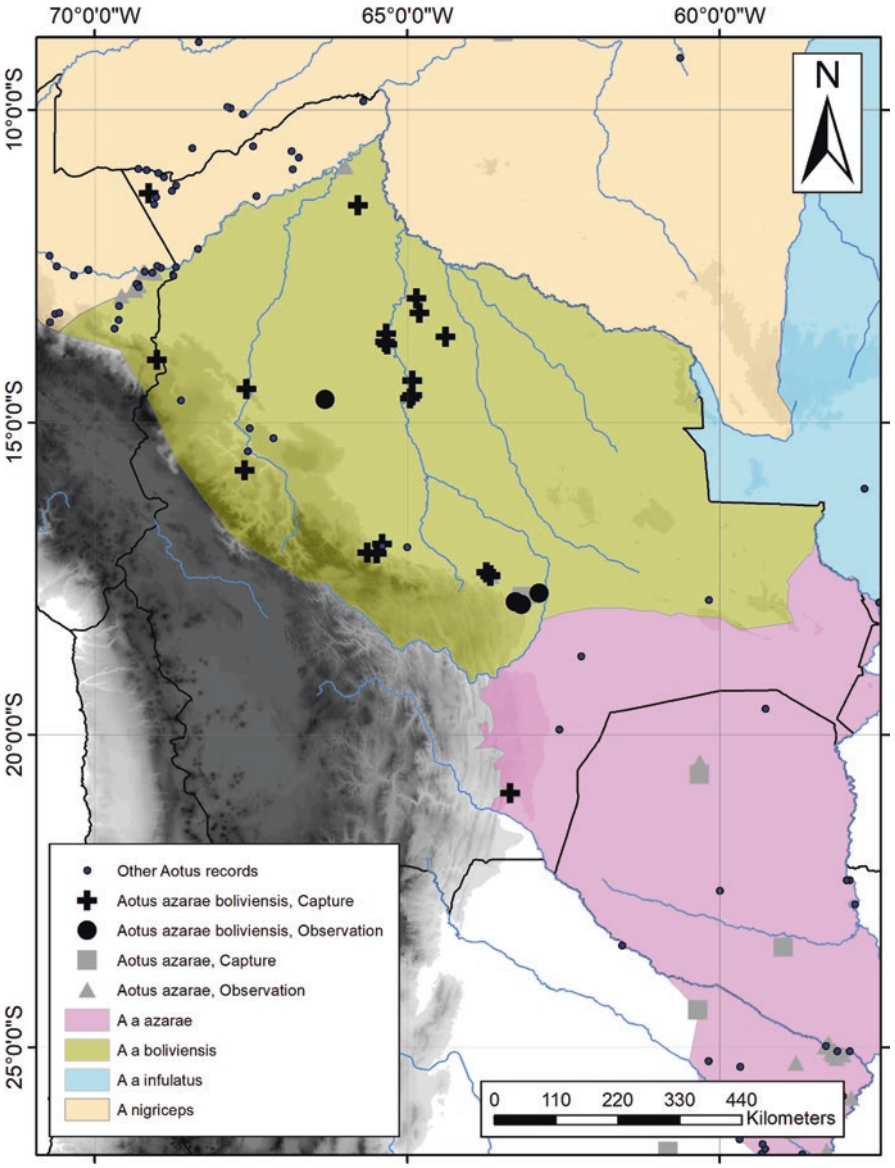

Fig. 2.3 Proposed distribution of *A. a. boliviensis* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

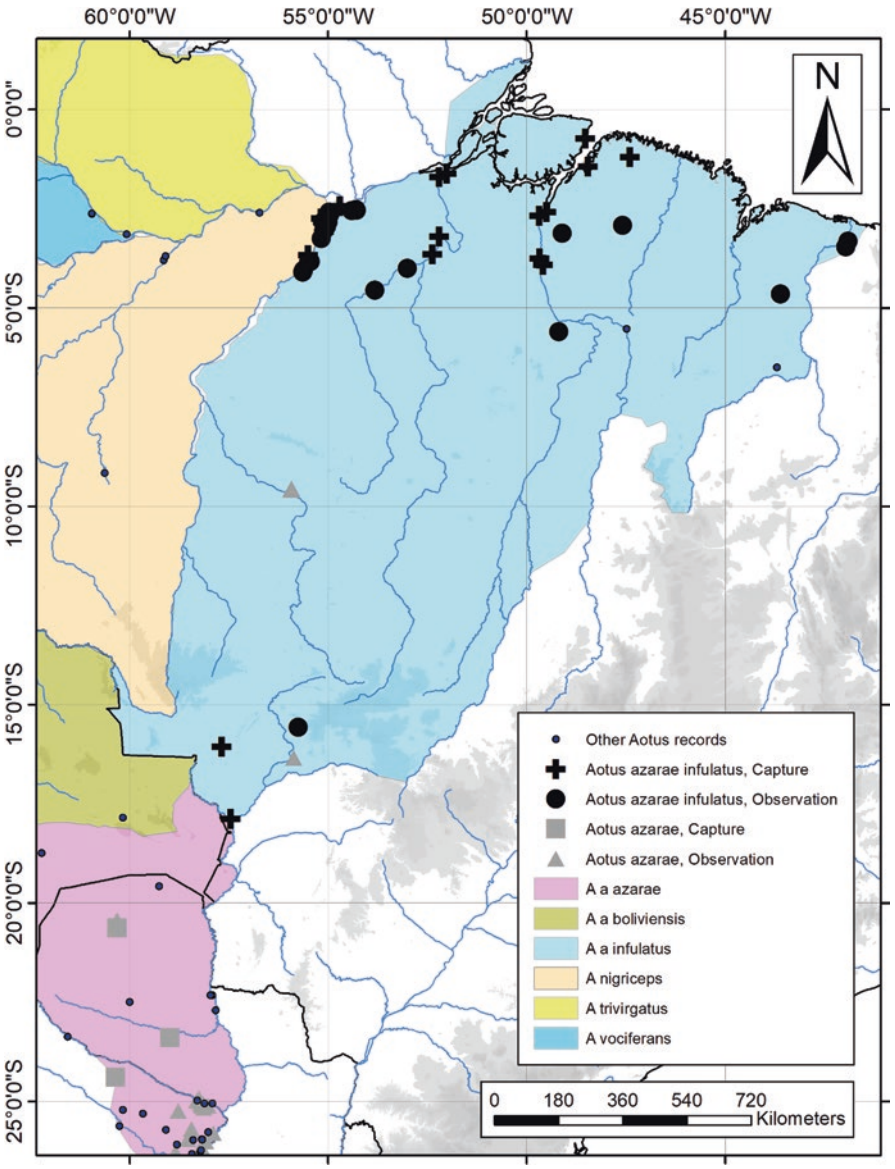

Fig. 2.4 Proposed distribution of *A. a. infulatus* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

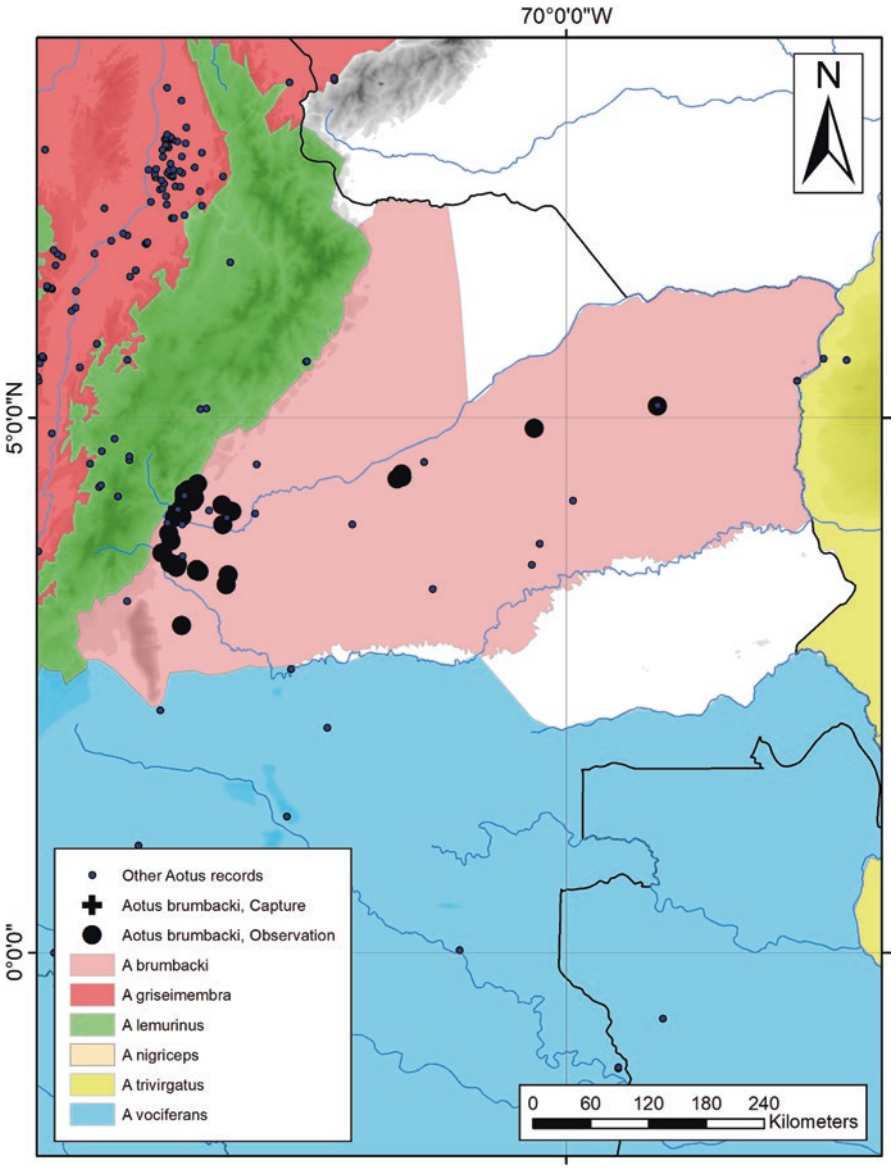

Fig. 2.5 Proposed distribution of *A. brumbacki* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

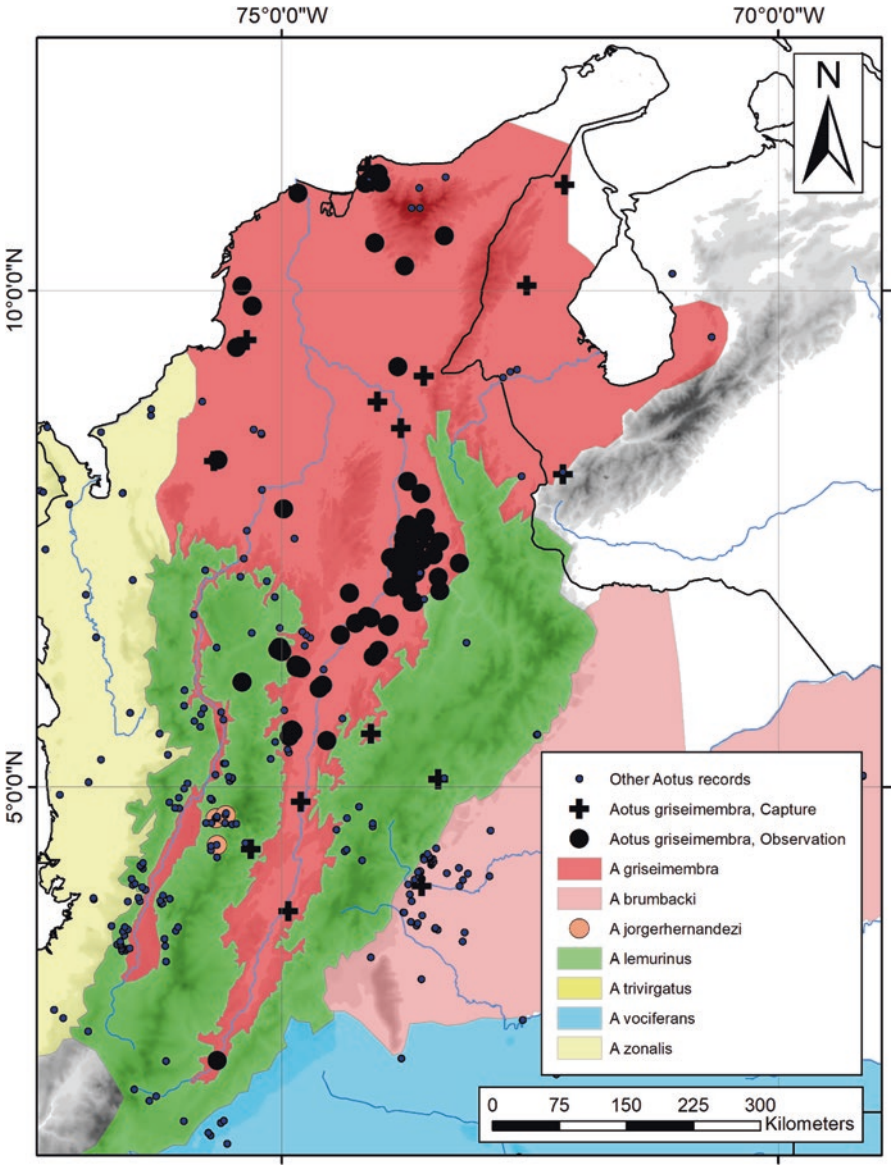

Fig. 2.6 Proposed distribution of *A. griseimembra* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

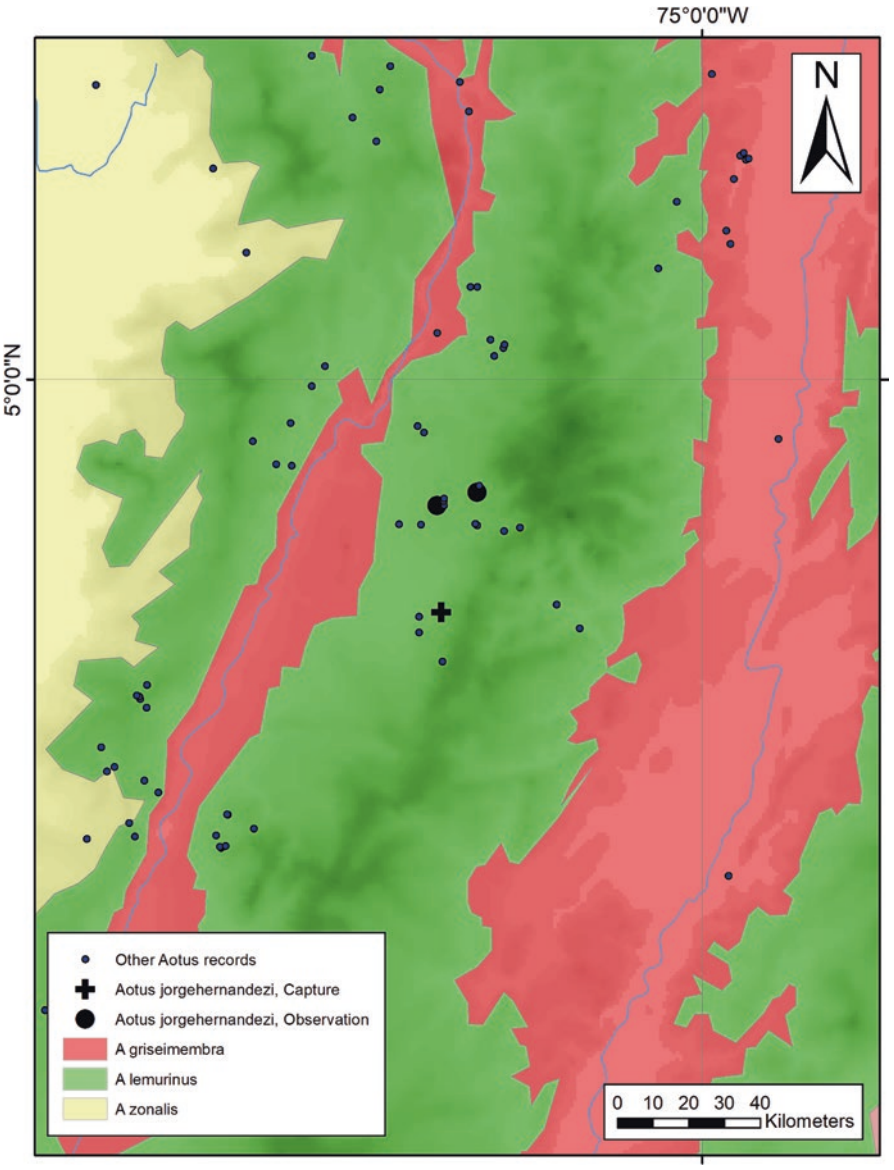

Fig. 2.7 Proposed distribution of *A. jorgehernandezi* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

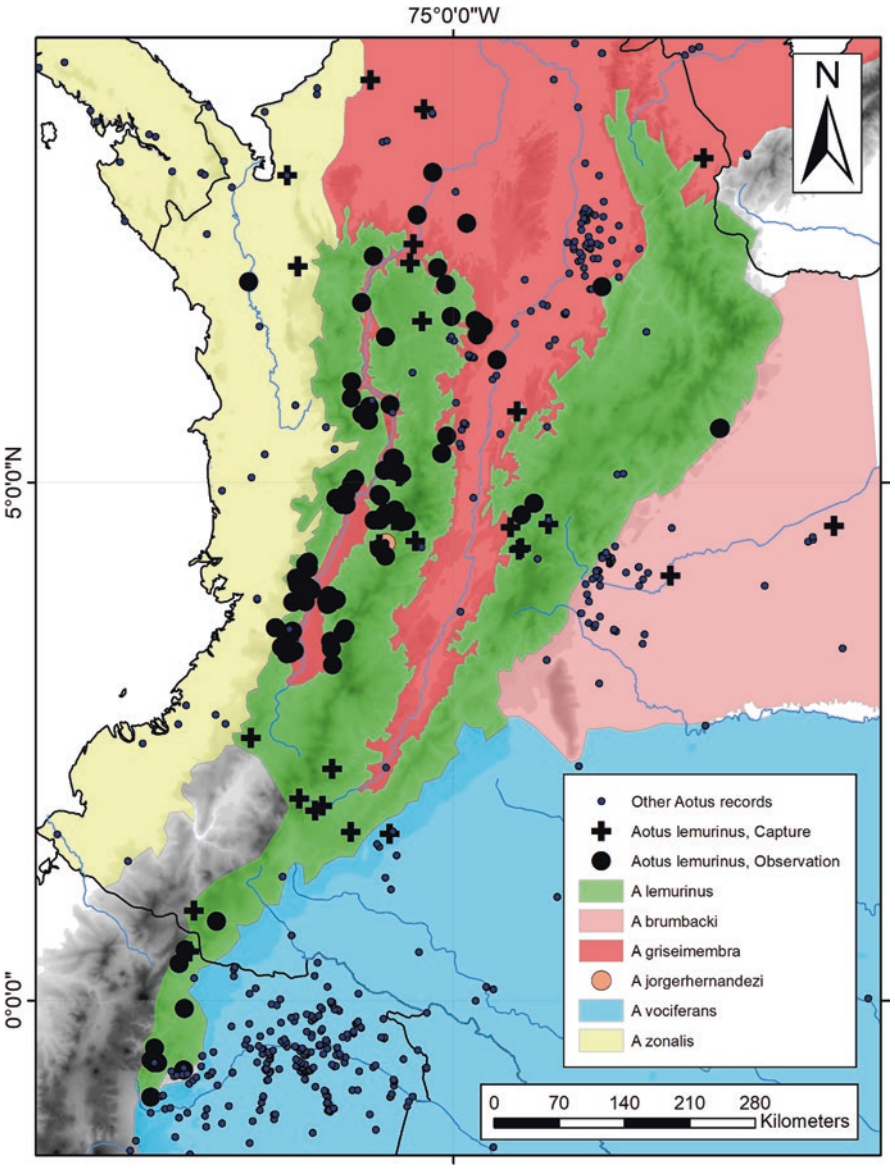

Fig. 2.8 Proposed distribution of *A. lemurinus* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

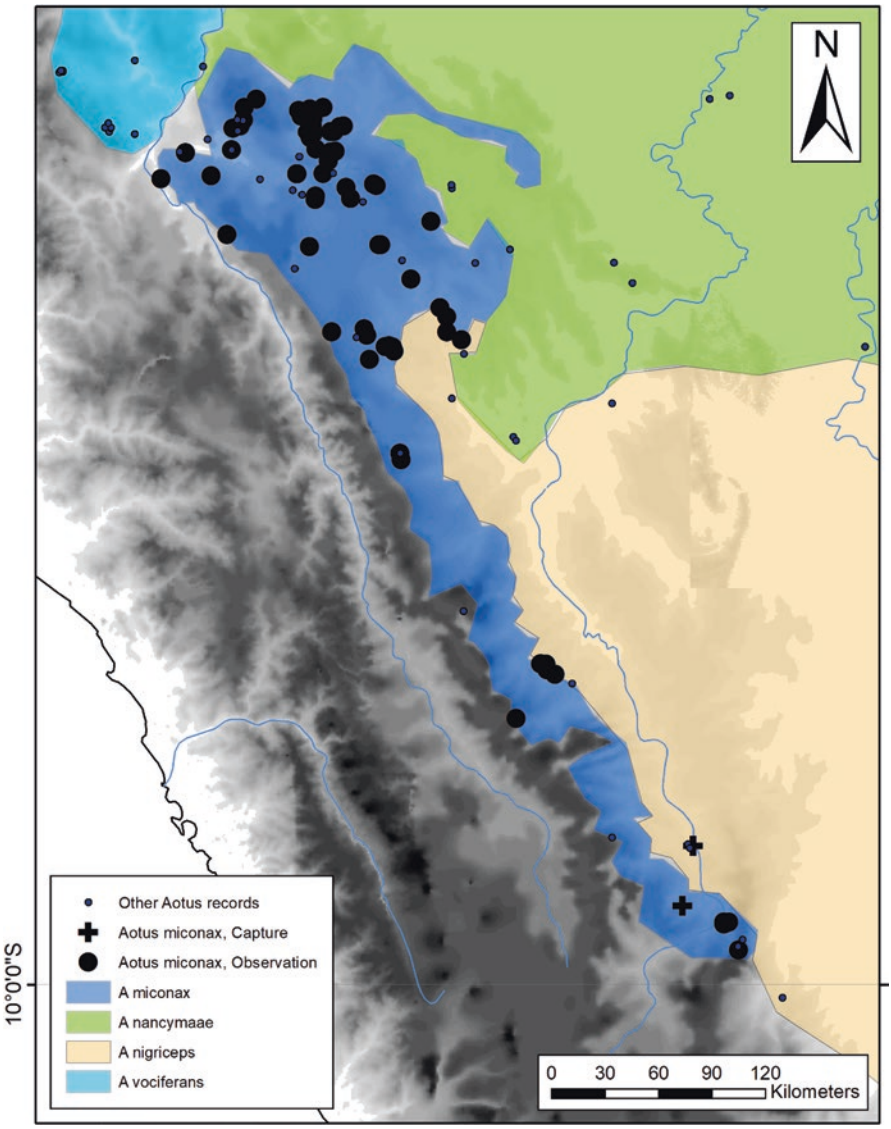

Fig. 2.9 Proposed distribution of *A. miconax* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

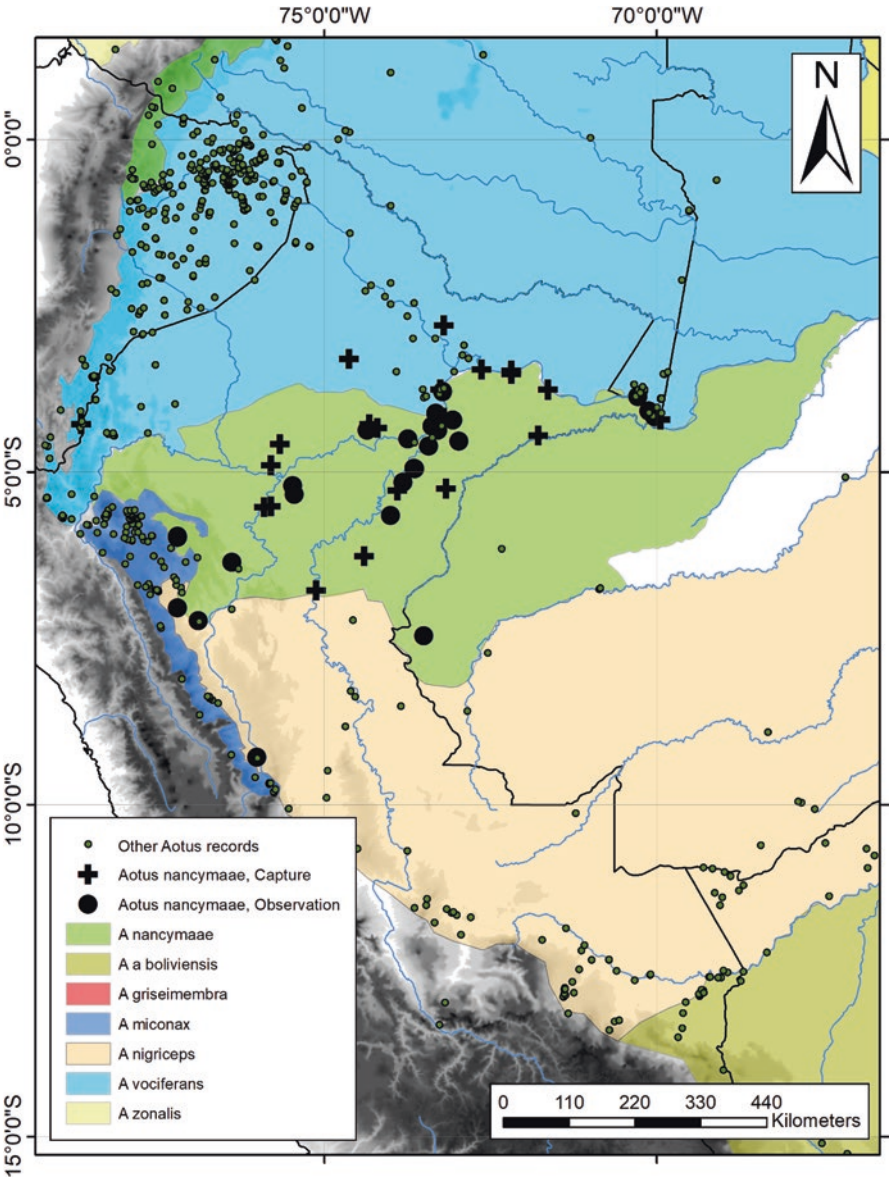

Fig. 2.10 Proposed distribution of *A. nancymaae* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

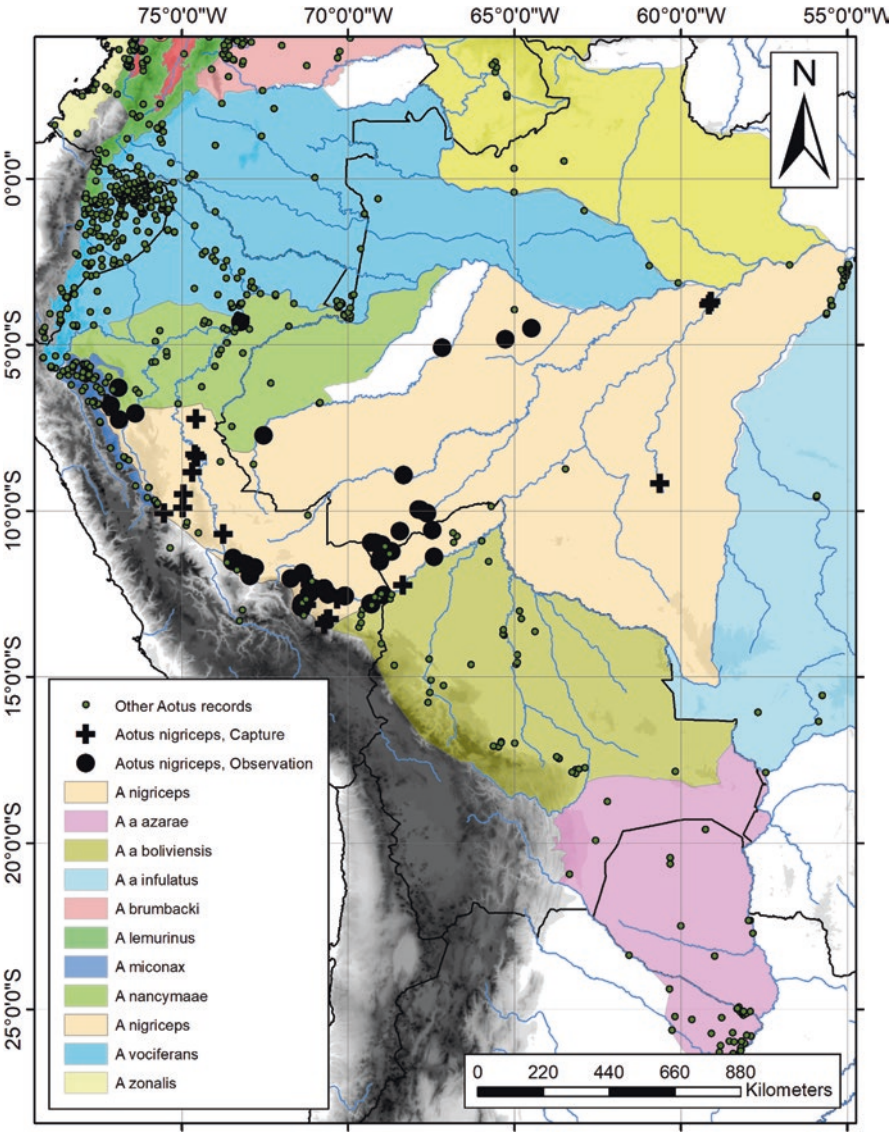

Fig. 2.11 Proposed distribution of *A. nigriceps* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

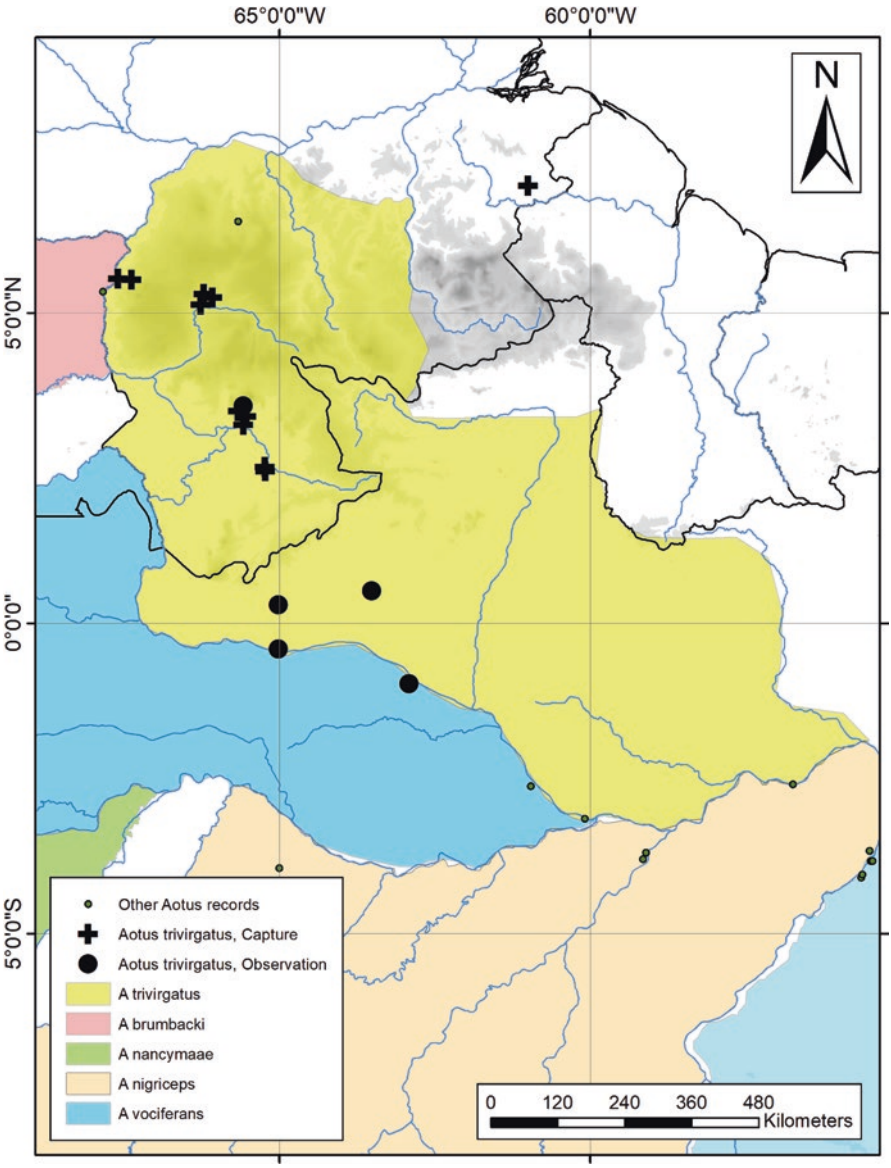

Fig. 2.12 Proposed distribution of *A. trivirgatus* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

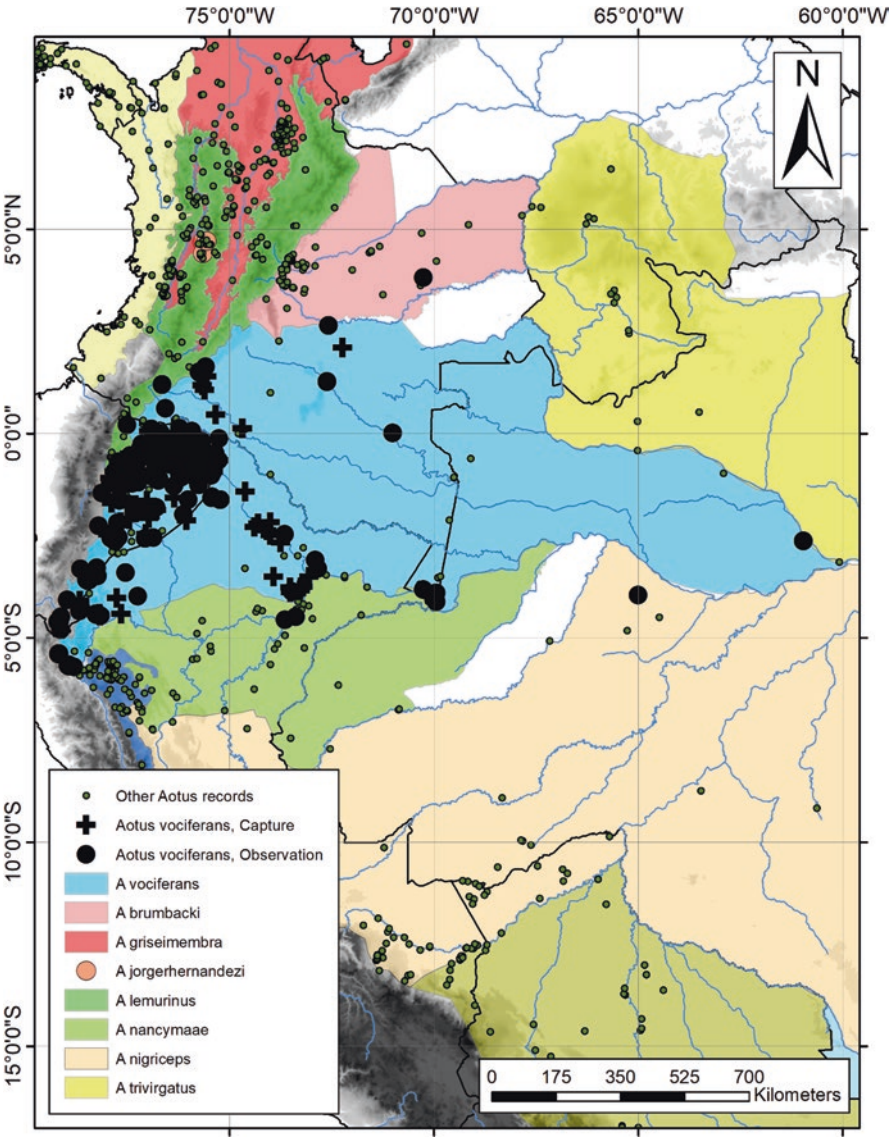

Fig. 2.13 Proposed distribution of *A. vociferans* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

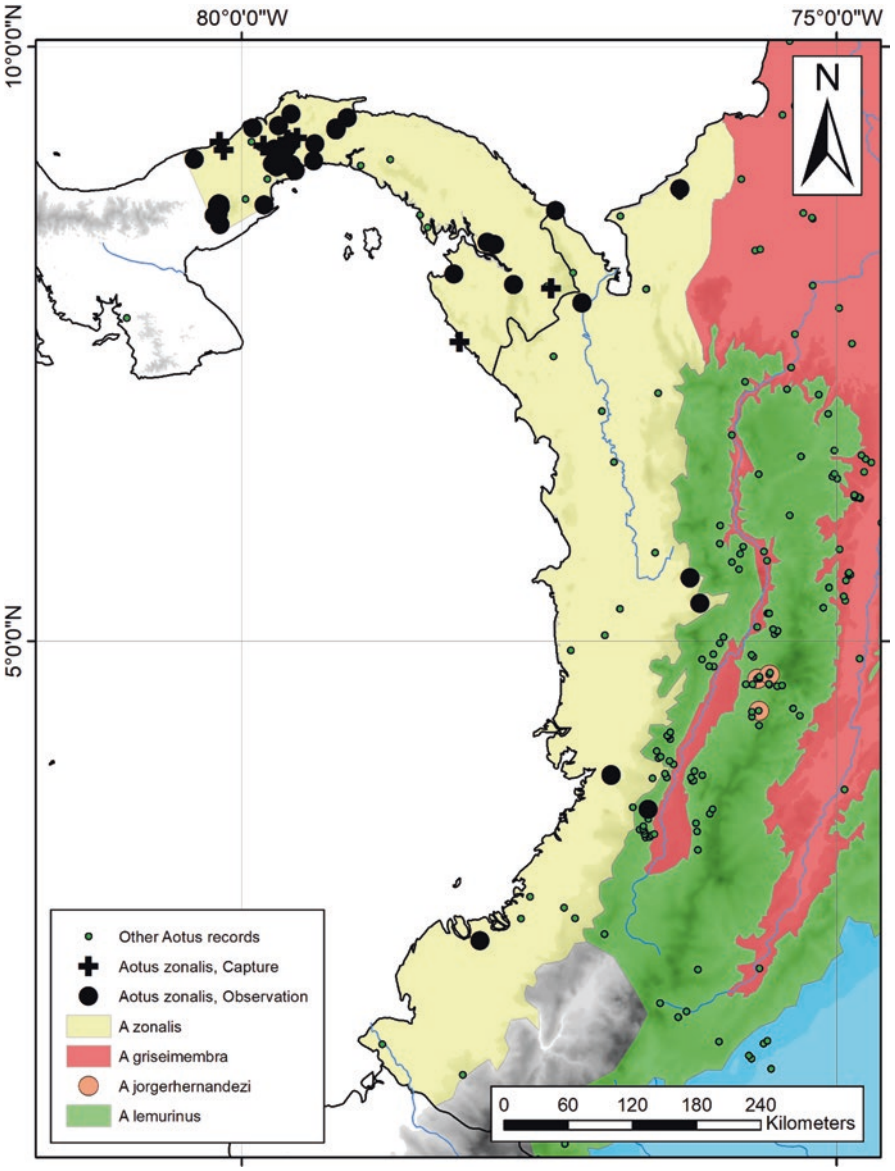

Fig. 2.14 Proposed distribution of *A. zonalis* and neighboring species, showing major rivers, relief, and national borders. Points represent species localities

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