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The Amazon River dolphin, *Inia geoffrensis*: What have we learned in the last two decades of research?

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Abstract

In the last decades, knowledge about the biology of the Amazon River dolphin *Inia geoffrensis* has increased considerably. Accordingly, we present a review of the published literature on this river dolphin, with a focus on the topics with the most advancements and those that are important to the species' conservation. We also present new information, including emerging knowledge on the other putative species of *Inia*. We summarize the current knowledge of the biology of *Inia*, covering aspects of taxonomy, distribution, life history and reproduction, genetics, anatomy and physiology, health, behavior, ecology, demographic parameters, and population trends. We also highlight the main anthropogenic threats affecting the species and the resulting conservation efforts.

Keywords:
boto, bufeo, South American river dolphins, *Inia boliviensis, Inia araguaiaensis*

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Context and content/Taxonomy

Prior to 2014, the genus *Inia* was considered monotypic with three recognized subspecies. Then, a new species, *Inia araguaiaensis*, was described in the Tocantins-Araguaia River Basin, Brazil (Hrbek et al., 2014; Siciliano et al., 2016). Additionally, *Inia boliviensis* was reestablished and its distributional area expanded along the Madeira River in Brazil (Banguera-Hinestroza et al., 2002; Gravena et al., 2014a, b). Nonetheless, the Society for Marine Mammalogy's Committee on Taxonomy still recognizes a single species in the genus, *Inia geoffrensis*, the Amazon River dolphin, with two subspecies: *I. g. boliviensis* (d' Orbigny, 1834), the Bolivian bufeo, and *I. g. geoffrensis* (Blainville, 1817), the boto (Committee on Taxonomy, 2022). According to the Committee, this classification was justified by the lack of isolation between the Bolivian bufeo and the boto, and a lack of robust sampling; however, these concerns were addressed by Gravena et al. (2014, 2015). *Inia araguaiaensis* is also not recognized as a separate species because of limited sampling throughout the species' distribution. However, the Brazilian environmental agency (ICMBio) accepts the Araguaian dolphin as an endemic species with its range completely confined inside Brazilian territory (ICMBio, 2018). The Bolivian government considers the Bolivian bufeo a national treasure (Law No. 284/2012; Aliaga-Rossel & Duran,

Figure 1. Group of Amazon River dolphins or botos, *Inia geoffrensis* (Photo credit: Projeto Boto).

2020) and a separate species from *I. geoffrensis*. In terms of conservation, these decisions are very important because they give governments and society the responsibility to protect these dolphins in their territories. In this account, we will consider the genus *Inia* to be comprised of three living species as follows: order Artiodactyla, infraorder Cetacea, family Iniidae: *Inia geoffrensis, Inia boliviensis,* and *Inia araguaiaensis*. We will focus on *I. geoffrensis* (Fig. 1) but also highlight relevant information on *I. boliviensis* and *I. araguaiaensis.* The common name "boto", or Amazon River dolphin, will be used to refer to *I. geoffrensis.*

General characters, form, and function

Inia is the largest of the freshwater dolphins. The boto shows remarkable sexual dimorphism, with males larger and more robust than females (Best & da Silva, 1989a, b; da Silva, 1994; Martin & da Silva, 2006). Males reach the mean asymptotic body length at 231.5 ± 1.53 cm (n = 24, range 219 - 249 cm) and females at 199.8 ± 1.22 cm (n = 45, range 182 - 218 cm), with a ratio of 1.16. With males 16% longer and 55% heavier than females, the species is one of the most sexually dimorphic of all cetaceans (Martin & da Silva, 2006). The longest male ever measured in the Amazon was 250 cm (n = 193), and the longest female was 225 cm (n = 185) (Martin & da Silva, 2006). The heaviest male was 207 kg, and the heaviest, non-pregnant adult female was 141 kg. Including pregnant females (n = 185), the maximum female body mass was 153.5 kg (Martin & da Silva, 2006). In the Orinoco, the largest boto that has been measured was 227 cm in length and 200 kg in weight (Mosquera-Guerra et al., 2021). The largest *I. boliviensis* measured was a pregnant female, 240 cm (holotype of the species) in 1834 by d'Orbigny, at Princípe da Beira in the Guaporé River (Pilleri & Gihr, 1977), but it is not clear if the measurement was taken in a straight line. Aliaga-Rossel & Escobar-Ww (2020) measured 26 Bolivian dolphins of different age classes, with the largest male measuring 235.6 cm and the largest female 239 cm.

Botos are very well adapted to navigate in all types of riverine habitats throughout their distribution. Their body is very flexible and is capable of twisting laterally. The head is thick and strong, with a long and cylindrical rostrum that is well separated from the small melon, which is rounded and bulbous. The melon is not compact and firm like in other dolphins but protuberant and soft, capable of changing its shape by voluntary muscle contraction and during echolocation.

The small, round eyes are functional and provide good vision, both under and above water (Best & da Silva, 1989a, b). Non-fused cervical vertebrae allow movements of the head in all directions, a characteristic not frequent in other species of dolphins. The cheeks are large and protruding, revealing a strong muscle mass necessary for the wide opening of the large mouth with a long rostrum and a powerful bite. The area of the throat in adults is flaccid and externally presents vertical pleats that expand during deglutition of large prey. The dorsal fin is long, thick, low, and keel-shaped. The flippers are large, broad, paddle-like (thick in the external border but thinner inside), and highly articulated. The joining of the bones of the sternum and the shoulder enables fine swimming movements and swimming backward (da Silva & Martin, 2014, 2018; Bastida et al., 2018). The broad and thick flukes, at the end of a laterally flattened caudal peduncle, are often frayed or ragged along their rear margin as a result of intraspecific interaction (Martin & da Silva, 2006; da Silva & Martin, 2018). Many of these morphological characteristics reduce speed and performance of aerial activities and high jumps, but they allow the boto to move and capture its prey in hard-to-reach places (*i.e.*, between branches and trunks in the flooded forest and under extensive mats of aquatic plants that form during the high-water period and harbor fish) (Martin & da Silva, 2006; da Silva & Martin, 2014).

Another distinctive characteristic of the boto is the pink color of its body. Although there are some pink females, males are generally much more pink than females. Martin & da Silva (2006) inferred that pinkness is a result of progressive loss of dark pigmentation with age and intraspecific aggressive interaction, not an indication of general health, but an honest signal of maturity, and it can also have a visual display effect. Fetuses and neonates are dark gray, and they change to light gray, and then pink as they age. There is no defined line separating the color of the dorsal and ventral regions, but the ventral area is usually lighter than the dorsal (Bastida et al., 2018; da Silva & Martin, 2018).

Martin & da Silva (2006) described skin lesions in adult male botos with a body length of 219 cm or more. These "cobblestone" lesions occurred on the leading edge of the dorsal fin. These lesions are either scar tissue or an inherited characteristic serving as a shield or weapon during intraspecific agonistic behavior.

Few descriptions of the internal morphology of the boto have been published. The respiratory tract has similarities with other dolphins, with the presence of a small trachea, a tracheal bronchus, and the right and left main bronchi, all with flat C-shaped cartilage rings dorsally opened. The right and left lungs exhibit a single cylinder lobe with a length greater than its width (Santos Jr et al., 2017). However, in the nasal tract, the vestibular air sac complex has developed into one large diverticulum, different from other dolphin species (Schenkkan, 1977). Schenkkan (1977) suggested that this morphology influences the sound production in the species. The structure of the bullae also has some specific features, which are apparently related to the ecological specificity of this species (Solntseva, 2009).

The stomach has three portions: the forestomach (muscular), the main stomach (glandular), and the pyloric stomach (muscular), showing morphological differences compared to *Platanista*, *Pontoporia* and *Lipotes* (Yamazaki & Kamiya, 1981). Different from

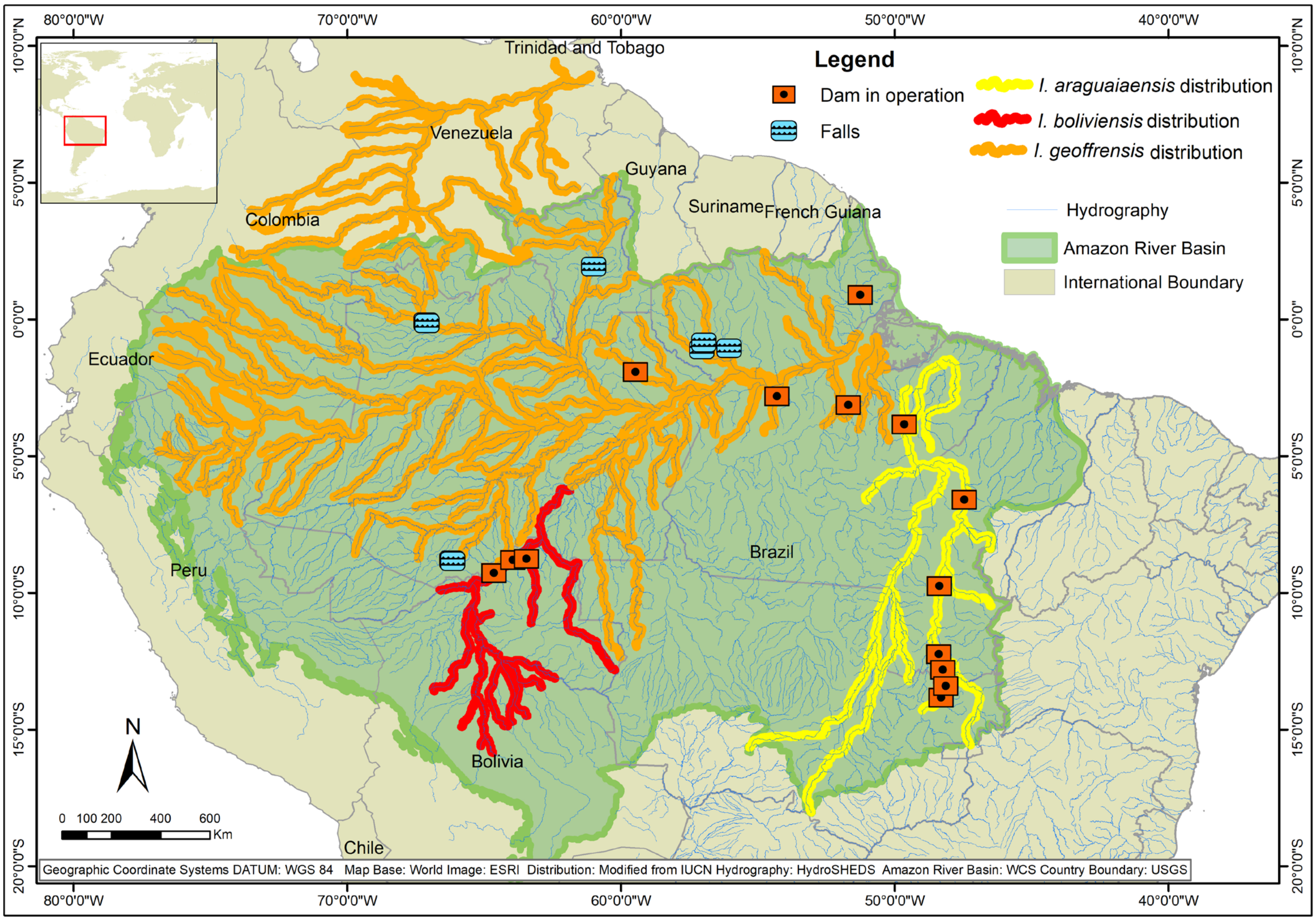

Figure 2. Map displaying records of botos (*Inia* sp.) in the main river basins in the Amazon region, as well as the main hydroelectric dams in operation in the Amazon and Orinoco River basins and the main falls that have the potential as barriers to the boto distribution. Spatial data from IUCN (2018).

other species, in *Inia* the food may enter the forestomach and main stomach at the same time or the main stomach first. This seemingly facilitates the action of gastric juice on the digestion process (Yamazaki & Kamiya, 1981; da Silva, 1983).

Observations on the morphology of the reproductive tract were made by Best & da Silva (1980) and da Silva (1994). Both ovaries are well developed and active. In males, the total testes weight is of the order of 1.2% of the total body weight. This relatively small percentage of testes weight is probably related to the high level of male competition and the promiscuous mating system. The head morphology of spermatozoa is similar to that of some other odontocete species but differs from that of delphinids (Amaral et al., 2017). The placenta is diffuse epitheliochorial, like in other cetaceans (da Silva et al., 2007).

Age-class physiological parameters of wild individuals have been evaluated in two locations in Brazil. The mean cardiac rate (CR, beats/min) of juvenile and adult individuals captured in the Mamirauá Sustainable Development Reserve, Amazonas (see da Silva & Martin, 2000 for details of study area), was 79 (ranging from 60 to 113). In botos captured in the Balbina Dam reservoir, Presidente Figueiredo, Amazonas, the rate ranged from 36 to 136 with a mean of 90. The respiratory frequency (RF, breaths/min) in juveniles and adults from the Mamirauá Reserve ranged from 3 to 18 (de Mello & da Silva, 2019), and in juveniles and adults from Balbina, from 3 to 14 (de Mello et al., unpub. data). Calves from the Mamirauá Reserve presented higher CR and RF given their normally elevated metabolism (Mann, 1999), with means of 102 beats/min and 11 breaths/min (de Mello & da Silva, 2019).

Distribution

Despite its endangered status, *Inia* is still abundant and has a broad distribution along the main rivers and tributaries of the Amazon and Orinoco rivers. Its range is limited by large impassable rapids, waterfalls, and very small or shallow rivers (Fig. 2). Its occurrence is directly related to the water level of the rivers in relation to the hydrological pulse (da Silva & Martin, 2018). In the last century, extreme droughts and floods in the Amazonian rivers may have altered the historical distribution of these dolphins by allowing individuals to pass flooded rapids and less steep falls.

Goulding et al. (2003) divided the Amazon River Basin into 13 separate river basins, including the Tocantins-Araguaia River Basin. In contrast to other authors, they considered the Tocantins River as part of the Amazon Basin because it discharges into the Pará River south of the Amazon River, it is linked ecologically to the Amazon River mouth, and its fauna and flora are related to

Amazon Basin species. The Tocantins-Araguaia River Basin is where the new species *I. araguaiaensis* was recently described (Hrbek et al., 2014). The Tocantins River was one of the first rivers to be dammed in the region, with the construction of the Tucuruí Hydroelectric Dam. This dam divided the river in 1986, blocking its access to the Pará River and isolating the *Inia* population of this basin from the Amazon River Basin.

The boundaries of *I. araguaiaensis* and *I. geoffrensis* in the Tocantins River estuary below the Tucuruí dam are unclear. Genetic analysis of stranded individuals near Soure and along the Marajó Bay revealed that these specimens from the east coast of Pará represent a different and isolated geographic form of *Inia*, and based on the genetic distances and morphological features are *I. araguaiaensis* (Siciliano et al., 2016). These findings confirm that the Tucuruí dam fragmented the *I. araguaiaensis* population.

In Brazil, the Xingu is a clearwater river, and along with most of its tributaries, has many rapids. The Volta Grande do Xingu is the main barrier to the botos, that are not found above this rapid - but they have been recorded in the lower reaches of the Xingu River (Goulding et al., 2003). The clear-water river Tapajós and its main tributaries - Juruena, Arapiuns, Teles Pires, and Jamanxim - flow through the relatively high terrain of the Brazilian Shield with numerous rapids. The main one is São Luiz do Tapajós, about 200 km upward from the river's mouth. During the dry season, these rapids act as a barrier to botos, but during the high water season and exceptional floods, botos, as well as migratory fish, are able to navigate them. Recent studies recorded the presence of botos in the middle Tapajós River, near Jacareacanga city (Pará) (Pavanato et al., 2016).

Before the construction of dams in the Madeira River, several rapids and falls stretched along 360 km between the cities of Porto Velho and Guajará-Mirim at the Brazil-Bolivia border. The Esperanza rapids, in the lower Beni River (Bolivia), is a geographical barrier for Bolivian bufeos. Today, *Inia* populations along the Madeira River are blocked and fragmented by the two large hydroelectric dams, the Usina Hidrelétrica (UHE) de Santo Antônio, and the UHE Jirau. These dams flood the Teotônio Falls and all other rapids, eliminating the barriers that may have existed in this area (Gravena et al., 2014a). One important recent finding on the distribution of *Inia* in this area was the extension of the distribution of *I. boliviensis* below the falls and the existence of hybrids along the Madeira River up to near Borba in Brazil (Gravena et al., 2014b). *I. boliviensis* is present along the Mamoré River and in most of its tributaries in Bolivian territory, and along the Guaporé-Itenez rivers (Aliaga-Rossel, 2002, 2010; Aliaga-Rossel & Duran, 2020).

The Purus and Juruá rivers are ecologically similar, with an extensive floodplain area and a complex *ria* system (lakes with dendritic patterns) inhabited by botos. A recent expedition (2022) recorded the presence of botos in the upper São José Rapids, in the Endimari River, a tributary of the Purus River (S. Brum et al., unpub. data).

The Negro and Branco River basins (Brazil and Venezuela) have numerous rapids in their upper sections. Nevertheless, botos occur along these rivers and in their main tributaries. In the Negro River, botos were recorded from the mouth of the river up to above São Gabriel da Cachoeira and throughout the Cassiquiare Channel (Best & da Silva, 1993; Romero et al., 2001; Rodríguez & Rojas-Suárez, 2008; Portocarrero-Aya et al., 2010). In the Branco River, botos were recorded upriver from Boa Vista in the tributaries Uraricoera and Tacutu rivers (Pilleri & Gihr, 1977; Meade & Koehnken, 1991; Best & da Silva, 1993; Farias, 2015). The Trombetas River rises near the Guyana-Suriname border and its main tributaries are studded with rapids and rocky riverbeds. The major falls is near Cachoeira Porteira, about 260 km from the mouth. Botos are only found in the floodplains and lakes of the lower Trombetas River.

Two major tributaries of the Amazon, the Jari and Araguari rivers, run through the state of Amapá in Brazil. The occurrence of botos in Amapá was recorded in estuarine and coastal habitats, in the Araguari River (at the mouth of the Amazon) and in the Cassiporé River (Siciliano et al., 2008; Marmontel et al., 2021). In the lower Araguari River, botos were recorded in part of the Piratuba Lake, in Tabaco and Piranhas creeks, and in the Flexal River in the areas of Retiro Boa Esperança, Primavera, Tapado, Tracajá Gordo, and Andiroba villages (Melo, 2006). For more detailed information on boto distribution in the Amapá State (North Coastal basins) see Marmontel et al. (2021).

The Ucayali and the Marañón River basins run mainly in Peruvian territory and have records of botos in the main river channels and in several tributaries such as Napo, Tigre, Pastaza, Morona, Santiago, and Huallaga in the Marañón to the mouth of Cenepa, Pucallpa, and Pacaya-Samiria (McGuire & Henningsen, 2007; Gomez-Salazar et al., 2012a; Campbell et al., 2017; Mosquera-Guerra et al., 2022). In Ecuadorian Amazon below 260 m of altitude, botos are well distributed along several rivers (Utreras et al., 2013), but there are no records on the Morona River (Utreras et al., 2010).

Botos also occur along the Caquetá-Japurá Basin in Colombia, with records up to the Araracuara Rapids to the mouth of the Apaporis River and its tributaries Yarí, Quinche, El Sol, Cahuinarí, El Bernardo, Mirití-Paraná, Córdoba, and in the Putumayo River. In the Colombian Orinoquia, botos were recorded in the following rivers: Arauca, Meta, Casanare, Bita, Tuparro, Tomo, Orinoco, Vichada, Guaviare, Inírida below the Córdoba Rapids, Antures, and La Concordia (Trujillo et al., 2010; Mosquera-Guerra et al., 2021, 2022).

The Orinoco Basin is in Venezuela and Colombia, and botos are found in the main rivers and tributaries. In Venezuela, records exist from the delta region upstream of Ciudad Bolivar, Caicara del Orinoco, and near Puerto Ayacucho, and in the tributaries of the Apure (Portuguesa, Guanare and Guaritico rivers), Capanaparo, Cinaruco, and Caura rivers (Best & da Silva, 1993; Romero et al., 2001; Portocarrero-Aya et al., 2010). The largest continuous area of the Orinoco basin uninhabited by botos is the Caroni River basin, which is blocked near its mouth by waterfalls and, since the 1960s, by the Guri Dam (Meade & Koehnken, 1991; Best & da Silva, 1993).

Genetics

In the past two decades, new information has been obtained using molecular markers in different populations of botos, including the discovery of a new species (Hrbek et al., 2014). Hamilton et al. (2001) attempted to construct the river dolphins' phylogeny based on mitochondrial markers and verified the possible existence of at least three different lineages of *Inia*, corroborating previous morphological analyses (Pilleri & Gihr, 1977; da Silva, 1994). Since these studies, the effort to collect biological samples from several rivers that could be used in molecular studies has increased considerably. Banguera-Hinestroza et al. (2002) reinforced the results already observed in morphological studies and in Hamilton et al. (2001), but the distance between sampling localities and the low number of samples weakened some of their conclusions. Conservatively, the authors recognized the existence of at least two Evolutionarily Significant Units (ESUs), one from the Itenéz-Mamoré River Basin, upstream of the Madeira River Rapids, and one from the Amazon Basin, possibly with another lineage or distinct population from the Orinoco River (Banguera-Hinestroza et al., 2002). Thereafter, research efforts were aimed at confirming the existence of these lineages with different molecular markers. The Major Histocompatibility Complex (MHC) (Martínez-Agüero et al., 2006), different intron sequences, Y chromosome regions (Ruiz-Garcia et al., 2008), multiple mitochondrial regions (*e.g.,* control region (D-loop), cytochrome b (Cytb), cytochrome c oxidase subunit I (COI) (Gravena et al., 2014a, 2015; Hrbek et al., 2014; Siciliano et al., 2016; Ruiz-Garcia et al., 2018), and highly polymorphic nuclear regions like microsatellites have been used (Hollatz et al., 2011; Gravena et al., 2014a, 2015; Hrbek et al., 2014). The vast majority of these studies confirm the existence of different lineages or species of *Inia* that are in accordance with their distribution: the Amazon River dolphin *Inia geoffrensis*, divided into two subspecies, *I. g. geoffrensis* and *I. g. humboldtiana*; the Bolivian bufeo, *I. boliviensis*; and lastly, *I. araguaiaensis*, the newest described species (Hamilton et al., 2001; Banguera-Hinestroza et al., 2002; Ruiz-Garcia et al., 2008; Hollatz et al., 2011; Gravena et al., 2014a, 2015; Hrbek et al., 2014; Siciliano et al., 2016).

The only molecular study that contradicts the results presented above is Ruiz-Garcia et al. (2018). They used two mitochondrial regions already utilized in other studies (Hamilton et al., 2001; Banguera-Hinestroza et al., 2002; Hollatz et al., 2011; Gravena et al., 2014a, 2015; Hrbek et al., 2014), and they also observed distinct lineages, but the authors attributed these differences to gene drift and founder events in the Bolivian bufeo populations and suggested that the Araguaian River dolphin was created by a vicariance barrier, contradicting all diversification theories previously proposed.

In addition to validating morphologic and phylogenetic studies, genetic studies are also applied in species conservation. The most important objective of these studies has been to determine whether there are different populations, and if they are experiencing a decline in genetic diversity. Regarding genetic variability, *I. boliviensis* populations present lower heterozygosity and genetic diversity, compared to *I. geoffrensis* (Gravena, 2013). Although no population genetics studies have been conducted on *I. araguaiaensis*, Hrbek et al. (2014) asserted that this species appears to have low levels of genetic diversity. The confirmation of hybrid individuals between *I. geoffrensis/I. boliviensis* and *I. geoffrensis/I. araguaiaensis* (Gravena et al., 2015; Farias et al., 2018), and the complete interruption of gene flow between populations caused by the construction of hydroelectric dams, is a major concern for all *Inia* species because it can further reduce the genetic variability of populations. Moreover, the fact that hybrid individuals have been found in a contact zone does not invalidate the fact that they are different species with independent evolutionary trajectories, as has been shown to occur in several species of cetaceans (Crossman et al., 2016).

Few studies have been conducted to determine the chromosomal composition of *Inia*. Kulu et al. (1971) described that *I. geoffrensis* shares the same diploid number (2n = 44) found in other cetaceans (Arnason, 1974; Heinzelmann et al., 2008). The karyotype structure of the Amazon River dolphin was considered conserved among cetacean species; however, using modern techniques, Bonifácio et al. (2012) observed a different karyotype formula (12m + 14sm + 6st + 10t + XX/XY). The main difference is the presence of only five pairs of submetacentric chromosomes (10sm) and five pairs of subtelocentric chromosomes (10st) (Kulu et al., 1971). Furthermore, significant variations in the heterochromatin distributions along chromosomes and nucleolar organizer region (NOR) location were also found (Bonifácio et al., 2012).

Recently, the karyotype of *I. boliviensis* was described, showing differences between the proposed formula described by Kulu et al. (1971) and by Bonifácio et al. (2012). The Bolivian bufeo presents the karyotype formula 14m + 12sm + 6st + 10t + XX/XY, differing from *I. geoffrensis* by having one metacentric chromosome pair more and one submetacentric pair less. The two species also differ in constitutive heterochromatic patterns (Hamada-Fearnside et al., 2017). These results can contribute to the better understanding of the karyoevolution of the group. Therefore, more samples should be collected and modern techniques applied.

Ecology

Inia can be found in most types of riverine habitats including main rivers, tributaries, smaller channels, confluences, bays, lagoons, and flooded forests (Martin et al., 2004; Aliaga-Rossel, 2010; Gomez-Salazar et al., 2012a, b; Mosquera-Guerra et al., 2021, 2022; Belanger et al., 2022). Their habitat use and movement patterns are largely dictated by the flood pulse and corresponding prey movements. During the dry season, animals are mostly restricted to the main rivers, deep lakes and channels. On the contrary, at high water, they inhabit flooded areas, including grasslands and flooded forests (Martin et al., 2004; Martin & da Silva, 2004a, b; Mintzer et al., 2016). Long-term research has confirmed the predictability of these movement patterns, with an exodus of individuals occurring from flooded areas at falling water (Martin et al., 2004; Martin & da Silva, 2004a, b; Mintzer et al., 2016).

In major rivers throughout their range, most individuals are found in areas of low current, such as riverbanks (within ~150 m), beaches, and confluences (McGuire & Winemiller, 1998; Martin et al., 2004; Aliaga-Rossel, 2010; Gomez Salazar et al., 2012a, b; Belanger et al., 2022). In the central Amazon Basin, females with calves and immature botos tend to use flooded areas at higher densities than solitary adults, which show preference for river habitat (Martin & da Silva, 2004b; Mintzer et al., 2016). In Venezuela, juveniles also showed preference for lagoons (McGuire & Winemiller, 1998).

Botos can exhibit strong site fidelity. In the central Brazilian Amazon, the same individuals have been recorded using the

Mamirauá floodplain for over 25 years (Martin & da Silva, 2004a, b). In Peru, a study in the Pacaya-Samiria Reserve also confirmed long-term site fidelity, with individual sighting histories of up to seven years (McGuire & Henningsen, 2007). Preliminary data from the Colombian Amazon also suggest a decade-long site fidelity in Lake Tarapoto near Puerto Nariño (F. Trujillo, Fundación Omacha, pers. comm., 9 August 2018). Long-term studies are needed on *I. boliviensis*, but one individual in the Tijamuchi River was resighted four times in a span of 239 days (Aliaga-Rossel, 2002).

Inia home range sizes have been estimated in the Amazon and Orinoco basins utilizing various methods. Most recently, home ranges were determined with satellite telemetry and ranged up to 186.8 km^2 for *I. geoffrensis* and 233.9 km^2 for *I. boliviensis* (Mosquera-Guerra et al., 2021, 2022). The corresponding core use areas for these individuals were calculated to be 54.9 km^2 and 32.3 km^2 (Mosquera-Guerra et al., 2021). Previous radio-telemetry and visual observation studies recorded maximum linear ranges for *I. geoffrensis* individuals in Brazil and Peru as 225 km and 220 km, respectively (Martin & da Silva, 1998; McGuire & Henningsen, 2007). Denkinger (2010) estimated linear ranges of over 200 km in Ecuador that extended to different rivers; however, most identified dolphins remained within 50 km. In Bolivia, a maximum linear range of 60 km was recorded in the Tijamuchi River (Aliaga-Rossel, 2000). Studies have generally been consistent in suggesting that males have larger home ranges than females, although more rigorous comparative quantitative analyses are needed. Furthermore, it is important to note that all home range studies have been limited by the timing and duration of data collection. Year-round home ranges that encompass all hydrological periods and corresponding shifting habitats are likely larger in area and total length than what is currently reported. Nevertheless, it is important to note that studies have confirmed international transboundary movements (Mosquera-Guerra et al., 2021).

Basic information on the feeding ecology and food habits of *I. geoffrensis* has been available since the 1980s, and these early studies established *Inia* to be a generalist that eats a wide variety of fishes (da Silva, 1983; Best & da Silva, 1993). Additionally, the heterodont dentition makes the boto unique among cetaceans, allowing it to feed on hard prey like river crabs (*Poppiana argentiniana*; Pilleri, 1972) and small turtles (*Podocnemis sextuberculata*; da Silva & Best, 1982). Moreover, botos are able to cut large armored fish and catfish into smaller pieces before swallowing them (da Silva, 1983).

Over 40 species of prey (19 different families) have been found in the stomach contents of botos in the central Amazon, with the freshwater croaker (*Plagioscion* spp.) being the most prominent (da Silva, 1983; Best & da Silva, 1993). Examination of stomach contents from one boto in the Venezuelan Orinoquia identified four prey species, all of which were identified in the Amazonian study. An evaluation of the stomach contents of a juvenile Bolivian bufeo also showed high prey diversity, with fishes from four families (Aliaga-Rossel et al., 2010). A recent study from three rivers in Brazil and Bolivia used stable isotopes to look at diet composition of *I. geoffrensis* and *I. boliviensis,* confirming the species as top predators feeding mostly on piscivorous fishes (Echeverria et al., 2022). Although *Inia* may engage in depredation, there is no published evidence to suggest that *Inia* are in meaningful dietary competition with fishers, as the main species targeted in local fisheries have not been found in great quantities (if at all) in stomach contents in the mentioned studies.

Reproduction and life history

It is essential to study reproduction to understand a cetacean's life history. Until the last decade, little was known about boto reproduction. Most information was based on opportunistic examination of a small number of carcasses from individuals caught in fisheries, or that were hunted or stranded, and from botos transported to American, European, and Japanese aquariums, in the 1960s and 1970s, for public display (Collet, 1984; da Silva, 1994). Boede et al. (2018) reported on pregnancy and birth in captivity.

Most of the available information on *Inia* breeding comes from studies of botos of the Brazilian Amazon, but it is reasonable to presume that *Inia* in other regions have similar reproductive parameters. Projeto Boto, through the long-term study (~25 years) of individually recognizable animals in western Brazilian Amazon, produced unique information on reproductive parameters of the boto (Martin & da Silva, 2018). These authors found that female botos start reproducing late in life, with the mean age at first birth of 9.7 years and a body length of 180 to 200 cm at first pregnancy. A single fetus is produced after a gestation period of about one year (12.3 to 13 months after conception). Calves are born throughout the year, but calving peaks when the river water level is at its lowest (McGuire & Aliaga-Rossel, 2007; Martin & da Silva, 2018). During low water levels, fish are more concentrated, making their capture easier during the period of high energetic demand for adult female dolphins – the last months of pregnancy and the beginning of lactation (da Silva, 1994). With rising waters, the dolphins re-enter the lakes and channels of the flooded forest, full of small fish (Martin & da Silva, 2004b). With gestation lasting slightly more than a year, conception occurs frequently during this season, when dolphins are more aggregated and food is abundant. This also coincides with the period when socio-sexual object-carrying displays are at their peak (Martin et al., 2008; Martin & da Silva, 2018).

Females can be pregnant and lactating at the same time, and still have an older associated calf when producing a neonate. Consequently, reproductively active females spend most of their lives accompanied by a dependent offspring. Calves are born with a body length of 84 cm (range 78 - 90 cm) and body mass of 12 kg. Parental care is long and lactation lasts between 1.5 and 5.8 years (mean 2.8 years). Seven females were known to lactate for at least 50 months (Martin & da Silva, 2018).

The life span of female botos is unknown, but the oldest female in the Central Amazon population was estimated to be 32.3 years old in November 2017 (Martin & da Silva, 2018). In the same study, females over 25 years of age were still reproductively active, with no indication of reproductive senescence. These authors highlighted the fact that, despite adaptations over millions of years to a life in freshwater ecosystem, the reproductive characteristics of the boto are very similar to those of marine odontocetes.

Another important parameter in the life cycle, life history, and evolution of organisms is the generation time (*i.e.*, the average age of parents of the current cohort, reflecting the turnover rate of breeding individuals in a population). In boto populations, generation time was estimated as 22 years (Moore et al., 2018).

Behavior

Socio-sexual behavior

Because of the turbidity of the waters in the Amazon rivers, underwater observation is very difficult, and boto mating behavior has not been documented in the wild. Recently, opportunistic footage recorded an underwater copulation attempt between two males, in a group with other individuals swimming around at a short distance. The larger boto, with its penis erected, was swimming belly up under the smaller boto, with their heads in opposite directions, attempting the penetration of the former's penis into the smaller boto's genital slit (Associação dos Amigos do Peixe-boi, unpub. data). Homosexual behavior was previously recorded by two male botos in captivity at the Duisburg Zoo in Germany (Sylvestre, 1985). As in many other species of mammals, including cetaceans, homosexual behavior could be key to the social organization of the species' males, helping to form bonds and establish dominance. Östman (1991) characterized adult male homosexual behavior among captive dolphins as dominance-related.

In captivity, masturbation and mating behavior have been recorded several times in females and males from a very early age. A female born at the Valencia Aquarium in Venezuela started copulating at the age of two, when she was 134 cm long and weighed 35.7 kg. These activities were commonly observed in Orinoco River dolphins but are not hormonal-dependent (Boede et al., 2018).

Male botos are known to perform agonist behavior against conspecifics and other aquatic animals. Reports of direct aggression toward boto calves (Bowler et al., 2018; da Silva et al., 2021) have been reported. However, most of these known attacks did not result in the death of the calf, suggesting that mortality would be an inadvertent consequence of the aggressive behavior rather than the motive. Males engaging in this behavior likely do not gain direct fitness benefits in terms of an accelerated return of females to reproductive condition (da Silva et al., 2021).

Adult male botos have been observed carrying objects such as sticks, branches, and clumps of grass, and they repeatedly toss them at the surface. According to Martin et al. (2008), object carrying in this sexually dimorphic species is socio-sexual display behavior, either of ancient origin or as one that has evolved independently in several geographically isolated populations.

Interspecific Interactions

Interactions between *Inia* and other aquatic animals are not rare. There are numerous records of botos throwing electric eel (*Gymnotus* sp.) into the air several times, holding and throwing small turtles, and playing with large pirarucus (*Arapaima gigas*) (Projeto Boto, unpub. data). Object play with a large anaconda (*Eunectes beniensis*) by two adult male Bolivian bufeos was recorded in the Tijamuchi River, Bolivia (Entiauspe-Neto et al., 2022). These authors also suggested that this could be a socio-sexual behavior.

Aggression towards Amazonian manatee calves has also been reported. The wounds on the examined calves were extensive but superficial. Teeth scratch marks were mainly on the body extremities, such as flippers and fluke, with no marks on the head and neck. Since the majority of calves were in low nutritional condition and there should be no nutritional or sexual competition between botos and manatees, the authors suggested that separation of the manatee calves from their mothers occurred before the encounters with botos and the interactions were opportunistic, without the intention of killing (da Silva et al., 2022).

Sound and vocalization

Botos produce a wide variety of sounds. Research on these sounds started with individuals in captivity, with their sounds described and categorized into four groups: echolocation clicks, single intense clicks, jaw-snaps, and burst-pulses (sounds formed by pulses with a high repetition rate and short interval between pulses) (Caldwell & Caldwell, 1970).

The first reports of the occurrence of whistles emitted by botos began with studies of wild populations (Nakasai & Takemura, 1965; Wang et al., 2001; Diazgranados & Trujillo, 2002). Wang et al. (2001) described simple low-frequency (below 5 kHz) contour whistles for Peruvian botos. However, there was uncertainty about these findings due to the presence of the tucuxi (*Sotalia fluviatilis*) in the area, a species known to produce whistles. Podos et al. (2002) did not record whistles in *I. geoffrensis* in the wild. Later, May-Collado & Wartzok (2007) confirmed that botos emit short whistles (0.002 - 0.080 s), with much higher frequencies (up to 48.1 kHz) than reported in previous studies. However, botos rarely emit whistles, suggesting that this type of sound plays a different function than that described for marine dolphins. The authors hypothesized that botos emit whistles to maintain distance between them, rather than promoting group cohesion (May-Collado & Wartzok, 2007).

In the last couple of years, whistles and repetitive sequences of downsweep whistles have been described as part of the diverse vocal repertoire of *I. araguaiaensis*, but the functions of these sounds have not yet been elucidated (Melo-Santos et al., 2019, 2020). Due to the rarity of downsweep whistle sequences, these authors suggest that they are probably associated with specific contexts, such as nursing or mating (Melo-Santos et al., 2020).

Conversely, pulsed calls are frequently emitted by boto and have been labeled based on how they sound to the human ear (*e.g.*, screams, barks, squeaks, squeals, squawks, creaks, cracks, squeaky-squawks, and whimpers) (Caldwell et al., 1966; Caldwell & Caldwell, 1970; Diazgranados & Trujillo, 2002). Although these calls are typical sounds in *Inia*'s vocal repertoire, they are still poorly described, and the behavioral context under which certain sounds are produced is still not fully understood.

Podos et al. (2002) described low-frequency pulsed sounds produced by the botos in the Mamirauá Reserve consisting of heterogeneous series of notes (from 1 to 16) of short duration (on average 0.103 to 0.720 s) and suggested that they are related to foraging. Amorim et al. (2016) found the same type of sound in the population of the Estação Ecológica Juami-Japurá but observed that they had significant differences in acoustic parameters between individuals of the two areas. The authors also concluded that the frequency and time parameters may differ in relation to the physical and chemical characteristics of the water. For example, to avoid information loss during sound propagation in white water, which contains a large amount of suspended material, the use of lower frequencies would be more advantageous for these dolphins (Hamilton, 1980; Amorim et al., 2016). More recently, de Melo et al. (2021) recognized six types of sounds (emitted in the minimum and maximum average range of 1.1 kHz to 25.7 kHz), four of which had not been described.

Melo-Santos et al. (2019) described, for the first time, the sounds of *I. araguaiaensis*, consisting of 237 types (at frequencies ranging from 1 - 10 kHz). The repertoire was composed mainly of pulsed calls and the short two-component calls (pulsed calls lasting less than 0.200 s and with the presence of biphonation). The most produced and documented sound occurred during a possible mother-calf interaction, suggesting its function as a contact call for such pairs.

Overall, there are relatively few studies on the sound production of *Inia*. More information is needed to fill gaps in the repertoire, define the functions of the sounds, and understand the geographic and environmental variations throughout these dolphins' distribution. Herein, we mainly discussed the sounds related to communication and not the clicks used for echolocation.

Demographic parameters and population trends

Information on boto densities has been published since the 1980s; however, comparable studies estimating densities and abundance in different areas have only been completed in the last 10 years (Trujillo et al., 2019; Paschoalini et al., 2021). Densities vary greatly between areas, ranging from areas with relatively low densities, like the clearwater rivers Tocantins (0.5 boto/km^2) and Tapajós (0.47 boto/km^2) (Pavanato et al., 2016; Paschoalini et al., 2020), to areas with higher densities, like the whitewater Purus River (10 – 14 botos/km^2) (Brum, 2021; Paschoalini et al., 2021). It is difficult to make inferences relating these densities to habitat preferences or human impacts because the comparable studies are recent and data on potential covariates are scarce.

Population parameter estimates, like fecundity and survival, are sparse and are available only from studies conducted by Projeto Boto in the Mamirauá Reserve. Information on reproductive parameters was published by Martin & da Silva (2018) and indicated an annual birth rate of 0.22 (calculated based on 71 reproductive females), suggesting that there is low potential for population increase (3% per year; Moore et al., 2018). Importantly, da Silva et al. (2018a) analyzed standardized monthly counts of botos in a portion of the Mamirauá Reserve from 1994 to 2017, and found that the population was declining at an average rate of 7.4% (halving every 10 years). Mintzer et al. (2013) estimated apparent survival using mark-recapture modeling and showed that apparent survival in this population decreased significantly from 0.97 to 0.90 when direct hunting for use as bait began in the region in 2000. Average apparent annual survival for this population was estimated to be 0.91 for the entire study period (1994 - 2011). Although apparent survival estimates have increased in more recent years (Mintzer et al., 2013; Projeto Boto, unpub. data), they have not reached pre-harvest levels. Using other mark-recapture models, Brum (2021) found relatively constant survival from 2003 to 2018, differing slightly between males (96%) and females (97%).

The parameter estimates available for this boto population make it a good candidate for population modeling, including population viability analysis (PVA). Martin & da Silva (2022) conducted a PVA that estimated a loss of 95% of the Mamirauá Reserve boto population in the next 50 years. This result was consistent with the results of separate population modeling conducted by Mintzer et al. (2020). However, these models were based on survival probabilities estimated for the peak of the harvest of boto in the Mamirauá Reserve (Mintzer et al., 2013), and thus could be updated with more recent survival estimates. Brum (2021), using population estimates for Solimões, Purus, and Negro rivers, recently found that survival of adults and juveniles is critical for maintaining boto populations. These analyses also indicated that the boto population of the Solimões River is highly threatened by the killing for use as bait in the piracatinga fishery. To date, population modeling results are very consistent in that the incidental and deliberate killing of botos needs to be reduced to maintain and/or enhance boto populations.

Health, diseases and parasites

The first observations related to a health condition in the genus *Inia* were made on skulls examined in the British Museum of Natural History collection in the 1960s. "Dental caries", later referred to as cavities, were observed in tooth crowns with an apparent destructive process from the surface of the enamel to the underlying dentine in four *I. geoffrensis* specimens (Ness, 1966). Other information gathered from necropsies of free-ranging *Inia* provided evidence of a high prevalence of lung disease, including lung carcinoma, verminous pneumonia (*Halocercus brasiliensis*), and bacterial pneumonia (Geraci et al., 1987; Rodrigues et al., 2018). Furthermore, medical records and necropsies performed on 153 individuals from 1956 to 2006 (from 22 different oceanaria in the United States, Venezuela, and Germany) revealed pneumonia and skin lesions (cutaneous and subcutaneous ulcerations and abscesses) to be the most common findings. Additional necropsy results included cachexia, and renal and hepatic pathology (Bonar et al., 2007).

Capture-release programs have allowed the determination of reference health parameters of wild individuals. Baseline hematological and serum chemistry values were determined for wild, healthy individuals in 2004 - 2005 in the Mamirauá Reserve (de Mello & da Silva, 2019; de Mello et al., 2021). Previously, the only available data on blood values of *I. geoffrensis* were from the 22 animals kept in aquariums in the USA in the 1970s (Ridgway et al., 1970). In general, most of the hematological and serum chemistry values from Mamirauá Reserve dolphins were within the range of those found in delphinids (Bossart et al., 2001; de Mello & da Silva, 2019; de Mello et al., 2021). Calves have higher white blood cell counts (24.54×10^9/l) than juveniles and adults (16.62×10^9/l), and this is attributed to their developing immune systems while they face a broader range of novel antigenic stimuli. Higher serum calcium and alkaline phosphatase were also observed in calves (21.12 mg/dl and 158.25 mg/dl), compared to juveniles (16.08 mg/dl and 122.67 mg/dl) and adults (13.98 mg/dl and 80.67 mg/dl). This difference was expected, given the bone growth and body development of younger animals (de Mello et al., 2021). Creatine kinase (CK), which is a tissue-specific isoenzyme present in the skeletal muscle, myocardium, and brain of mammals, can be elevated during capture and transportation as a result of muscle exertion (Bossart et al., 2001). CK activity was correlated with observed stress levels in *I. geoffrensis*, and this may serve as a bioindicator of stress for the species.

Bacterial and parasitic infectious diseases have been described in living captive and wild individuals. *Streptococcus iniae* was first isolated and described in 1976 from cutaneous lesions of a captive *I. geoffrensis* at the Steinhart Aquarium in San Francisco, California, USA. At the time, the species was found to be resistant to eight of the 24 antibiotics tested (Pier & Madin, 1976). Two years later, a second strain of *Streptococcus iniae* was isolated and characterized at the Niagara Falls Aquarium in New York state, USA (Pier et al., 1978). These are known to cause the “golf ball disease” in *Inia*, which is a potentially severe dermatologic syndrome, characterized by the occurrence of slow-growing, nodular, subcutaneous abscesses (Bonar & Wagner, 2003). A serological survey of toxoplasmosis, a zoonotic disease, revealed that 86.3% of botos sampled in the Mamirauá Reserve had antibodies against *T. gondii*, suggesting high-level contamination of the aquatic environment in this area (Santos et al., 2011).

Threats, uses and conservation

The International Union for Conservation of Nature (IUCN) has changed the classification of the boto three times, evidencing how relevant information, as well as threats, have increased in the last 25 years. The boto was first listed as vulnerable (VU) in the IUCN Red List in 1996. It was downgraded to data deficient (DD) in 2008 because the information available was considered insufficient for an assessment. In 2018, as a result of new information on ecology, population trends, and threats, it was listed as endangered (EN) (da Silva et al., 2018c). Threats to boto populations come from many sources. Herein, we highlight biological resource use (*e.g.*, intentional hunting for bait, entanglement in fishing nets) and modification of natural systems (*e.g.*, dam construction) as the most important threats to the species (da Silva et al., 2018c; CMP, 2020; Brum et al., 2021; Campbell et al., 2022).

Biological resource use, primarily related to fisheries-boto interactions, is the most urgent threat. Fishing in the Amazon is an important social, cultural, and economic activity, providing food and income for human populations. The popular nylon gillnets, introduced in the 1960s, considerably increased conflicts between humans and botos. Botos are vulnerable to entanglement in a wide variety of nets, but reports identify frequent entanglement in fixed and drift gillnets, as well as seine nets (Brum, 2011; Iriarte & Marmontel, 2013b; Campbell et al., 2020). Boto mortality related to this threat is not quantified, but it is likely significant for some populations. Analysis of fish landing data from the middle Solimões River estimated that 176 botos were killed by entanglement in one year (Brum, 2011).

Fishers may perceive dolphins as competitors due to the high frequency of negative interactions (Trujillo et al., 2010; Brum, 2011; Alves et al., 2012; Guizada & Aliaga-Rossel, 2016; Campbell et al., 2020; Brum et al., 2021). Botos may disrupt fishing operations and cause financial losses by frightening fish, taking and damaging fish from nets, and becoming entangled. As a result, some fishers kill botos intentionally, even though they will not use the carcass for bait (da Silva & Best, 1996; Loch et al., 2009; Alves et al., 2012; Mintzer et al., 2015; Brum & da Silva, 2021). Botos are featured in legends and mysticism, and riverine people may fear the species as a result of these stories (Dutra & Santos, 2014; da Silva et al., 2017).

Conflicts between *I. araguaiaensis* and sport fishers have been reported. Fishers reported that these dolphins chase the target fish and also steal bait. Informal conversations with sport fishers and professionals in the Araguaia River in the city of Luiz Alves, Goiás State in 2018 were unanimous in stating that this conflict has been increasing (S. Brum, unpub. data). These fishers also correlated an observed reduction of the target fishes with their perception of an increase in *I. araguaiaensis* abundance in the area. Trapped *I. araguaiaensis* rescued from shallow lakes produced by water pumping showed scars and wounds from gunfire shots. As *I. araguaiaensis* is a newly described species with a small population (Araújo & da Silva, 2014), this increasing conflict could considerably affect the species.

Unlike other aquatic mammals in the Amazon, including manatees (*Trichechus inunguis*) and giant otters (*Pteronura brasiliensis*), the boto was not traditionally hunted or commercially exploited. For many years, the main source of anthropogenic mortality was incidental entanglement. However, in the last 20 years, this changed dramatically, and boto hunting for use as bait in the piracatinga fishery became one of the major threats to the species (da Silva et al., 2018c).

The piracatinga (*Calophysus macropterus*) is a medium-sized scavenger catfish that is abundant in whitewater rivers and has low commercial value. This catfish was not fished in the Brazilian Amazon until around the year 2000 when it replaced an overexploited species of siluriform food fish commonly consumed in Colombia (da Silva et al., 2011; Brum et al., 2015; Pimenta et al., 2018). Since then, the use of botos for bait in the piracatinga fishery has caused concern among researchers and managers due to its adverse effects on boto and caiman populations (Mintzer et al., 2013, 2020; Iriarte & Marmontel, 2013a, b; da Silva et al., 2018a, c).

Estimates of boto mortality for bait in the documented piracatinga fishery in Brazil range from 300 to 4,000 animals per year (da Silva et al., 2011; Brum et al., 2021). Despite the uncertainty in these numbers, a reduction in survival and a steep population decline of this species in the central Solimões River region have been related to this activity (Mintzer et al., 2013, 2020; da Silva et al., 2018a; Martin & da Silva, 2022). Currently, the commercialization of piracatinga is prohibited in Colombia and Brazil. However, there is evidence that this trade persists (da Silva et al., 2018b), and the use of botos to fish piracatinga has expanded to other regions such as Venezuela, Peru, and Bolivia, where there are no data on its impact (da Silva et al., 2018b; Mintzer et al., 2018; Campbell et al., 2020; Trujillo et al., 2020).

The construction of dams for hydroelectric power plants is probably the most impactful natural system modification affecting Amazon rivers and consequently *Inia*. Dams alter the flood pulse regime, block fish movement, and fragment animal populations (Winemiller et al., 2016; Forsberg et al., 2017; Resende et al., 2019). About 277 hydroelectric dams are planned across the Amazon Basin, and 175 dams are already in operation or under construction (Castello & Macedo, 2016).

Despite the increasing attention, more research is needed to understand the impact of hydroelectric dams on the botos, particularly given the growing demand for energy and documented adverse impacts to other species (Braulik et al., 2014; Benchimol & Peres, 2015). Hydroelectric dams fragment and isolate populations, reducing gene flow and consequently genetic diversity (Best & da Silva, 1989b; Araújo & Wang, 2015; Pavanato et al., 2016). It is a serious threat to the two lesser known boto species, *I. boliviensis* and *I. araguaiaensis,* as they are endemic to the Madeira and Tocantins-Araguaia, the basins most impacted by dams (Akama, 2017; Latrubesse et al., 2017).

The Santo Antônio and Jirau hydroelectric dams on the Madeira River, in Rondônia, Brazil now act as barriers between the species *I. geoffrensis* and *I. boliviensis* and also isolated a group of *Inia* between these two dams. Although the distribution limits and population size of both species in the region have not been identified, hybrids were found more than 300 km downriver from Jirau (Gravena et al., 2015). In addition to the isolation of *Inia* species with unresolved taxonomic issues, adverse impacts of these dams on fishing activity have already been reported, with a reduction in captured stocks (Santos et al., 2018). This reduction could affect the long-term survival of dolphins in the region, as fish is their main food, and a decrease of fish stocks tends to exacerbate conflicts between dolphins and fishers.

The *I. araguaiaensis* population(s) occurring in the Tocantins River is(are) highly fragmented, although there are no studies regarding the impacts of this fragmentation. This river currently has seven operating hydroelectric dams, another one is already licensed, and three more are being planned (Akama, 2017). Surveys of *I. araguaiaensis* in this river revealed low densities (Paschoalini et al., 2020), leading to greater concerns for this population's conservation. High concentrations of parasites in dolphins (*e.g.*, candiru catfish, *Ochmacantus* sp.) and fish, just downriver from dam reservoirs, suggest that dams may impact the health of this population (Araújo-Wang et al., 2019). A study in the Peixe Angical reservoir that used boat surveys and fixed observational points in a 263 km^2 area, recorded a total of 20 *I. araguaiaensis* sightings. The dolphins were concentrated in waters just downstream of the dam and near the dam (Araújo & Wang, 2015). Further monitoring and genetic studies in areas near dams, including reservoirs, would be beneficial.

The population of *I. geoffrensis* from the Tapajós River Basin is also threatened by the construction of several hydroelectric dams, as it has low population density and its fragmentation could impede its long-term conservation (Pavanato et al., 2016). One of the botos translocated from Balbina dam cofferdam, Uatumã River, Brazil, in 1989, was captured alive inside the reservoir in 2019 (V.M.F. da Silva, unpub. data). This suggests that there is no impediment to the survival of individuals in those hydroelectric dam reservoirs and they may even benefit from the higher productivity of some fish species due to damming (Agostinho et al., 2016). However, multidisciplinary long-term studies are needed to understand the impact of dams on the population dynamics of the botos.

Although the Araguaia River does not have hydroelectric dams, this river has been undergoing severe siltation due to soil modification and water use for agriculture and livestock, which could also present a threat to its small *I. araguaiaensis* population. In 2016, 12 Araguaian botos were rescued from ponds that lost connectivity with the main river very quickly, preventing animals from leaving the site (Emin-Lima et al., 2018). This was an unusual occurrence for a species that is adapted to the flood pulse.

*Ini*a plays an important role in the culture and legends of indigenous Amazon communities (Gravena et al., 2008; da Silva et al., 2017). In these legends, dolphins are believed to shape-shift to a male form and seduce women in riparian villages. This has led to dolphin body parts being used as love charms and amulets, specifically the gonads, eyes, and teeth (Alves & Rosa, 2008; Gravena et al., 2008; da Silva et al., 2017). These products can be readily found in most Amazon cities; however, research has shown that some products sold as boto parts are mislabeled (Gravena et al., 2008; Sholl, 2008; Siciliano et al., 2018). Molecular studies on charms found in large city markets in the Brazilian Amazon indicated that these products came from domestic animals such as pigs and sheep, or from the marine dolphin *Sotalia guianensis* (Gravena et al., 2008; dos Santos et al., 2018). This finding suggests that mortality of *Inia* for this market is not significant. There are old records of *Inia* meat consumption by indigenous people (da Silva et al., 2018b), but these reports are anecdotal, and there is no direct market for human consumption in the Amazon and Orinoco basins (Trujillo et al., 2010; Alves et al., 2012).

The boto is a popular tourist attraction in the Amazon (Alves et al., 2011; Romagnoli et al., 2011; D'Cruze et al., 2017). In villages across the Amazon-Orinoco Basin, mainly in Brazil, tourism-related activities such as swimming with, feeding, and watching dolphins have emerged. Well-managed tourism can be advantageous to local communities and can raise residents' and visitors' awareness of conservation issues as well as reduce residents' negative perception toward dolphins (Romagnoli et al., 2011; Das & Chatterjee, 2015; S. Brum et al., unpub. data). In the Amazon, effective conservation strategies have been inclusive of local communities (Schwartzman et al., 2000, 2010). In this context, nature-oriented tourism has grown as a potentially sustainable activity, combining conservation with economic benefits for communities (Stronza & Pêgas, 2008). However, research indicates that tourism could be better managed and generate better outcome for local communities if stricter rules were implemented, and if there were more ways for local communities to be involved. Tourism activities would also benefit from stronger conservation messaging (Alves et al., 2011; Romagnoli, 2011; Aliaga-Rossel et al., 2014; D'Cruze et al., 2017).

In Brazil, tourists can interact directly with botos. In Amazonas State, since 1998, wild botos have been habituated to receive fish provisions and remain close to tourists in the water. This activity has expanded and occurs in floating houses in multiple locations (Alves et al., 2011, 2012; Gravena et al., 2019; Rodrigues et al., 2019). Boto-focused tourism has attracted the attention of management agencies and tourism entrepreneurs, which led to a Resolution of the Amazonas State Environmental Council (CEMAAM Resolution No. 28 of 22 January 2018) regulating tourist interactions with *I. geoffrensis* and *I. boliviensis* in the Amazon state. This resolution was an important milestone to manage boto-based tourism, which should not be considered a threat to the species, but for which monitoring and inspection are essential (Brum et al., unpub. data). Organized dolphin-watching activities focused on botos also occur in Colombia, Ecuador, Peru and Bolivia. In Venezuela, it is an opportunistic activity (CMP, 2020; V. Utreras, pers. comm, Instituto Nacional de Biodiversidad, Ecuador, 18 March 2021).

Although botos are protected by both national and international laws and agreements, there is little joint international effort to effectively conserve the species. At the national level, the conservation status of *Inia* is being assessed and published in National Action Plans (NAPs). Although these efforts unite researchers and government agencies, use the standard international methods for defining conservation status, and define the main actions necessary for conservation, the Brazilian NAP, for example, does not identify government investments to carry out the proposed actions. Therefore, it is up to the researchers and conservationists to obtain the necessary resources, which are usually very scarce, especially for long-term monitoring. Furthermore, enforcement of existing laws is almost nonexistent due to federal resource constraints.

International cooperation is a crucial component to conserve a species inhabiting a transnational biome, such as the Amazon. The International Whaling Commission (IWC) provides a worldwide discussion forum for the conservation of cetaceans. In recent years, botos have been the focus of some discussions of the Small Cetacean Committee, mainly regarding the use of botos as bait in the piracatinga fishery. Botos are also the focus of a Conservation Management Plan (CMP, 2020) of the IWC. Within the context of the international Amazon biome, this CMP is an important instrument and identifies problems and joint actions for the conservation of the species. Due to the international scope of the IWC that creates some accountability between members, these recommendations are usually applied by the appropriate agencies of the member countries.

In Brazil, the Amazonian country that includes most of *Inia*'s range, botos have been protected since 1967 (Law No. 5197 of 3 January), when hunting of Brazilian wild fauna became prohibited. Additionally, fishing regulations such as the maximum size of fishing nets and minimum distances from lake entrances and small tributaries, if enforced, should benefit this species. Despite the legal protective framework, the population trend of the boto is declining (da Silva et al., 2018c), which reinforces that enacting laws alone is not sufficient to ensure long-term conservation of species.

In the last decade, prohibitions of piracatinga fishing have been the main public policies aimed at protecting botos in Brazil and Colombia. In Colombia, the commercialization of piracatinga is prohibited (Aunap Resolution 1710 of 23 August, 2017). In 2014, Brazil's Interministerial Normative Instruction (INI) No. 6 of 17 July prohibited the piracatinga fishery for five years to allow the recovery of populations of botos used as bait in this activity. This regulation has been the only enacted protection measure established specifically for botos in Brazil in almost 40 years. This INI was renewed for three more years, until August 2023. The prohibition has seemingly had repercussions on the fishing industry of Amazonas state, which have claimed great losses. However, Brum et al. (2015) and Pimenta et al. (2018) indicated that piracatinga fishing was an activity performed only to supplement fishers' income, and interviews with fishers' associations during the moratorium period confirmed these authors statements (V.M.F. da Silva, unpub. data). Brum et al. (2015) expressed concern about the moratorium's potential to lead to the concealment of the fishery (*i.e.*, a black market for piracatinga), especially since the fishery was already marginalized due to the use of a protected species as bait. This effectively has happened, as the few enforcement actions that have been carried out have seized piracatinga. Interviews with fishers in the middle Solimões River region in early 2019 revealed the continued illegal export of this fish to Colombia (V.M.F. da Silva, unpub. data). Recent surveys (2021 and 2022) showed that piracatinga fishing still occurs in Manacapuru and the middle Solimões River region (Brum et al., 2022). Despite these problems, the moratorium has provided brief relief from the piracatinga fishery for at least some boto populations in Brazil.

Methodologies in river dolphin research

River dolphin research has been conducted using a variety of methods, many of which have been adapted from marine to riverine environments. For example, distance sampling is one of the most common methods for estimating abundance. This approach has been used in surveys for *Inia* in Brazil, Colombia, Ecuador, Peru, and Venezuela, with modifications to improve dolphin detectability (Gomez-Salazar et al., 2012a; Paschoalini et al., 2021).

Mark-recapture studies have also been applied with varying degrees of success. A few studies have applied mark-recapture methods using photo-identification in Peru and Colombia (McGuire & Henningsen, 2007; Gómez-Salazar et al., 2014). In Brazil, the long-term study by Projeto Boto has monitored dolphins by marking individuals with freeze-branded characters (da Silva & Martin, 2000). This has yielded significant advances in understanding trends in abundance, survival, behavior, movement, reproduction, and life history (*e.g.*, Martin & da Silva, 2004b; 2018; Mintzer et al., 2013, 2016, 2020; da Silva et al., 2018a). Projeto Boto has also employed direct counts, generating data regarding habitat use and preference (*e.g.*, Martin & da Silva, 2004a; Martin et al., 2004).

To study movement patterns and site fidelity, VHF radios and satellite transmitters have been deployed in some areas (Martin & da Silva, 1998; Mosquera-Guerra et al., 2021). Martin & da Silva (1998) deployed 34 1mW-output VHF transmitters and monitored the animals by hand-tracking from a small boat and automated tracking stations atop trees and towers. Transmission lasted from 1.5 to 15.2 months, revealing strong site fidelity and spatial segregation by sex. Mosquera-Guerra et al. (2021) tracked 23 individual botos from different river basins with satellite transmitters. Days of transmission ranged from 24 to 336, and acquired data were adequate to calculate home range size and core use areas with kernel density estimation.

Drones (Fürstenau Oliveira et al., 2017; Oliveira-da-Costa et al., 2019) and passive acoustic monitoring (Campbell et al., 2017) have been used in tandem with traditional boat-based surveys to test their applicability in terms of cost- and time-effectiveness methods, with promising results. For example, in the Juruá River in Brazil the use of drones produced more accurate estimates of group sizes as it allowed researchers to recount the observed dolphins after fieldwork ended (Oliveira-Da-Costa et al., 2019). Similarly, drones were able to record calves and detect more individuals in a study conducted in the Parque Estadual do Cantão, Brazil (Fürstenau Oliveira et al., 2017). Passive acoustics monitoring (PAM) methods have the advantage of working during bad weather conditions, addressing one of the major logistical difficulties with traditional survey methods (that need calm water and low levels of glare). This has led to comparisons between visual surveys and PAM, and has provided insights into *Inia* diurnal patterns (Campbell et al., 2017).

Using stereo acoustic data loggers, Yamamoto et al. (2016) monitored the underwater behavior of botos at the Mamirauá Reserve, observing local habitat use and diel changes. These authors recorded a higher index of presence of dolphins in lakes and junctions during nighttime as well as the frequency of click trains, suggesting that botos use lakes as their primary habitat for foraging, especially at night.

Conclusion

In the last two decades, knowledge of the life history, ecology, and behavior of *Inia* spp. has increased considerably. This is thanks to the commendable efforts of researchers in all countries where these dolphins occur. Although we now have a better understanding of the species, and there are more organizations and NGOs operating in the region toward the conservation of *Inia*, the challenges imposed by the Amazonian habitat and insufficient financial support for research still hamper advances in science. The dolphins of the genus *Inia* are distributed along the rivers of six countries in South America with extensive international boundaries that do not act as physical barriers. This fact alone reinforces the need for more intense collaboration among not only the scientific community but also with the governments of these countries to guarantee the protection of these river dolphins internationally.

The threats to the species, mainly due to human activities, are still present and some are increasing, regardless of new laws and conservation actions. Therefore, efforts should be directed at conducting studies on populations to verify the impacts of direct and indirect threats affecting their abundance, and focus should be directed at quantifying the effect of fisheries on dolphin populations and their prey. Fisheries conflicts are a major threat, causing the direct killing of dolphins and affecting the whole conservation chain. Thus, involvement of local communities in conservation activities is a necessity. Other primary threats are the contamination of the rivers and lakes and the modification of the environment by development projects, as mining and hydroelectric dams. These threats reinforce the need for more societal involvement and the importance of engaging local people in conservation activities aimed at the protection of the dolphins of the genus *Inia* and their habitats.

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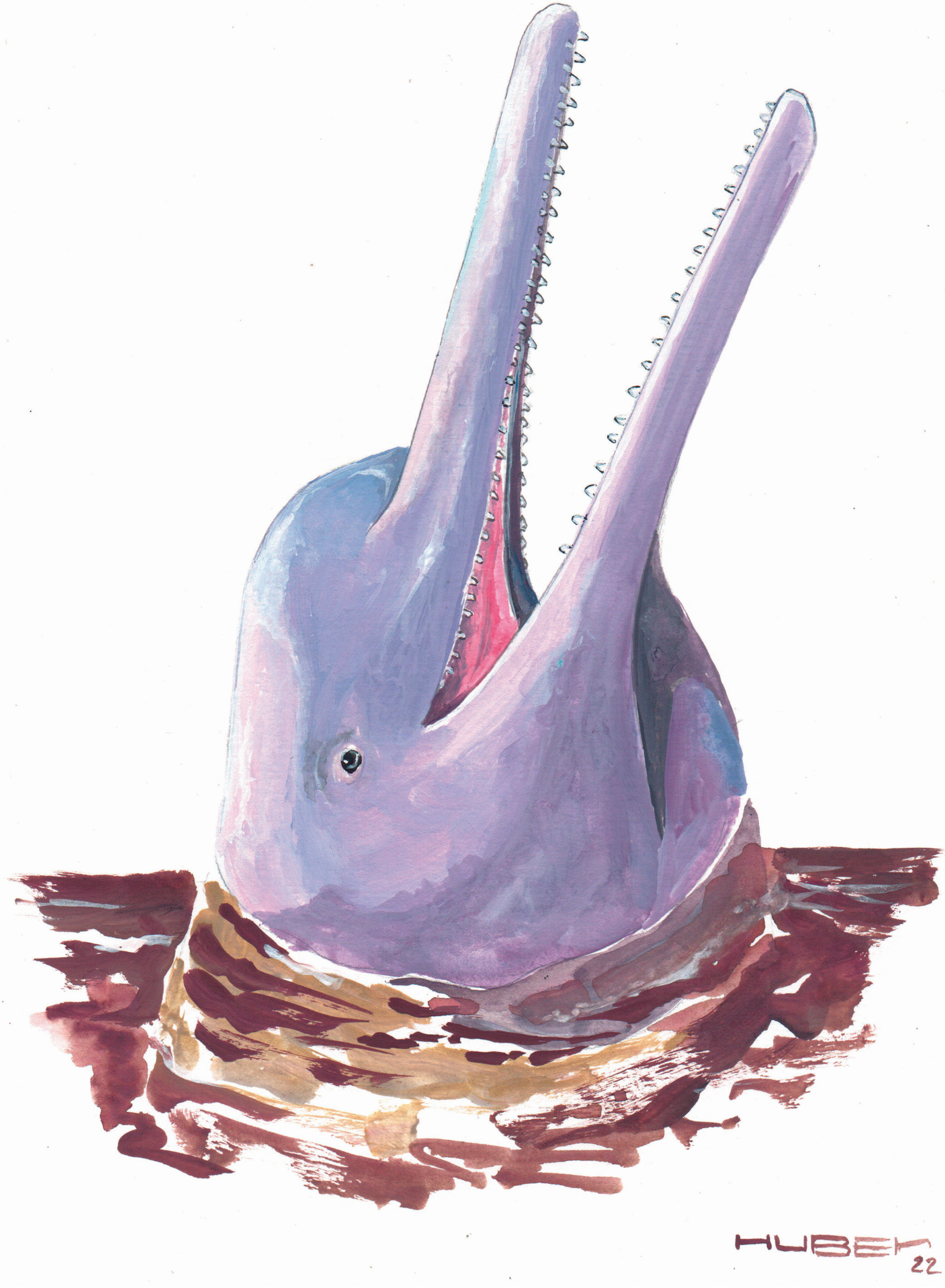
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