Bolivian River Dolphin *Inia boliviensis* (d'Orbigny, 1834)

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Common Names

English	Bolivian river dolphin, Bolivian bufeo
Spanish	Delfín de rio boliviano, Bufeo, bufeo boliviano
Portuguese	Boto boliviano
French	Dauphin de rivière bolivien
Italian	Delfini di fiume boliviani
German	Bolivianischer Flussdelfin
Dutch	Bolivian Amazonedolfijn
Guarayos (Bolivia)	Inia

Taxonomy and Systematics

Overview

The genus *Inia* belongs to the suborder Odontoceti, superfamily Platanistoidea, family Iniidae. The genus and species were described in the Bolivian Amazon in 1834 by the naturalist Alcide d'Orbigny. Since then, the genus *Inia* has been the focus of constant debate. Traditionally, the genus is considered to consist of a single species with three geographically structured subspecies, *Inia geoffrensis geoffrensis* in the Amazon (except in the Bolivian Amazon rivers), *I. g. humboldtiana* in the Orinoquia, and *I. g. boliviensis* in the Bolivian Amazon (Aliaga-Rossel, 2002). Later, the presence of two *Inia* species (*I. geoffrensis* and *I. boliviensis)* was proposed, and in 2014 a third species, *Inia araguaiensis,* was described in the Tocantins Basin of Brazil. However, the separation as different species has been controversial based on the fact that the characters used to differentiate them are highly variable and derived from small sample sizes.

Pilleri and Gihr (1977) again suggested the uniqueness of *Inia boliviensis* d'Orbigny 1834: (Fig. 1), later supported by morphological studies comparing coloration, cranial characteristics, brain size, and the number of teeth, among others (Da Silva, 1994). As a result of the increasing use of molecular techniques, a comparative study of mitochondrial DNA provided further evidence to separate *I. boliviensis* as a distinct species (Hamilton et al., 2001; Banguera-Hinestroza et al., 2002). In addition, new evidence for the separation of the genus into two distinct species was presented by Martinez-Aguero et al. (2006) using loci of the major histocompatibility complex (MHC).

The divergence of the Bolivian bufeo from the Amazonian form, also shown by Ruiz-Garcia et al. (2006), further suggests that the *Inia boliviensis* population is the result of a founder effect that occurred between 5 and 6 million years ago. Later, Ruiz-García et al. (2008) and Ruiz-Garcia (2010) reported that the diversification of *I. boliviensis* occurred more recently, between 50,000 and 500,000 years ago, using microsatellite and mitochondrial markers.



Fig. 1 Bolivian river dolphin (*Inia boliviensis*) leaping in the Tijamuchi River, Beni Bolivia. (© Enzo Aliaga-Rossel)

Gravena et al. (2014) divided *I. boliviensis* into two isolated groups, including populations upriver (in the Madeira sub-basin of Bolivia) and downriver (in Brazil). All genetic analyses have consistently shown that *Inia boliviensis* and *I. geoffrensis* are disjunct populations with sufficient differentiation to justify their specific status (Emin-Lima et al., 2022).

However, probably based on a misinterpretation of Gravena et al. (2014) and ignoring Gravena et al. (2015), who presented further genetic studies to identify *I. boliviensis* as a separate species, the Taxonomy Committee of the Society for Marine Mammals does not accept the evidence supporting the uniqueness of the species and maintains it as a subspecies (Society for Marine Mammalogy Committee on Taxonomy, 2021; Emin-Lima et al., 2022). Strong morphometric statistical research has also shown that the diversity within the genus *Inia* is incompatible with the idea of a single taxon, providing additional evidence that *Inia boliviensis* is a distinct species (Emin-Lima et al., 2022).

The Bolivian bufeo has a diploid chromosome number of 2n = 44, with FN = 74, and the karyotype formula 14 m + 12sm + 6st + 10 t + XX/XY. This formula has one more metacentric pair of chromosomes and one less submetacentric pair than *I. geoffrensis*. Furthermore, the constitutive heterochromatic patterns of the two species differ, with C-positive heterochromatin found in the pericentromeric, interstitial, and terminal regions of *I. boliviensis* (Hamada-Fearnside et al., 2017).

Inia boliviensis d'Orbigny, 1834 is officially recognized and known in Bolivia only by the name "bufeo", and is usually referred to in English as "the Bolivian river dolphin" (Aguirre et al., 2019). The name "Bolivian boto" has also been proposed only in Brazil. The International Whaling Commission (IWC) has given the Brazilian label "boto," which is unknown in Bolivia, Colombia, Ecuador, Peru, and Venezuela (Aliaga-Rossel, 2010; Aliaga-Rossel & Guizada, 2020a). Therefore, *Inia boliviensis* will be referred to as Bolivian bufeo throughout this chapter.

Fossil Records

Both Inidae and Pontoporidae are represented by South American fossil relatives. Most of the previously described "iniids" have been found in other extinct groups (Muizon, 1988; Cozzuol, 2010),

suggesting that the family can be considered endemic to the freshwater habitats of South America. The only fossil remains outside of South America that could plausibly be classified as Iniidae are partial skull fragments of *Goniodelphis* from the Early Pliocene Palmetto Fauna of central Florida (Morgan, 1994).

Ischyrorhynchus and *Saurocetes*, two fossil genera that unambiguously belong to the Iniidae, discovered well south of the current distribution of *Inia*, specifically in the Late Miocene Ituzaingó River deposit of the Paraná Basin in Argentina. However, in 1943, Miranda-Ribeiro described a tooth of *Plicodontina mourai* from the Juruá River in Brazil and suggested that this animal was a close ancestor of *I. geoffrensis.* Godfrey et al. (2021) described a new odontocete belonging to the family Inioidea, named *Isoninia borealis*, which exhibits a combination of characteristics that warrant the creation of a new genus and species within the Odontoceti. This new find, along with other inioid genera, supports the hypothesis that extant inioids have a relict distribution, indicating their ancient origin.

Current Distribution

Global

About 15 million years ago, *Inia* may have migrated from the Pacific Ocean into the Amazon basin (Grabbert, 1983). *Inia*'s ancestors remained in the vast inland sea. During the middle to late Miocene (12 million years ago), the inland sea was drained, separating the northern and southern river basins as a result of the uplift of the Andean Cordillera Oriental de Los Andes and a global decrease in sea levels (Hamilton et al., 2001). These events isolated the Bolivian population from the Amazon River dolphin populations (*I. geoffrensis* and *S. fluviatilis*). This isolation continued, facilitated by a series of rapids and cascades on the river between Guayaramerin in northern Bolivia and Porto Velho, Brazil (Hamilton et al., 2001).

The distribution of *Inia boliviensis* is mostly limited to the north and northeast of Bolivia, in the tropical rivers of the Amazon basin, due to the aforementioned barriers, cascades, and rapids. Limited to three main sub-basins: Mamoré, Iténez, and Abuna in the departments of Beni, Santa Cruz, Cochabamba, and Pando (Fig. 2) (Aliaga-Rossel, 2003, 2010; Aliaga-Rossel & Guizada, 2020a). In particular, some of these rivers run along the border between Bolivia and Brazil (Itenez-Guapore rivers) and to the north in the Abuná River (Aliaga-Rossel, 2003). Additionally, rapids and cascades along the rivers in Bolivia towards Brazil can drag the Bolivian bufeo downstream, creating a relatively isolated population; however, they are unable to return due to the cascades and therefore their genetic structure is different (Gravena et al., 2015).

Bolivian bufeos are found in Bolivian rivers that contain mainly two types of water: *whitewater*, which is a turbid river of Andean origin, rich in nutrients, with a neutral pH and suspended solids. The species is also found in *clear waters* with low levels of nutrients and dissolved or suspended solids. The clear waters typically flow from the dense rainforest, but it is also possible to find transparent waters stained dark by tannic acids from decaying vegetation (Aliaga-Rossel, 2002; Aliaga-Rossel & Guizada, 2020b). Some river areas are mixed during the rainy season. They are also found in several lagoons formed by the meanders of ancient rivers; these lagoons are unique for their physicochemical characteristics and their geomorphology.

Populations

Genetics

Despite existing research and published information, there is much confusion about the population structure of the Bolivian bufeo. In addition, its taxonomy as a separate species is still under debate. The first genetic study of *I. boliviensis* using mitochondrial markers showed the three lineages of the genus *Inia* (Hamilton et al., 2001); this was supported by a similar study that indicated two evolutionary significant units (ESUs) (Banguera-Hinestroza et al., 2002).

Using a separate marker, the major histocompatibility complex (MHC), Martínez-Aguero et al. in 2006 hypothesized the presence of two distinct species. Other studies with different intron sequences have been used, including Y chromosome regions by Ruiz-García et al. (2008), and in 2015, Gravena et al. studied individuals from the Madeira and the Upper Madeira Basin using various mitochondrial regions (control region, cytochrome b, and cytochrome oxidase I). All these studies concluded that the genus *Inia* has different species along its distribution; the Amazon River dolphin *Inia geoffrensis* is divided into two subspecies, *I. g. geoffrensis* and *I. g. humboldtiana*, and the Bolivian river dolphin, *I. boliviensis.* It is worth noting that Hrbek et al. (2014) described a new species from Brazil named *Inia araguaiaensis.*

Low heterozygosity and genetic diversity in Bolivian river dolphin populations is a factor of vulnerability for the species, recognized by both the International Union for Conservation of Nature (IUCN) and Bolivia's Red Book of Vertebrates (Ruiz-García et al., 2008; Gravena et al., 2015).

The study by Gravena et al. (2015) highlights that gene flow is unidirectional from the upstream group (upper part in Bolivia) to the downstream group in Brazil (Fig. 2), and the divergence time between the two groups was estimated to have occurred ~122,000 years ago. The study also revealed the existence of an *I. geoffrensis/I. boliviensis/I. geoffrensis* hybrid, highlighting the fact that the construction of hydroelectric dams will stop the spread of the species' genes from the original populations, thereby reducing genetic

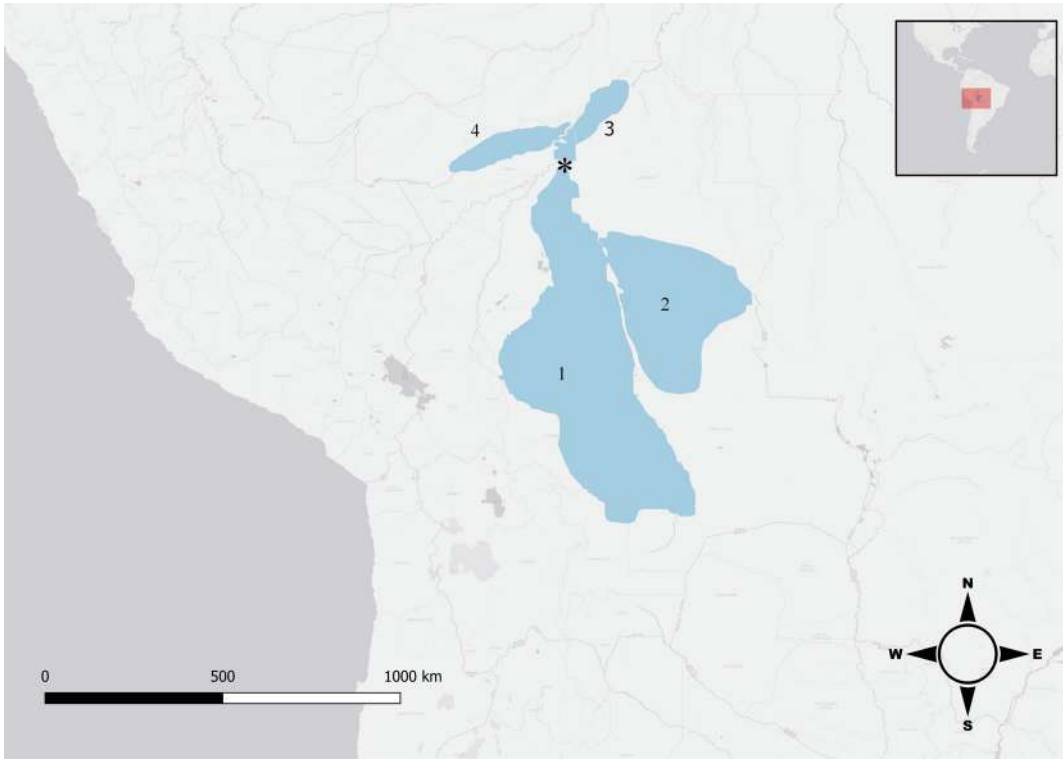


Fig. 2 Main distribution of the Bolivian bufeo (*Inia boliviensis*). Located in tributaries, rivers, and lagoons of each of the Upper Madeira sub-basin; 1 = Mamore Sub-Basin, 2 = Itenez or Guapore Sub-Basin, 3 = Madeira River up to Porto Velho town, 4 = Abuna Sub-Basin. Asterisk = Cachuela Esperanza area; this is one of the barriers preventing the occurrence in the Beni or Madre de Dios rivers

diversity. Cetacean hybridization is not uncommon, and the development and increase in genetic studies in recent years have confirmed this (Pampoulie et al., 2020).

Abundance

Numerous research on abundance have been published, mostly in the Mamore sub-basin and with fewer studies in the Itenez sub-basin (Aliaga-Rossel, 2002; Aliaga-Rossel et al., 2006; Aliaga-Rossel & Quevedo, 2011; Aliaga-Rossel et al., 2012; Gomez-Salazar et al., 2012; Aliaga-Rossel & Guizada, 2017; Trujillo-Gonzáles et al., 2019; Guizada & Aliaga-Rossel, 2016; Paschoalini et al., 2021). The relative abundance reported ranges from the Madera River's lowest estimate of 0.02 bufeos/km to the Tijamuchi River's highest estimate of 9.50 bufeos/km (Aliaga-Rossel & Guizada, 2020a). Reasons for these differences have been addressed by Aliaga-Rossel and Guizada (2020a), depending on the field effort (kilometers surveyed) and the season of the year (Table 1). Based on all published estimations, the mean relative abundance is 0.92 ± 0.75 bufeos/km (mean ± SD). There are still gaps in the data on population size, which should be assessed in understudied areas, such as rivers in the Pando department.

Table 1 Abundance of the Bolivian river dolphin *Inia boliviensis* in Bolivian rivers (min: minimum; max: maximum). Sa 10 = Salinas et al. (2010); AR 06 = Aliaga-Rossel et al. (2006); AR 12 = Aliaga-Rossel et al. (2012); Mo 12 = Morales (2012); Pa 94 = Painter (1994); ARG 17 = Aliaga-Rossel and Guizada (2017); Pi 69 = Pilleri (1969), PG 77 = Pilleri and Gihr (1977); ARQ 11 = Aliaga-Rossel and Quevedo (2011); T 10 = Trujillo et al. (2010); GS 12 = Gomez-Salazar et al. (2012); MAR 07 = McGuire and Aliaga-Rossel (2007); GAR 16 = Guizada and Aliaga-Rossel (2016); Sa 07 = Salinas (2007); AR 02 = Aliaga-Rossel (2002); UP = unpublished Data Aliaga-Rossel. (Table modified from Aliaga-Rossel & Guizada, 2020a)

River	Variable	# Surveys	Min	Max	Reference
Abuna	Abundance	1	0.12	0.12	Sa 10
Apere	Abundance	2	1.27	2.81*	AR 06, AR 12, Mo 12
Bajo Mamore	Abundance	1	0.35	0.35	Sa 06
Blanco	Abundance	3	0.16	1.62	Pa 94
Blanco-baures	Abundance	1	0.13	0.13	ARG 17
Ibare	Abundance	9	0.39	7.2	Pi 69, ARQ 11, AR 12
Ichilo	Abundance	1	0.25	0.25	PG 77
Ichilo-Mamore	Abundance	2	1.22	1.29	T 10, MO 12
Ipurupuru	Abundance	1	1.17	1.17	PG 77
Itenez	Abundance	3	0.47	1.55	GS 12
Itonamas	Abundance	2	0.26	0.66	ARG 17
Machupo	Abundance	2	0.1	2.7	ARG 17
Madeira	Abundance	1	0.02	0.02	SA 10
Mamore	Abundance	8	0.46	3.74	AR 06, MAR 07, GS 12, GAR 16
Negro	Abundance	4	0.00	0.6	UP
Negro de Caimanes	Abundance	1	0.22	0.22	Pa 94
Niquisi	Abundance	1	2.54	2.54	AR 12
Rapulo	Abundance	1	2.64	2.64	AR 06
San Martin	Abundance	1	0.77	0.77	Sa 07
Secure	Abundance	1	0.67	0.67	UP
Tijamuchi	Abundance	6	0.77	9.55*	AR 02, AR 06, ARQ 11, AR 12
Yacuma	Abundance	2	1.85	2.35*	AR 06
Yata	Abundance	2	0.16	0.6	Sa 10

Table 2 Morphometrics of the Bolivian river dolphin (*Inia boliviensis).* Authors: PG 77 = Pilleri and Gihr (1977); BDS 93 = Best and Da Silva (1993); DS 94 = Da Silva (1994); RG 06 = Ruíz-García et al. (2006); ARM 10 = Aliaga-Rossel and McGuire (2010); ARE 20 = Aliaga-Rossel and Escobar (2020); AR 02 = Aliaga-Rossel (2002)

Measure	Mean	SD	Range	Author
Total length (mm)	2160			PG 77
	2071.6		2000–2150	BDS 93, DS 94
	1800		1600–1980	BDS 93
	2022	148.2		RG 06
	1937.7	91.5		RG 06
	2071.6		2000–2150	ARM 10
	1965.6	399,6	1100–2400	ARE 20
Muzzle length (mm)	330		310–350	ARM 10
	257.29	103.5	80–400	ARE 20
Length from jaw tip to melon (mm)	248.2	27.1		RG 06
	209.7	43		RG 06
Length from jaw tip to mouth base (LTJMO) (mm)	330.9	37.5		RG 06
	290	44.7		RG 06
Length from jaw tip to spiracle (LTJS) (mm)	389.1	35.6		RG 06
	351.3	54.7		RG 06
Length from jaw tip to genital aperture (LTJGA) (mm)	890	92		RG 06
Width of the pectoral fin (WPF) (mm)	180.9	20.2		RG 06
	166.1	18.3		RG 06
	179.38	58.38	10–23	ARE 20
Length of dorsal fin (LDF) (mm)	66.4	9.7		RG 06
	58.5	8.8		RG 06
Width of fluke (WF) (mm)	153.6	25		RG 06
	145.3	13.9		RG 06
	420.9	181.69	21.5–55	ARE 20
Flukes tip to tip (FIT) (mm)	446.4	33.8		RG 06
	408.8	44.8		RG 06
Weight (kg)	49.5			AR 02
	75.4			AR 02

Description

Morphology and Coloration

River dolphins of the genus *Inia* are the largest freshwater dolphins in the world. Their bodies are robust and corpulent (Fig. 1), but these animals are fast swimmers and very flexible, capable of twisting laterally, performing quick U-turns and touching their caudal fin with their snout (Aliaga-Rossel, 2002; Trujillo et al., 2011).

There is a clear sexual dimorphism, with males larger than females according to da Silva (1994), while Ruiz-Garcia et al. (2006) show the opposite (females larger than males), although the difference does not seem to be significant (Table 2). The largest recorded total body length was a female of the species, 240 cm, registered in 1834 by d'Orbigny in the Guaporé River and in 2010 in the Rio Grande sub-basin of the Mamore River (Pilleri & Gihr, 1977; Aliaga-Rossel & Escobar-WW, 2020) (details in Table 2).

Adult Bolivian bufeos tend to be predominantly whitish, pink, or gray with patterns of darker shades of pink, showing, at most, a pink flush on the underside (Aliaga-Rossel, 2002). When they are involved in intense physical activity, such as diving or mating, they increase the

intensity of the pink coloration due to the capillary vessels being closer to the skin (Best & Da Silva, 1989; Aliaga-Rossel, 2000).

Adults often have visible scars on the body (and several notches, especially on the fins). Calves are uniformly dark gray, with short beaks with visible vibrissae on the lower jaw; with age, calves change coloration to light gray as they grow into juveniles, and finally to the white-pink tones (Aliaga-Rossel, 2002).

Skull Characteristics and Dentition

The skull of *Inia boliviensis* is robust, slightly asymmetrical, long-snouted, and narrow (Fig. 3) compared to marine cetaceans (Pilleri & Gihr, 1977). The orbit is incomplete with a semicircular shape and incomplete zygomatic arches. The lateral projections of the zygomatic arch give the cranium a trapezoidal shape. The squamosa covers only half of the parietal, and the tympanic bulla is wide and shows no flattening (Pilleri & Gihr, 1977). The supra-occipital region, which is located above the foramen magnum, has two small foramina.

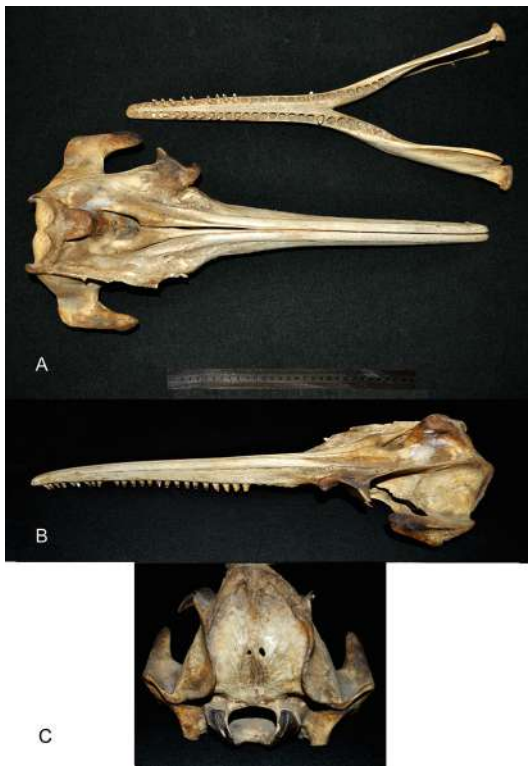


Fig. 3 Skull of Bolivian bufeo (*Inia boliviensis*): (**a**) mandible (lower jaw) and skull in dorsal view; (**b**) lateral view; (**c**) occipital view of the skull showing the foramen magnum. (© Enzo Aliaga-Rossel)

The mandibles are fused for about one-third of their total length (Miranda-Ribeiro, 1943; Emin-Lima et al., 2022). The premaxilla is extremely thickened and soon diminishes into a thin lamella (Pilleri & Gihr, 1977).

The Bolivian bufeo has heterodont teeth (which is unusual for a cetacean), with conical teeth in the front while the posterior teeth are slightly broader and flatter (i.e., molar-like). All the teeth have a rough surface with a wrinkled enamel layer. The number of teeth per ramus varies from 31 to 34 on the left side and 31 to 35 on the right side. The average is 33 teeth on each side, presenting a higher number of teeth in their jaws than *I. geoffrensis* (Pilleri & Gihr, 1977; Emin-Lima et al., 2022).

Anatomy

The head of the Bolivian bufeo is very distinctive, featuring a long, and pointed snout and a narrow V-shaped jaw (Fig. 4). The body is rounded dorsally when viewed from above, with a single smooth longitudinal dorsal ridge or crest that does not terminate in a triangular protuberance that serves as one blowhole.

Given that *Inia*'s ecosystems are typically murky and sediment-filled, evolutionary processes have favored the presence of the melon, a soft and protuberant structure found in the forehead. Its shape can be easily altered by muscle control and is used to position itself in space, locate prey, and communicate more effectively between individuals (Trujillo et al., 2011).

Despite having small but functional eyes, bufeos are not blind like Asian river dolphins. However, their functionality is useless when swimming in the murky, dark waters of tropical rivers. Because of the placement of both eyes on the side of the head, their vision is two-fielded



Fig. 4 Detail of the bufeo rostrum, characteristic long and pointed snout, small but functional eyes, prominent forehead, or melon. (© Enzo Aliaga-Rossel)

rather than binocular like that of humans and primates (Pilleri, 1969; Best & da Silva, 1989).

Behind the head the body is thicker, without resemblance to a neck. Their vertebral formula is C7, Th13, L3, Ca16 (+1) = 39 (+1) vertebrae. Nine chevron bones are present, of which the fourth and fifth on the right side are fused together. Another unique feature is that the seven cervical vertebrae are independent (not fused) (Pilleri & Gihr, 1977), allowing flexibility for the head to turn quickly and redirect its swimming.

Inia boliviensis always has 13 pairs of strong ribs united to the sternum, which is a long and broad forming a single robust plate. Flippers are located almost ventral, and both the dorsal fin and flippers are almost twice as long as the caudal fin. Flippers are robust, highly articulated, paddle-like, thick, long, and pointed (Pilleri & Gihr, 1977). The dorsal fin is triangular keel-shaped but not elevated.

Inia's stomach is divided into three chambers: the fore, main, and pyloric stomachs. The pyloric

stomach and the main stomach are connected by a small canal (Aliaga-Rossel, 2000). The genital entrance is situated very close to the anal opening in females, who have bicornuate uteruses. Both sexes have nipples near the anal slit (da Silva, 1994).

Life History

It is possible that Bolivian bufeos will mature at about the same time as other river dolphin species, such as *I. geoffrensis*, which sexually mature between 5 and 7 years of age. Female bufeos have a 2-year reproductive cycle, which includes 10–11 months of gestation, 6–12 months of nursing, and possibly 1 month of rest or recovery (McGuire & Aliaga-Rossel, 2007).

The duration of lactation is about 11 months, and it has been observed that a 1-year-old calf has no teeth. There is no information on when calves are weaned, although a mother and calf have been seen with a young juvenile, which was probably also her offspring (Aliaga-Rossel & Escobar-WW, 2020).

The breeding season is year-round, but the majority of births coincide with the dry season (June to October) when Bolivian bufeo give birth to a single calf (McGuire & Aliaga-Rossel, 2007). Twins have been mentioned anecdotally but this occurrence is uncommon and unrecorded, and the calf may actually be an older sibling.

There are no records of natural age mortality for Bolivian bufeos. The maximum life span is probably 30–35 years. The maximum recorded age in captivity for *I. geoffrensis* was 45 years and 9 months; an individual named Baby at the Duisburg Zoo in Germany was captured at a young age and raised there until it had to be put down due to an illness (World Animals Voice, 2020).

Ecology

Habitat Use

The habitat preferences of *Inia boliviensis* appear to be influenced more by the presence of their prey and specific habitat conditions than by physical factors such as pH, conductivity, temperature, transparency, or solid dissolution (Aliaga-Rossel, 2002; Guizada & Aliaga-Rossel, 2016; Aliaga-Rossel & Guizada, 2020b).

A long-term study found that Bolivian bufeos preferred both meandering and confluence habitats (Aliaga-Rossel & Guizada, 2020b). These sites are sections characterized by a slow river flow (Martin & da Silva, 2004). These locations are also favored by fish, and dolphins do not consume much energy in these habitats (Martin & da Silva, 2004). Confluences have also been considered areas of easy prey capture by river dolphins (McGuire & Winemiller, 1998; Aliaga-Rossel, 2002), which harbor high densities of fish due to the deep water and refuge they provide (Mosquera-Guerra et al., 2015; Trujillo-Gonzales et al., 2019; Aliaga-Rossel & Guizada, 2020b). Bufeos are large animals, and since meanders and confluences are places where the river expands, these ecosystems can support more individuals than the main river channel, particularly during the mating season, which occurs mainly during the dry season. Meanders and curves also have greater depths, which are preferred by river dolphins (Aliaga-Rossel et al., 2006; Aliaga-Rossel & Guizada, 2020b).

In general, potential foraging areas for Bolivian bufeos tend to be concentrated at the mouths of tributaries and lagoons during the dry season (Aliaga-Rossel, 2002; Aliaga-Rossel et al., 2006; Aliaga-Rossel & Guizada, 2020b). Although bufeos are thought to occupy the same area for more than 1 year, their seasonal movements are variable (McGuire & Hesningen, 2007). Through photo-identification, a maximum home range of 60 km was estimated in the Tijamuchi River (Aliaga-Rossel, 2000).

The bufeo is most vulnerable during the low-water season when habitat is limited and has to compete with increased activity of fishing boats and nets throughout its range (detailed below).

Diet and Feeding

The Bolivian bufeo can be categorized as a generalist predator (Fig. 5), feeding on prey of various sizes, including river crabs, eels, large fish, etc.



Fig. 5 Adult Bolivian river dolphins (*Inia boliviensis*) hunting a fish of the family Loricariidae, in the Tijamuchi River, Beni, Bolivia. (© Candice Arias)

(Pilleri, 1969). The stomach contents of one juvenile showed high prey diversity, with fish from the families Doradidae, Heptapteridae, Auchenipteridae, and Characidae (subfamily Tetragonopterinae), which are not commercial fish (Aliaga-Rossel et al., 2010).

Using stable isotope analysis to compare the relative prey consumption and isotopic niche breadth of the bufeo in the San Martín River in the Itenez basin (six individuals, five males, one female), Echeverria et al. (2022) found that fish were the main consumed group (0.67 ± 0.09 of contribution to the diet). Compared to other populations in Brazil, this isotopic niche breadth is smaller.

Behavior

Migrations and Movements

Bolivian bufeos can exhibit some degree of site fidelity (Aliaga-Rossel & Guizada, 2020b). They have been regularly observed year-round in some preferred areas (Tijamuchi River Mamore Sub Basin). Aliaga-Rossel (2000), by using photo-id, indicated a linear range of 60 km. A recent satellite telemetry study reported a home range of 233.9 km^2, with a core area use of 3.7–54.9 km^2 and an average daily movement of 1.6 + −0.79 km (0.4–3.9 km range) for the San Martin River, Itenez sub-basin (Mosquera-Guerra et al., 2021).

Swim and Dive Behavior

Bolivian bufeos are also excellent swimmers. Their sleek body shape and powerful muscles enable them to swim rapidly and efficiently, even swimming upstream against the current, propelled by their powerful caudal tail (Pilleri, 1969). As noted above, they have a highly flexible body that performs rapid U-turns and touches the caudal fin with the snout (Trujillo et al., 2011). When the Bolivian bufeo surfaces to breathe, it is practically horizontal. Only the melon and the blowhole are typically seen emerging from the water above the surface. Eyes and the beak are rarely seen (Pilleri & Gihr, 1977).

The onset of deep diving behavior in Bolivian bufeos is easy to notice; when they start deep diving, they bend the lower half of their body before diving. It is noteworthy, however, that the tails rarely protrude above the water surface. The head and throat fall, the dorsal fin rises above the water. At the end of the dive warning, the animal disappears completely and the parts of the body still above the water are triangular in shape (Pilleri & Gihr, 1977). They are rarely seen leaping.

The average dive duration for Bolivian bufeos is 2–5 min (Aliaga-Rossel pers obs), but they can hold their breath for up to 15 min. In general, they dive to find food, and while diving, they use echolocation to navigate and find food, although if a bufeo feels threatened, it will dive to the bottom of the river and hide longer as described by Aliaga-Rossel and Escobar-WW (2020).

Foraging Behavior

Bolivian bufeos have developed diverse foraging strategies to obtain food in their complex and changing riverine habitats. These strategies allow them to efficiently utilize available resources and ensure their survival. Potential foraging areas of the Bolivian bufeo tend to be concentrated at the mouths of tributaries and lagoons, especially during the dry season (Aliaga-Rossel, 2002).

They use echolocation as a fundamental foraging tool to generate an acoustic map of their environment (Trujillo et al., 2011). This allows them to detect the exact location of prey and determine their size, shape, and distance even in muddy water. Bolivian bufeos may venture into shallow waters, such as sandbanks or near-shore areas, or swim in the flooded forest taking advantage of the opportunity to catch fish and other prey there. This strategy enables them to access prey that would otherwise be out of their reach. They also use ambush techniques or swim rapidly to catch their prey. Once they detect their prey, dolphins swiftly lunge forward to capture it. They are able to take advantage of feeding opportunities, which may include capturing injured or weakened fish.

Social Behavior

Little is known about the social behavior of Bolivian bufeos; they are not acrobatic and breaching out of the water is rarely seen. They are usually observed as solitary individuals and the majority of observations were made in pairs, usually consisting of mother and calf (Aliaga-Rossel, 2002, 2010; Aliaga-Rossel & Guizada, 2020a). Cohesive groups of more than five individuals are infrequently observed. Published studies refer to bufeo groups but do not imply anything related to social cohesion (Fig. 6). Although there have been sporadic gatherings at feeding sites or during courtship and mating, 20–30 bufeos have been observed in the Pojije, Apere, San Martin, and Tijamuchi rivers in Bolivia. On the other hand, their ability to communicate acoustically over long distances allows bufeos to interact even when they are apparently swimming alone (Zurita Roca, 2019).

Bufeos react protectively to injured or captured individuals (Pilleri, 1969; Aliaga-Rossel & Escobar-WW, 2020). The authors observed protective behavior when a mother repeatedly attempted to bring her dead calf to the surface and then submerge it. Similarly, during a translocation, the mother bufeo stayed close to a captured calf with no visible agonistic or fear response to humans (Aliaga-Rossel & Escobar-WW, 2020).



Fig. 6 Several Bolivian river dolphins (*Inia boliviensis*) gathered in shallow water; aerial view captured by a drone. (c) PICB

Bufeos are playful, including curiosity behavior toward humans; occasionally picking up dropped objects, or interacting or "playing" with other animals (Aliaga-Rossel pers obs). Recently, two bufeos were observed playing with an anaconda (*Eunectes beniensis*) on the Tijamuchi River (Entiauspe-Neto et al., 2022). It has been noticed that some tour companies offering to swim with dolphins are taking advantage of their curiosity and yearning for physical contact. Bufeos may nip divers, play tag, seize the diver's hand under its flipper and pull him along, or even surround him while swimming (Layne & Caldwell, 1964). Although a recent report of river dolphins having negative interactions with humans (biting them) was reported and observed (authors pers. obs). Anecdotes of fishermen's paddles being dragged or bufeos bumping against canoes are common. Locals also report that bufeos can become quite tame (Aliaga-Rossel, 2010).

Reproductive Behavior

The genus *Inia* was previously thought to be monogamous (Best & da Silva, 1989), but small testicles of the males, the dominance of solitary individuals, sexual dimorphism, and reports of

interspecific aggression suggest that polygyny is practiced (da Silva, 1994; Trujillo et al., 1998). Bufeos appear to have a promiscuous and violent mating system, with several mating activities observed, especially during falling water and dry water seasons (McGuire & Aliaga-Rossel, 2007). The main characteristics of the mating activity were vigorous and frantic swimming, chasing, and splashing, although it is impossible to tell how much of the action was simply social interaction behavior and how much was reproductive in nature. This activity could involve several bufeos or just a few individuals.

A male juvenile Bolivian bufeo was found dead in the Mamore River, presumably as a result of intraspecific sexual aggression. The corpse was found after a night-long activity by several bufeos in the area, with lots of playing, splashing, and other violent behaviors. The necropsy revealed several bite marks on the fins, cuts, lesions in the blowhole, and internal hemorrhages (Aliaga-Rossel, 2000).

Acoustic Behavior

Zurita Roca (2019) analyzed 2121 sounds and classified them into tonal sounds or whistles and pulsed sounds or clicks. The study showed that the whistles have a duration of 0.082 s with a frequency range oscillating from 2.29 to 3.65 kHz. The pulsed sounds have a duration of 1.13 s and a minimum frequency range of 21.99 kHz; the maximum frequency could not be recorded due to the limitations of the hydrophone, but it is greater than 50 kHz. Bolivian bufeos show differences in vocal structure. For example, in areas with more boat traffic, they are quieter, have shorter sounds and higher frequency values. In addition, the surface behavior during the passage of the boats showed some kind of response (escape swimming, movement to another area, increase in the frequency of departure, etc.); however, the vocal repertoire has been poorly described to date.

Parasites and Diseases

Ectoparasites

The ectoparasites of this species have been insufficiently studied. Additionally, the bufeo has no known commensal or mutualistic species. Natural parasites include mainly macroparasites and microparasites such as bacteria and viruses (Bonar et al., 2007). In Bolivia, there are anecdotal observations of fish from the family Cetopsidae, *Cetopsis coecutiens*, attached to bufeos which the locals call piojo del bufeo ("bufeos flea"). Araujo-Wang et al. (2019) have described the presence of an "ectoparasite" of the genus *Ochmacanthus* (candiru) for *Inia boliviensis*. The interaction between the two species appears to have several disadvantages for the bufeo, including (1) reduced preference for infected individuals by potential mates; (2) reduced time to feed, reproduce, and rear offspring (e.g., including individuals that are fit to reproduce); and (3) loss of skin when candirus bite and eat the skin of the bufeo, causing uncomfortable wounds and subsequent infections.

Endoparasites

Information on endoparasites of *I. boliviensis* is lacking. Most of the information on endoparasites comes from *I. geoffrensis*, which had a significant number of nematodes in its stomach (Best & da Silva, 1993), although there is no evidence that these infections were harmful. Lung parasites seem to be common, such as the campulid trematode *Hunterotrema caballeroi* (Bonar et al., 2007).

Infectious Diseases

The occurrence of infectious diseases in the genus *Inia* is mainly limited to reports of captive individuals of *I. geoffrensis*. Reports include

pneumonia and skin lesions (ulcerations and cutaneous and subcutaneous abscesses), cachexia, renal pathology, hepatic pathology, bacterial sepsis (Woodard et al., 1969; Bonar et al., 2007), and bacterial and parasitic pneumonia caused by *Halocercus brasiliensis* in free-ranging Amazonian river dolphins (Rodrigues et al., 2018). A proliferative skin lesion on a Bolivian river dolphin from the Guaporé River, Brazil, was infected with gammaherpesvirus (Sacristan et al., 2019), one of the most studied infectious agents in cetaceans (Sacristan et al., 2019; Esperon et al., 2008; Maness et al., 2011). A new species of alphaherpesvirus was found in a skin sample. Because these riverine species diverged from other odontocete cetaceans millions of years ago, the high herpesvirus divergence, and the fact that these populations are currently quite isolated, the high prevalence of gammaherpesvirus (59.1%, 13/22) and the absence of associated lesions in most animals suggest that they are likely the result of virus–host coevolution (Exposto et al., 2021).

Conservation and Management

Serious concerns about the survival of river dolphins led the IUCN Species Survival Commission Expert Group to focus its efforts on developing a strategy to address these threats in the early 1980s. In the 1990s and 2000s, most of the important developments gained in the biology, identification, and distribution of threats were published. Since then, numerous regional and national workshops have identified direct and indirect threats, and as a result, recommendations have been made. There has also been an increase in our understanding of the ecology, behavior, population estimates, mortality from conflicts with fishing operations, and conservation recommendations for bufeos.

Human Threats

Habitat Degradation, Decreased Water Quality, and Contaminants

Because of deforestation, agriculture, mining, and/or urbanization, the rate at which the human population is growing is reducing the quality and quantity of water (Campbell et al., 2022). These threats have been identified and highlighted in every river dolphin action plan so far. The main biological impact of deforestation on aquatic ecosystems is the rapid loss of fish (prey), especially in small tributary rivers where many species depend on the availability of resources. The construction of new roads and increased boat traffic are unfavorable for bufeos because these activities erode riverbanks and destroy the habitats on which they depend, as already warned by Pilleri and Gihr (1977).

One of the main threats to the habitat of bufeos is river pollution, caused as well by the discharge of high levels of nutrients (i.e., high phosphorus loads), and the influx of toxins such as heavy metals (mercury, arsenic, and lead), DDT and chlorine compounds that come from pesticides, agricultural, and livestock activities (Aliaga-Rossel, 2010).

As for heavy metals, the main source of mercury comes from small-scale gold mining, where gold is separated from other elements. These pollutants are then discharged into the rivers, where they can bioaccumulate in the trophic chain (Barbosa et al., 2021; Mosquera-Guerra et al., 2019). Uncontrolled gold mining occurs along the Beni River, where no controls or specific laws are enforced regarding the pollutants discharged into the water. Studies conducted in the Beni River and among human populations along the Upper Madeira River in Brazil have shown that mercury levels exceed regulatory limits (Barbosa et al., 2021; Mosquera-Guerra et al., 2019). High levels of contamination harm not only those directly involved in or near mining operations, but also populations 120 km downstream, where mercury has been identified in the hair of those who consume a lot of fish (Schudel et al., 2018). Mercury is associated with lesions in the neurological system, motor dysfunction, and eye problems. Studies show the direct effects of biomagnification of contaminants in fish and humans (Barbosa et al., 2021; Mosquera-Guerra et al., 2019). Mercury levels in the blubber tissue of adult river dolphins are much higher than those of calves, indicating that bioaccumulation is an

ongoing process in dolphins in the Madeira River basin (Barbosa et al., 2021). Given that river dolphins are efficient fish consumers, consuming 2–3 kg of fish per day (Best & Da Silva, 1989), and are long-lived (Martin & Da Silva, 2018), they are particularly at risk of poisoning, demonstrating the potential impact of mining contaminants on bufeo populations.

Interactions with Fisheries, Hunting, and Bycatch

Some of the most significant threats to Bolivian bufeos are interactions with fishing activities. This has been extensively reported, and overexploitation of aquatic resources is increasingly forcing fishermen to use more aggressive fishing techniques that are detrimental to other aquatic species. The decreasing number of fish of appropriate size, the increasing number of nets and fishing effort in the river and the perception of competition for fish by fishermen are increasing the threats to bufeos. Long nets used at confluences and across the width of rivers increase the possibility of bufeos becoming entangled and drowning (Aliaga-Rossel et al., 2012; Trujillo et al., 2010). Few studies have focused on the effects of commercial fishing in Bolivia and the potential impacts on aquatic populations. There are reports that some members of indigenous groups occasionally hunt Bolivian bufeos to sell the blubber in the Trinidad area. This appears to be an income-generating practice for some locals. Bufeos are also shot for fun or by sport hunters practicing their aim (R. Cuellar, 2018, personal communication; Aliaga-Rossel, 2003, 2010).

Another major cause of mortality comes from the death of individuals accidentally trapped in fishing nets. Some of these are released by fishermen, who must leave them to die or kill them with machetes to avoid damaging their catch, nets, or "suffering of the animal". In these cases, it is common for fishermen to use the remains as bait, save the fat, or simply leave the carcass floating. As noted above, there are few reports of humans killing bufeos as a source of protein (Best & Da Silva, 1989; Reeves et al., 1999; Aliaga-Rossel, 2002). However, interviews with fishermen in the middle and lower Mamore River did not initially consider the bufeo to be a competitor for their fish, but this perception changed in 2022 (Aliaga-Rossel, 2002). In some areas, bufeos steal or damage the fish in the nets, increasing their negative perception and now being seen as a strong competitor for fish. This results in reported deaths or injuries to the animal, including shooting, poisoning, and beating.

A report from near Tefé in the Brazilian Amazon suggests that intentional killing for use as bait results in approximately 1650 dolphins being killed each year (da Silva et al., 2018; Marmontel et al., 2020). The same situation occurs in other countries, where the number of killings is increasing at an alarming rate (Trujillo et al., 2010; Brum et al., 2015). Limited employment opportunities for fishermen further complicate conservation efforts. In riverine fishing towns, wages and educational prospects are often relatively poor (Campbell et al., 2022). In Bolivia, bufeos are occasionally used as bait for blanquillo (*Calophysus macropterus*) fishing, especially when a dead bufeo is trapped in nets. Locals concur that the fat makes it more effective than other wild animals such as caimans, capybaras, or fish guts. Although the impact on bufeos populations was not measured, the effectiveness of this method may lead to its continued and intensive use in the future (Escobar-WW et al., 2020).

Boat Traffic and Noise

Aquatic life in rivers is negatively impacted by increased boat traffic (Berthinussen et al., 2021). River dolphins are seriously threatened by increased boat traffic since it can alter their feeding and spawning habits, cause stress to the animals, and contaminate their water with oil from leaking boats. Bolivian bufeos can easily interrupt their feeding behavior, or other activities if disturbed by the intense approach of outboard motorboats.

Collisions with boat propellers can injure or even kill them, although collisions are probably underreported. In the Tijamuchi River, Aliaga-Rossel (2000) found a dead adult male that had been struck by the propeller of an outboard motor. The left side of its beak was severely cut, and the

left lower jaw was broken; similar events have been documented in the Colombian Amazon (Trujillo, 1994). This threat increases during the low-water season when more calves are observed (McGuire & Aliaga-Rossel, 2007), and they use shallow river channels that are also used by fishing boats and other vessels. In some areas of the Yacuma and Ibare rivers, poor tourist practices offer swimming with Bolivian bufeos and increase boat traffic.

The amount of anthropogenic noise has also increased significantly. In addition, noise pollution can interfere with a species' ability to communicate and navigate. Bolivian bufeos can be harmed by such acoustic pollution (which is primarily caused by shipping traffic, military operations, and sounds associated with oil and gas exploration) in a variety of ways, ranging from physical impairment and hearing loss to behavioral effects or even effects on prey (Berthinussen et al., 2021).

Increasing noise pollution is evident in several commercial ports along the rivers, where dolphin densities are always low. Bolivia has seen an increase in commercial cetacean-watching activities over the past decade, which may increase this disturbance in tourist areas. The physical condition of the animals is significantly affected when tour guides drive the boats in circles to "attract" bufeos (although this may be an agonistic response to the noise) (Aliaga-Rossel et al., 2014).

Dams' Constructions

Studies on the cumulative impacts of dams on Bolivian bufeos are scarce or non-existent. However, due to substantial habitat fragmentation, dam development directly endangers river dolphin populations by isolating them (Da Silva et al., 2018). This has occurred in rivers in Asia and in the Brazilian Amazon (da Silva et al., 2018; Paschoalini et al., 2020), impacting the movement and migration of both dolphins and fish, which in turn affects the food chain (Paschoalini et al., 2020). The golden catfish (*Brachyplatystoma rousseauxiien*), whose numbers in Bolivia have been dangerously reduced by the construction of the Jirau and Santo Antonio dams on the Madeira River in Brazil, is a notable example of the impact of dams in disrupting long-distance migration.

The alteration and loss of habitats make them unviable for the species. For example, since 2012, the Santo Antonio and Jirau plants have kept a population of dolphins isolated in a 100-km stretch between the two dams. This could have an impact on the two biological groups of *I. boliviensis*, which are likely to be lost soon before their evolutionary history can be understood (Gravena et al., 2015).

In Bolivia, new dams have been proposed for the Madeira River complex and the Madeira–-Madre de Dios–Beni Corridor, despite all the negative impacts already presented elsewhere (SARDI, 2022).

Use of Bufeos Products

Meat. The indigenous group "the Yuracaré" in the central Mamore occasionally engages in subsistence hunting and eats bufeo meat, although there are no records of the number of dolphins killed by them. Bufeo meat is typically considered being too fatty and unpleasant for frequent consumption (Aliaga-Rossel, 2010). The people of Costa Márquez, in northern Bolivia, consider this meat as harmful, unhealthy, and even toxic (Anderson, 1997).

Traditional Medicine. Inhabitants of several villages along the rivers and tropical towns and cities agree that the fat can be used as a very effective traditional medicine to cure respiratory problems (tuberculosis) and some lung infections (Aliaga-Rossel, 2003, 2010), including sequels to COVID-19, but this should be studied further.

Traditional Charms and Myths. Bufeo teeth are sold in the local market of Riberalta (northern Bolivia) as sexual magnets, love, or lucky charms. Although rare, some indigenous chimanes or witch doctors use the bufeo's genitalia, eyes, or other body parts for a variety of purposes.

Natural Mortality

There is no direct evidence of predation by other large vertebrates because the bufeo is the dominant predator in the aquatic ecosystems of the

Bolivian Amazon. Best and Da Silva (1993) suggested that the jaguar (*Panthera onca*) and the black caiman (*Melanosuchus niger*) are potential predators. Anecdotal evidence suggests that a newborn bufeo was seen in the mouth of a caiman (*Caiman yacare*), although it is uncertain whether the newborn was truly killed by a caiman or if it was already dead (L. Cuellar, 2009, personal communication; Aliaga-Rossel, 2010). In another case, a dead bufeo was reported in the Mamoré River, possibly caused by intraspecific sexual aggression (Aliaga-Rossel, 2002, 2010).

As a result of climate change, prolonged water shortages and droughts are becoming more common and are being recorded at the national level. Although some droughts occur naturally and fluctuate frequently, this problem is intensifying and may indirectly affect bufeo populations by reducing the availability or quality of habitat.

Legislation and Management

The IUCN Red List classifies *Inia geoffrensis* as Endangered A2acd + 3 cd + 4acd (EN) and includes the subspecies *I. g. boliviensis*, recognizing entanglement ("bycatch"), habitat modification and degradation, and activities other than fishing (dam construction, port development, mining, boat traffic, etc.) as the main threats (da Silva et al., 2018). The Red Book of Endangered Vertebrates of Bolivia and recognizes *I. boliviensis* as vulnerable (VU) (Aliaga-Rossel, 2009).

The Bolivian river dolphin is protected directly and indirectly by the following Bolivian regulations:

- Supreme Decree 25,458, the "*Veda General Indefinida*" (enacted in July 1999), which prohibits the harassment, capture, and harvesting of wildlife and their derivatives. However, its effectiveness is debated, and it does not directly refer to bufeos.
- Departmental Law—this local regional law declares the Bolivian river dolphin as Natural Heritage of the Department of Beni (enacted in March 2008) and recognizes the need for additional protection and further understanding of the species.
- Law No. 284/2012 of Bolivia. The bufeo has been declared a Natural Heritage of the Plurinational State of Bolivia (enacted in September 2012), the second article of which states: "The Executive party of the Central State Level, in coordination with the Autonomous Territorial Entities, will prioritize the protection and conservation of the Bufeo or river dolphin and its habitat, through policies, programs and projects in the short, medium, and long term."
- Municipal Law No.12/2012 declares the bufeo as Natural Heritage and symbol of Santísima Trinidad City.
- Municipal Law No. 122/2019 declares the bufeo as Natural Heritage of Puerto Villarroel in the department of Cochabamba.
- The National Action plan for conserving the Bolivian dolphin (*Inia boliviensis*) 2022–2025. Administrative Resolution VMABCCGDF N 049/20 22 (enacted in October 2020) includes several activities to be carried out for the conservation of the species. Although to date there is no budget from the government to carry out any of the proposed activities, these are being developed independently by researchers.
- Supreme Decree 4489, *Protection of wildlife* (enacted in March 2021), within the framework of the exclusive jurisdiction of the Central State Level, prohibits sport hunting.

Future Challenges for Research and Management

There are many knowledge gaps relevant to the conservation management of the Bolivian bufeo. The biology, life history, population size and structure, and migratory behavior of the species are insufficiently studied. According to the most recent IUCN assessment (da Silva et al., 2018), there are significant knowledge gaps regarding range-wide population structure, annual fluctuation behavior, and medium- and long-term changes. Monitoring populations is key to identifying ongoing changes in tropical ecosystems and understanding distribution and abundance in relation to risks from anthropogenic activities and climate change.

Currently, there are no complete population estimates for bufeos in many rivers and aquatic systems throughout their range. However, research done in recent years has attempted to increase knowledge by using non-conventional methods, but also by combining conventional visual methods, aerial visual methods (with unmanned vehicles), and passive acoustic monitoring. These efforts will provide a complete distribution and abundance estimate of river dolphins and help establish a baseline for any national monitoring or research programs.

Population genetic studies are increasing, but more comprehensive genetic analyses that include samples from each region of the distribution are still needed. This is a crucial area to address in the coming years, as it will advance our understanding and inform actions taken to protect Bolivia's bufeo populations.

Since the distribution of bufeos occurs in international rivers (Bolivia–Brazil), conservation and management efforts must be undertaken by both countries through intergovernmental agencies, indigenous communities, industry, and NGOs.

The effects of deforestation, human settlements along rivers, pollution from gold mines, and the impact of industry and pesticides on water quality and fish populations need to be studied. More research is also needed on how human fishing affects fish communities.

The ecotourism industry, community-based tourism, and tourism focused on citizen science (e.g., bird and cetacean watching) are of growing interest in the country. The department of Beni (in the sectors of Trinidad, Santa Rosa del Yacuma, and Rurrenabaque) is committed to the development of ecotourism. Therefore, efforts to improve infrastructure and continue to train and certify specialized guides will promote responsible and quality tourism related to river dolphin conservation.

Last but not least, it is imperative to raise awareness about the bufeos. People may be inspired to understand and become involved in conservation issues involving charismatic or emblematic species. By adopting this species, it will be possible to launch sustainable educational initiatives like those in Brazil or Colombia. A strong educational component combined with an effective conservation strategy can even solve problems related to negative perceptions of river dolphins by local people.

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