Vol. 45: 269–282, 2021
https://doi.org/10.3354/esr01133

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published July 29

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Home range and movements of Amazon river dolphins *Inia geoffrensis* in the Amazon and Orinoco river basins

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ABSTRACT: Studying the variables that describe the spatial ecology of threatened species allows us to identify and prioritize areas that are critical for species conservation. To estimate the home range and core area of the Endangered (EN) Amazon river dolphin *Inia geoffrensis*, 23 individuals (6♀, 17♂) were tagged during the rising water period in the Amazon and Orinoco river basins between 2017 and 2018. The satellite tracking period ranged from 24 to 336 d (mean ± SE = 107 ± 15.7 d), and river dolphin movements ranged from 7.5 to 298 km (58 ± 13.4 km). Kernel density estimates were used to determine minimum home ranges at 95% (K_{95} = 6.2 to 233.9 km^2; mean = 59 ± 13.5 km^2) and core areas at 50% (K_{50} = 0.6 to 54.9 km^2; mean = 9 ± 2.6 km^2). Protected areas accounted for 45% of the K_{50} estimated core area. We observed dolphin individuals crossing country borders between Colombia and Peru in the Amazon basin, and between Colombia and Venezuela in the Orinoco basin. Satellite tracking allowed us to determine the different uses of riverine habitat types: main rivers (channels and bays, 52% of recorded locations), confluences (32%), lagoons (9.6%), and tributaries (6.2%). Satellite monitoring allowed us to better understand the ecological preferences of the species and demonstrated the importance of maintaining aquatic landscape heterogeneity and spatial connectivity for effective river dolphin conservation.

KEY WORDS: South America · Satellite telemetry · Kernel density · Cetaceans · Neotropical rivers · Conservation · Protected areas · Transboundary

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Publisher: Inter-Research · www.int-res.com

1. INTRODUCTION

The home range of animals is an important spatial ecological variable operating as a proxy for a species' biological needs (Kenward 2001, Hemson et al. 2005), and its key resource supply (Flores & Bazzalo 2004). Among other biological variables, the home range of some cetacean species is related to (1) animal body mass (Harestad & Bunnel 1979, Swihart et al. 1988, Gubbins 2002); (2) sex and age (Wells 1991); (3) the density of conspecifics; and (4) the distribution of mates (Ostfeld 1990). In addition, home ranges are good predictors of productivity and habitat heterogeneity, enabling ecological comparisons among geographically distinct populations (Ballance 1992, Gubbins 2002, Ouellette & Cardille 2011).

Areas within home ranges are not occupied homogeneously (Dixon & Chapman 1980, Samuel et al. 1985); some of the areas that are used more frequently are called 'core areas', and are often associated with greater resource density (Samuel et al. 1985, Powell 2000, Oshima et al. 2010). When identifying the extent of home ranges and, in particular, core areas, it is also essential to identify a species' critical habitats to help guide population management (Ingram & Rogan 2002, Seminoff et al. 2002, Rayment et al. 2009) and design protected areas.

There are several methodological approaches that can be used to estimate home ranges and core areas. From location data points it is possible to produce utility distributions (UD) that describe the differences in the intensity of home range use (Powell 2000, Oshima et al. 2010). Kernel density estimators are useful for quantifying the intensity of habitat use (Worton 1989, Ouellette & Cardille 2011) and are among the most robust and widely applied non-parametric statistical methods for estimating the probability of the occurrence of individuals (Seaman & Powell 1996, Seaman et al. 1999, Powell 2000, Oshima et al. 2010).

Spatial ecological assessments for aquatic species have been conducted for a number of cetaceans, including harbor porpoise *Phocoena phocoena* (Sveegaard et al. 2011), Hector's dolphin *Cephalorhynchus hectori* (Rayment et al. 2009), common bottlenose dolphin *Tursiops truncatus* (Defran et al. 1999, Gubbins 2002, Wells et al. 2017), franciscana dolphin *Pontoporia blainvillei* (Bordino et al. 2008), Guiana dolphin *Sotalia guianensis* (Flores & Bazzalo 2004, Rossi-Santos et al. 2006, Azevedo et al. 2007, Wedekin et al. 2007, Oshima et al. 2010), and Amazon river dolphin (Martin & da Silva 1998, 2004a). This last study was conducted in the Mamirauá Sustainable Development Reserve in Brazil and represents the first long-term home range study of adult river dolphins (N = 53) using VHF radio transmitters.

The dynamic nature of hydrological systems presents a considerable challenge for numerically determining the spatial ecological variables of aquatic organisms, especially due to the logistical constraints related to individual detection and identification. The latter is particularly true for Amazon river dolphins, which are highly mobile top predators able to cover long distances (hundreds of kilometers) in relatively short periods (days) with a possible differential use of habitat by males and females (Martin & da Silva 1998, 2004a, Trujillo 2000, Gómez-Salazar et al. 2012c, Mosquera-Guerra et al. 2018).

Amazon river dolphins are subdivided into 2 subspecies: *Inia geoffrensis geoffrensis* that are distributed across the Amazon (da Silva 2002) and Orinoco basins (Herrera et al. 2017), and *I. g. boliviensis*, found along the Mamoré, Iténez, and Madeira rivers (Aliaga-Rossel 2002, Aliaga-Rossel et al. 2006, Gravena et al. 2014). Considered as Endangered (da Silva et al. 2018), Amazon river dolphins are among the most threatened aquatic mammals. Their populations are declining due to (1) deliberate killing and bycatch (Trujillo et al. 2010, Mintzer et al. 2016, da Silva et al. 2018); (2) habitat degradation through timber exploitation, agricultural expansion, and gold mining; (3) climate change (Mosquera-Guerra et al. 2015, 2019, 2020); and (4) the construction of hydropower dams, primarily in Brazil (Anderson et al. 2018). To date, there are 175 dams that are operating or are under construction in the Amazon basin, as well as at least 428 more planned over the next 30 yr, including 21 large dams (Forsberg et al. 2017, Latrubesse et al. 2017, Anderson et al. 2018, Almeida et al. 2020). Dams have transformed 16.4% of the distribution of *I. g. geoffrensis* in the Amazon basin, 22.9% in the Orinoco basin, and 54.9% in the Tocantins-Araguaia hydrographic complex (Mosquera-Guerra et al. 2018). Currently, 2 dams exist within the range of *I. g. boliviensis* in the Madeira River (Gravena et al. 2014, 2015).

The intensity and scale of threats to *Inia* populations in South America require urgent action to quantitatively determine the spatial requirements of these cetaceans in different ecosystems throughout their range. In this study, we used satellite tracking to collect quantitative spatial information on Amazon river dolphins across 5 rivers in the Amazon and Orinoco basins with special attention to an assessment of home ranges and core areas, use of protected areas, and transboundary movements.

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted from October 2017 to December 2018 across 5 rivers in the Amazon and Orinoco basins. Captures were made along transects: (1) from the lower Juruena River sub-basin in Brazil and the Cururu River, including its confluence with the Teles Pires River in the Tapajós River basin; (2) in the main channel of the San Martín River in Bolivia, from its confluence with the San Joaquin River to the border between Beni and Santa Cruz provinces; (3) from the confluence of the Atacuari and the Amazon River in Colombia to the Zaragoza Creek, including the Tarapoto wetland complex, and the confluence of the Loretoyacu and the Amazon rivers; (4) from the mid-basin of the Orinoco River in Colombia, including its confluences with the Bita and Meta rivers; and (5) from the confluence of the Huallaga and Marañón rivers in Peru to the confluence of the Ucayali and the Marañón rivers, including the confluence with the Marañón and Tigre rivers (Fig. 1).

Ecological and threat variables considered here included: (1) biogeographic influence and water types, i.e. black, clear, white, and mixed (Sioli 1984, Junk & Furch 1993, Hoorn & Wesselingh 2010); (2) habitat types, i.e. main rivers (channels and bays) with *várzea* (forests flooded by whitewater), confluences, tributaries, and lagoons with *igapó* (Amazon forests flooded by blackwaters) (Trujillo 2000, Martin & da Silva 2004b, Gómez-Salazar et al. 2012c); (3) proximity to protected areas, i.e. national and regional natural parks, reserves, and Ramsar sites; and (4) threats to river dolphin populations, i.e. gold mining, dams, and by-catch (Table 1).

2.2. Dolphin capture protocol and measurement recording

Only adult individuals were selected for tagging, and their age class was estimated based on body length, following the methods of da Silva (2009) and Martin & da Silva (2018), and avoiding females with calves (see Table 2).

Field work was conducted in locations previously investigated by Gómez-Salazar et al. (2012a, 2012b), Mosquera-Guerra et al. (2019), and Trujillo et al. (2019) in the Colombian and Peruvian Amazon and the Orinoco River in Colombia (conservation and abundance estimates); Pavanato et al. (2016) in the Tapajos River, Brazil (conservation and abundance estimates); and Aliaga-Rossel & Guizada Duran (2020) in San Martín and Iténez, Bolivia (abundance estimates).

Capture locations were chosen based on accessibility, river width, and water depth. We implemented 2 different capture techniques depending on the river width. The first technique was employed in water courses less than 300 m wide. Two small boats (6–8 m length, propelled by 20–40 hp outboard motors) were used to set two 300 m nets with 5 cm mesh size. The first net was placed 100 m upstream and 100 m downstream from the observed target group. Fishermen walking along the banks of the river then slowly moved the upstream net toward the dolphin group. Once the net had been moved 50 m downstream, a third net was deployed by a boat without an outboard motor to avoid scaring the animals. The aim of this operation was to steer the individuals in the direction of the riverbank. The second technique was used in water courses wider than 300 m. One end of the net was fixed to a 3 m pole held by a fisherman close to the riverbank. From this fixed point, the net was rapidly extended around the target dolphin group by a motorboat, forming a half-moon with a radius of 100 m upstream. As dolphins were caught in the nets, they were immediately untangled and carefully transported to the riverbank or to a processing platform in a motorboat.

As part of our protocol, a veterinary team was present throughout the capture procedure to monitor the health of the animals according to cardiac and respiratory rates. The whole procedure lasted around 10 to 45 min. There was no evidence that individuals experienced excessive stress. No increase in heart and respiratory rates, or sudden movements of head or caudal fins were noted, as have been previously documented as signs of stress (Martin et al. 2006). In the event of excessive stress, our safety protocol required that the capture operation would immediately be halted and the dolphin released.

2.3. Tag specification, permissions, and method of attachment

The tags used were SPOT-299A and SPOT6-F single-point fin mounted satellite tags (Wildlife Computers), 20.8 cm long, 2.0 cm wide, 2.5 cm high, and weighing 62 g. The tags had an 18 cm long flexible antenna, plastic wings, and a 6.5 × 2.0 cm tail. The tags were positioned on each side of the trailing edge of the dorsal fin, with a matching 0.8 cm diameter hole in each for attaching the tag 3.5 cm anterior to

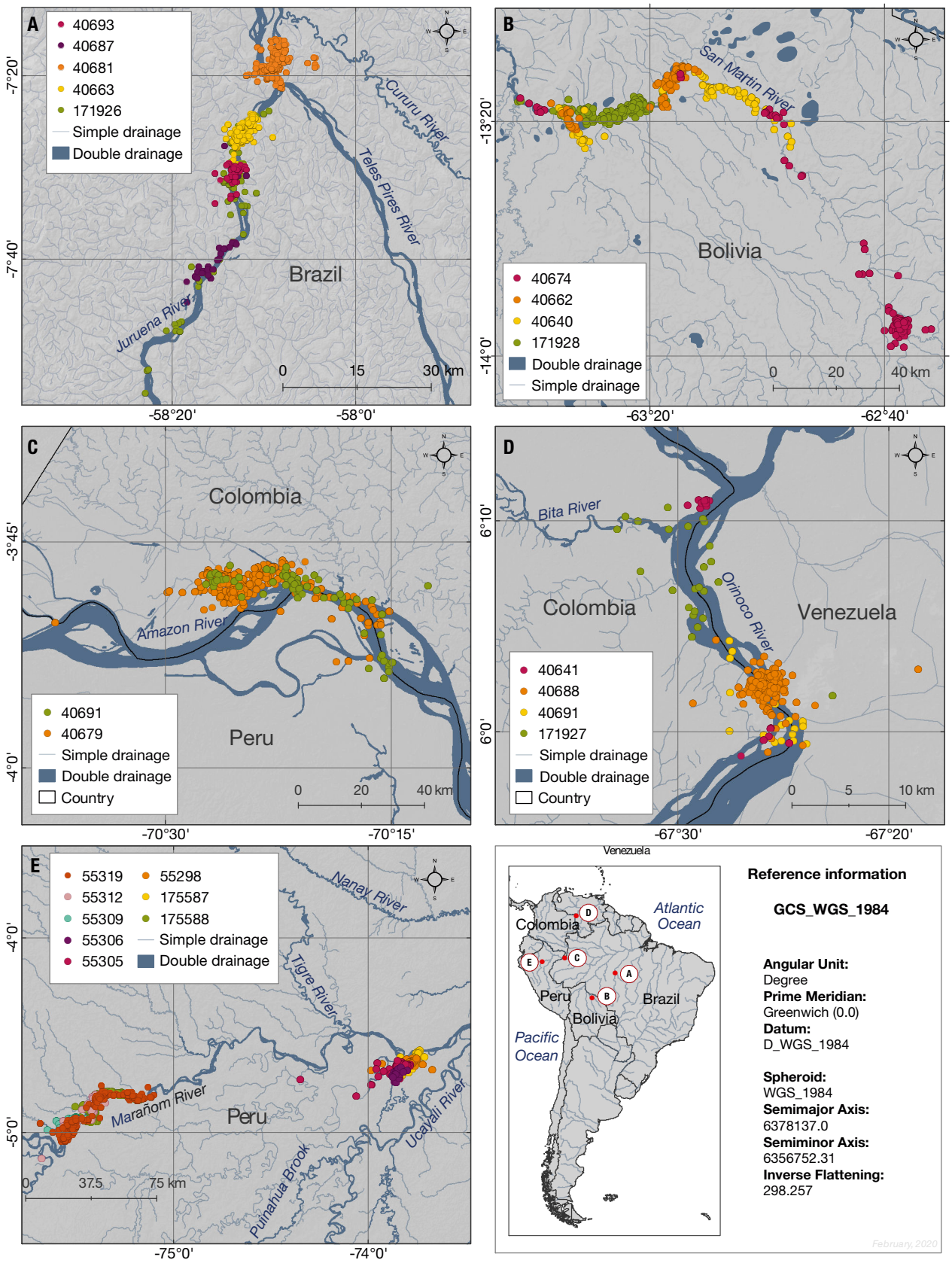

Fig. 1. Satellite-linked locations for the 23 Amazon river dolphins tagged in the Amazon and Orinoco basins. Rivers: (A) Juruena, Brazil, (B) San Martín, Bolivia, (C) Amazon, Colombia, (D) Orinoco, Colombia, and (E) Marañón, Peru. Simple drainage: minor water bodies, generally small tributaries; double drainage: main rivers

Table 1. Information on Amazon river dolphins *Inia geoffrensis* tagged with satellite-linked transmitters in the Amazon and Orinoco basins, 2017–2018. ♀: female; ♂: male

Country	Basin	Subbasin	Rivers	Biogeographic influence of the basin	Water type	Taxon	Number and sex
Brazil[a]	Amazon	Tapajós	Juruena	Amazon-Brazilian Shield	Clear	*I. g. geoffrensis*	1♀, 4♂
Colombia[b]	Amazon	Amazon	Amazon	Andean-Amazon	Mixed	*I. g. geoffrensis*	1♀
Bolivia[a]	Amazon	Iténez	San Martín	Amazon-Brazilian Shield	Clear	*I. g. boliviensis*	1♀, 3♂
Colombia	Orinoco	Orinoco	Orinoco	Orinoco-Guiana Shield	White	*I. g. geoffrensis*	2♀, 2♂
Peru[a]	Amazon	Marañón	Marañón	Andean-Amazon	White	*I. g. geoffrensis*	1♀, 7♂
Colombia[b]	Amazon	Amazon	Amazon	Andean-Amazon	Mixed	*I. g. geoffrensis*	1♂

[a]Protected area; [b]Ramsar site

the fin's trailing edge, following Balmer et al. (2011, 2014) and Wells et al. (2013, 2017). The tags were programmed for continuous transmission (24 h), up to 250 times a day, to an ARGOS satellite constellation, providing location and tag status data, and yielding up to 240 tracking days based on battery life. Satellite tagging was conducted under research permits for each country (Bolivia: DGBAP/MEG No. 0515/2017; Brazil: SISBIO 60171-1; Colombia: No. DTA 0898/2018; Peru: RD 515-2018 PRODUCE, RJ 003-2018).

2.4. Location data and filtering

Estimates of the tagged Amazon river dolphin locations were received and processed by the ARGOS Data Collection and Location System and downloaded from CLS-ARGOS. ARGOS uses multiple, polar-orbiting satellites to receive data from tags, and transmits this data to ground-based processing centers. Tag locations were calculated using the Doppler effect on transmission frequency and a location-processing algorithm (Collecte Localization Satellites [CLS] 2011).

Locations were classified by the ARGOS system into 1 of 6 location classes (LCs) based on the level of accuracy measured in kilometers of uncertainty for latitude and longitude. ARGOS classifies location quality relative to an estimated error radius in the following location classes: 3 (accurate to <250 m), 2 (accurate to 250–500 m), 1 (accurate to 500–1500 m), and A and B (1–2 messages received but no accuracy estimation). In our study, we used only the most accurate data, LCs 3 and 2, after filtering the data with SAS-routine and ARGOS-Filter (Witt et al. 2010, Wells et al. 2017, Dolton et al. 2020). Data with low accuracy, LC1 (500–1500 m), and data in classes A and B, with no accuracy estimations, were not used in our analysis.

2.5. Kernel density estimate and movement

A kernel density estimate at a 95% probability UD (K_{95}) was used to calculate home range, whereas a kernel density estimate at a 50% probability UD (K_{50}) was used to measure the core area. Home ranges calculated using the kernel density estimator (KDE) were used to estimate UDs. In addition, the longest distance between 2 locations was estimated following Gubbins (2002), Seminoff et al. (2002), Flores & Bazzalo (2004), Rayment et al. (2009), Oshima et al. (2010), and Wells et al. (2017). A UD represents the probability of finding a given individual in a certain place and describes the use of space (White & Garrott 1990, Wells et al. 2017). It also identifies areas of intense use (Powell 2000, Wells et al. 2017). Mapping was performed using the Geostatistical Analyst and Spatial Analyst extensions in ESRI ArcGIS version 10.2.2. (ESRI 2014), and the smoothing parameter of the Beizer interpolation was used following Worton (1989), MacLeod (2013), Wells et al. (2017), and Dolton et al. (2020).

River dolphin tagging was carried out during the rising water period for Colombia and Peru, and during the maximum water levels for Brazil and Bolivia. River depth in our sampling locations ranged from 8 m in Juruena to 44 m in the Amazon (Goulding et al. 2003). Permanent islands and shoreline areas were subtracted from the home range and core area calculations, based upon satellite images for the study period (Copernicus Sentinel 2020). We followed the habitat types proposed by Gómez-Salazar et al. (2012a). The main river, confluences, tributaries, and lagoons were delimited in satellite images downloaded from the Copernicus Sentinel platform, and processed through the Geostatistical Analyst and Spatial Analyst extensions in ESRI ArcGIS version 10.2.2 (ESRI 2014). The number of locations (95% significance level) per habitat type were quantified

and classified using the ArcGIS version 10.2.2 software tools (ESRI 2014, Copernicus Sentinel 2020). Mean values ± SE are reported throughout this paper and were calculated using RStudio version 1.1.383 (R Studio Team 2014), running R version 3.5.2 (R Core Team 2017).

3. RESULTS

3.1. Tracking effort

Satellite tag-linked locations were analyzed for 23 adult Amazon river dolphins (6♀, 17♂) between 2017 and 2018. The transmitters were installed on individuals in the (1) Juruena River in Brazil (n = 5, 1♀, 4♂); (2) San Martín River in Bolivia (n = 4, 1♀, 3♂); (3) Amazon River in Colombia (n = 2, 1♀, 1♂); (4) Orinoco River in Colombia (n = 4, 2♀, 2♂); and (5) Ucayali River in Peru (n = 8, 1♀, 7♂). The body length of tracked individuals ranged from 159 to 227 cm (mean 190 ± 3.7 cm) and their weight from 49 to 200 kg (mean 94 ± 7.4 kg). The number of satellite locations with accuracy classes of 2 and 3 ranged from 96 to 1697 (mean 626 ± 103 locations) and the tracking duration ranged from 24 to 336 d (mean 107 ± 16 d; Table 2).

3.2. Ranging patterns

The longest total distance traveled by a tagged individual in our study was 297.9 km, recorded by an *Inia geoffrensis boliviensis* male in the San Martín River, Bolivia. The shortest distance recorded was 7.5 km by an *I. g. geoffrensis* male in the Juruena River in Brazil (Table 2). The total and daily movements (ranges, mean, and SE) for all tagged individuals are reported in Table 3. The tagged dolphins made transnational movements, with 1 *I. g. geoffrensis* individual crossing between Colombia and Peru (36.2 km) along the Amazon River and 3 *I. g. geoffrensis* individuals crossing between Colombia and Venezuela (51.8 km) through the Orinoco River basin. Since the transmission of satellite data was set at intervals, it was difficult to determine how many times these transboundary movements occurred.

The mean numbers of satellite-tracking locations for all individuals in each habitat type were (1) confluences: 35.0 ± 11.3 in the Orinoco River, Colombia to 299.5 ± 68.5 in the Marañón River, Peru; (2) main river: 100.5 ± 32.5 in the Amazon River, Colombia to 438.1 ± 120.8 in the Marañón River, Peru; (3) lagoons: 10.8 ± 10.0 in the Marañón River, Peru to 588.0 ± 425.0 in the Amazon River, Colombia; and (4) tributaries: 11.7 ± 1.8 in the Orinoco River, Colombia to 67.0 ± 15.1 in the Juruena River, Brazil (Table 4).

3.3. Home range size

A minimum home range was measured using only locations with an estimated error radius of <500 m. The minimum home range (K_{95}) estimates varied from 12.1–27.9 km^2 (Juruena River, Brazil) to 60.5–233.9 km^2 (San Martín River, Bolivia), while the core area (K_{50}) estimates ranged from 0.6–9.1 km^2 (Juruena River, Brazil) to 3.7–54.9 km^2 (San Martín River, Bolivia; Fig. 2, Table 5).

The use of protected areas was calculated based only on the core areas of the monitored river dolphins. These proportions ranged from 10.3% (Orinoco River, Colombia) to 79% (San Martín River, Bolivia). Intermediate values were recorded for the Juruena River, Brazil (66.5%), Amazon River, Colombia (51.6%), and Marañón River, Peru (19.8%).

4. DISCUSSION

The spatial ecology of Amazon river dolphins (including estimates of home ranges, movements, and habitat use) has been assessed with a variety of methods, such as: (1) strip-width transects (McGuire & Winemiller 1998, Aliaga-Rossel 2002, Martin & da Silva 2004a, Denkinger 2010); (2) photo-identification (McGuire & Henningsen 2007); (3) capture-recapture (Martin & da Silva 2004a, Mintzer et al. 2016); and (4) tagging with VHF radio transmitters (Martin & da Silva 1998, 2004b). Nevertheless, there are still several unanswered questions regarding the habitat selection of dolphins. The use of satellite devices in this study allowed us to estimate the minimum home ranges, core areas, and movements of tracked individuals, providing more accurate and higher resolution versions of these variables. It also gave us the opportunity to address questions regarding habitat selection by Amazon river dolphins.

4.1. Ranging patterns and habitat heterogeneity

The movement values reported in our study (Tables 2 & 3) are comparable to those of Martin & da Silva (1998, 2004b), who reported that the maximum

Table 2. Amazon river dolphin *Inia geoffrensis* tag deployment and performance summary in South America (2017 and 2018). PPT ID: platform transmitter terminal identification number; ♀: female; ♂: male; locations: class 2 and 3 locations; K_{95}: home range 95% utilization distribution (UD); K_{50}: core area 50% UD. Dates are given as mm/dd/yy

Site/species	PTT ID	Length (cm)	Weight (kg)	Sex	Deployment coordinates (°N)	(°E)	Tracking interval	Days of emission	No. of locations	K_{95} (km^2)	K_{50} (km^2)	Total distance (km)
Juruena River (Brazil)												
I. g. geoffrensis	171926	197	89	♂	−7.416	58.190	10/10/2017–09/04/2018	336	645	23.6	0.6	69.9
I. g. geoffrensis	40663	162	49	♀	−7.516	58.208	10/08/2017–02/08/2018	125	437	17.6	1.4	11.7
I. g. geoffrensis	40687	182	60	♂	−7.516	58.208	10/10/2017–01/13/2018	108	138	27.9	9.1	27.9
I. g. geoffrensis	40681	193	56	♂	−7.347	58.144	11/10/2017–02/07/2018	119	1.489	15.5	1.0	11.2
I. g. geoffrensis	40693	205	91	♂	−7.516	58.208	10/10/2017–12/30/2017	114	156	12.1	1.8	7.5
Amazon River (Colombia)												
I. g. geoffrensis	40679	199	78.4	♀	−3.465	70.221	11/02/2017–03/19/2018	144	1262	30.7	2.4	36.2
San Martín River (Bolivia)												
I. g. boliviensis	40640	204	91.2	♂	−4.366	85.288	12/01/2017–04/29/2018	167	352	233.9	54.9	150.0
I. g. boliviensis	40662	209	83	♂	−4.366	85.288	12/01/2017–02/21/2018	83	462	89.2	11.4	93.6
I. g. boliviensis	40674	208	85.4	♂	−4.380	85.286	12/01/2017–02/08/2018	76	447	204.9	18.5	297.9
I. g. boliviensis	171928	211	69.2	♀	−4.365	85.301	12/02/2017–08/25/2018	266	1.369	60.5	3.7	101.7
Orinoco River (Colombia)												
I. g. geoffrensis	40688	214	180	♂	5.983	67.428	02/17/2018–04/10/2018	53	771	8.8	1.2	13.3
I. g. geoffrensis	40691	159	68	♀	5.997	67.432	02/17/2018–03/13/2018	24	96	18.9	3.9	11.3
I. g. geoffrensis	171927	188	107	♂	6.028	67.377	02/17/2018–05/31/2018	54	138	41.2	10.3	26.0
I. g. geoffrensis	40641	227	200	♀	5.996	67.427	02/26/2018–04/16/2018	57	96	76.4	18.5	51.8
Marañón River (Peru)												
I. g. geoffrensis	55305	197	97	♂	−4.649	73.825	08/13/2018–11/14/2018	118	446	20.9	2.9	80.3
I. g. geoffrensis	175587	177	63.9	♂	−4.636	73.813	08/13/2018–09/29/2018	47	560	32.2	2.1	20.7
I. g. geoffrensis	55298	182	72.5	♂	−4.666	73.833	08/14/2018–09/26/2018	44	414	11.8	0.6	37.3
I. g. geoffrensis	55306	173	101.9	♀	−4.738	73.861	08/14/2018–10/16/2018	151	109	6.2	1.5	9.5
I. g. geoffrensis	55309	170	92.6	♂	−4.936	75.513	08/21/2018–09/23/2018	33	857	20.1	2.2	27.5
I. g. geoffrensis	55312	182	111.7	♂	−4.939	75.566	08/21/2018–12/24/2018	153	818	64.9	8.4	70.4
I. g. geoffrensis	55319	176	99	♂	−4.977	75.545	08/21/2018–10/20/2018	60	1.337	186.8	32.2	91.8
I. g. geoffrensis	175588	180	97	♂	−4.941	75.514	08/21/2018–10/03/3018	43	1.697	88.3	10.0	50.7
Amazon River (Colombia)												
I. g. geoffrensis	40691-1	176	118	♂	−3.470	70.215	09/17/2018–11/24/2018	94	305	61.7	5.9	33.1

Table 3. Total and daily distances traveled and the habitats used. n: number of Amazon river dolphins tagged

Rivers	n	Habitats used	Total distance traveled (km) range (mean ± SE)	Daily movement (km) range (mean ± SE)
Juruena River (Brazil)	5	Juruena and Tapajós main rivers; confluences: Juruena River with Cururu and Teles Pires rivers	7.5–69.9 (25.6 ± 11.6)	0.070.26 (0.14 ± 0.03)
San Martín River (Bolivia)	4	San Martín main river; confluences: San Joaquin River and clearwater floodplain	93.6–297.9 (160.8 ± 47.3)	0.4–3.9 (1.6 ± 0.79)
Amazon River (Colombia)	2	Amazon and Loretoyacu main rivers; confluences: Amazon River with Loretoyacu and Atacuari rivers and the Zaragoza creek, and Tarapoto lagoons complex	33.1–36.2 (34.6 ± 1.5)	0.25–0.35 (0.30 ± 0.05)
Orinoco River (Orinoco)	4	Orinoco main river; confluences: Bita and Meta rivers and the Tesoro and Negro creeks	11.3–51.8 (25.6 ± 9.3)	0.25–0.9 (0.52 ± 0.13)
Marañón River (Peru)	8	Marañón main river; confluence: Ucayali and Tigre rivers	9.5–91.8 (48.2 ± 10.5)	0.06–1.5 (0.75 ± 0.16)

distance covered by 1 individual was 225 km. Their data were derived from 53 VHF radio-tagged adult individuals in the Japurá and Solimões rivers (Mamirauá Sustainable Development Reserve, Brazil) between 1994 and 1999. These authors verified the presence of resident and migrant individuals within the same population. Our results also agree with distance values reported from photo identification assessments (based on individual marks) by McGuire & Henningsen (2007) at the Pacaya-Samiria Reserve in Peru (maximum 220 km, mean 60.8 km), and Denkinger (2010) in the Cuyabeno and Lagartococha rivers (Cuyabeno Reserve, Ecuador), where the maximum distances traveled by *Inia geoffrensis geoffrensis* individuals ranged from 50 to 200 km.

Amazon river dolphins are one of the largest predators in the Amazon (Goulding et al. 1988, 2003, McGuire & Winemiller 1998, Gómez-Salazar et al. 2012c), contributing to fish community structure (Lowe-McConnell 1975, 1987). The diets of river dolphins include fish of different sizes (25–90 cm), belonging to more than 43 species and at least 19 families, many of which show migratory patterns influenced by flood pulses (da Silva 1983, Best & da Silva 1989). Long fish migrations from 500 km up to 3000 km (Zapata & Usma 2013, Duponchelle et al. 2016, Barthem et al. 2017, Hauser et al. 2018) can potentially explain the relatively long distance values recorded by tagged dolphins in our study. This aspect requires further analyses, comparing satellite tracking data from both Amazon river dolphins and their fish prey within the same temporal window.

Previous studies have pointed out the different use of heterogenous habitat by river dolphins (McGuire & Winemiller 1998, Martin & da Silva 1998, 2004a,b, Trujillo 2000, McGuire & Henningsen 2007, Denkinger 2010, Gómez-Salazar et al. 2012c, Mintzer et al. 2016). Trujillo (1994, 2000) and Trujillo & Morales-Betancourt (2009) reported seasonal lateral and longitudinal movements based on direct sightings and photo identification and suggested that these movements were influenced by the reproductive processes associated with low water periods (June to September in the Amazon River basin and December to April in the Orinoco River basin). Amazon river dolphins have adapted their foraging and reproductive behavior (mating and care of their calves) to the flood pulse, which determines habitat and prey availability within both the Amazon and Orinoco river basins (Martin & da Silva 2004b, Mintzer et al. 2016).

4.2. Home range

The kernel density estimator is considered to be one of the best methods for conducting spatial analyses on small cetaceans (Seaman & Powell 1996, Seaman et al. 1999, Powell 2000, Flores & Bazzalo 2004, Oshima et al. 2010). It has been applied to the study of home ranges, core areas, and movement patterns of harbor porpoises (Sveegaard et al. 2011), Hector's dolphins (Rayment et al. 2009), common bottlenose dolphins (Gubbins 2002, Wells et al. 2017, Balmer et al. 2019), and Guiana dolphins (Flores & Bazzalo

Table 4. Number of tracking locations (range, mean ± SE, percentage of total) for the Amazon river dolphins tagged in each habitat type in the Amazon and Orinoco basins. Blanks in Tributaries column: no data

Rivers	n	Number of tracking locations in each habitat type							
		Confluences		Main river		Lagoons		Tributaries	
		Range (mean ± SE)	%	Range (mean ± SE)	%	Range (mean ± SE)	%	Range (mean ± SE)	%
Jurueña River (Brazil)	5	15–996 (191.5 ± 176.5)	38.7	37–545 (296.6 ± 85.1)	50.2	10–95 (67± 15.1)	11.1		
San Martín River (Bolivia)	4	41–643 (216.2 ± 143)	32.9	141–680 (357.2 ± 116.4)	54.3	25–93 (29.5 ± 22)	4.5	16–102 (54.5 ± 21.3)	8.3
Amazon River (Colombia)	2	51–73 (62 ± 11)	7.9	68–133 (100.5 ± 32.5)	12.8	163–1013 (588 ± 425)	75	23– 43 (33 ± 10)	4.2
Orinoco River (Orinoco)	4	12–66 (35 ± 11.3)	12.8	19–742 (228.5 ± 172)	83.9	9–17 (11.7 ± 1.8)	3.3		
Marañón River (Peru)	8	116–601 (299.5 ± 68.5)	38.4	109–1073 (438.1 ± 120.8)	56.2	10–40 (10.8 ± 10)	1.4	23–184 (31.2 ± 36.8)	4

Table 5. K_{95}, K_{50}, and daily K_{95}, and K_{50}. Data are shown as range (mean ± SE). n: number of Amazon river dolphins tagged

Rivers	n	K_{95} (km^2)	Daily K_{95} (km^2)	K_{50} (km^2)	Daily K_{50} (km^2)
Jurueña River (Brazil)	5	12.1–27.9 (19.3 ± 2.8)	0.07–0.2 (0.14 ± 0.03)	0.6–9.1 (2.8 ± 1.6)	0.002–0.08 (0.02 ± 0.01)
San Martín River (Bolivia)	4	60.5–233.9 (147.1 ± 42.2)	0.2–2.7 (1.3 ± 0.5)	3.7–54.9 (22.1 ± 11.3)	0.01–0.3 (0.18 ± 0.06)
Amazon River (Colombia)	2	30.7–61.7 (46.2 ± 15.5)	0.2–0.6 (0.4 ± 0.2)	2.4–5.9 (4.1 ± 1.75)	0.01–0.06 (0.04 ± 0.02)
Orinoco River (Orinoco)	4	8.8–76.4 (36.3 ± 14.9)	0.2–1.3 (0.8 ± 0.2)	1.2–18.5 (8.1 ± 3.8)	0.02–0.3 (0.2 ± 0.06)
Marañón River (Peru)	8	6.2–186.8 (53.9 ± 21.4)	0.04–3.1 (0.9 ± 0.4)	0.6–32.2 (7.5 ± 3.7)	0.01–0.5 (0.12 ± 0.06)

2004, Oshima et al. 2010). These are all coastal species with home ranges reported in square kilometers. Because of the linearity of rivers, the spatial use of the water courses for riverine cetacean species has been reported in the literature using linear units (km) (Martin & da Silva 1998, 2004b, McGuire & Henningsen 2007, Denkinger 2010). A kernel analysis (KDE), as implemented in this study, allowed the calculation of the *Inia* home range areas in square kilometers (Table 2).

As already mentioned, home range as a spatial variable of dolphin ecology is determined by habitat heterogeneity, prey distribution, and dolphin foraging strategy; and these can be also influenced by physiological and ecological parameters, including social structure, reproductive status, and territoriality (Scott et al. 1990, Martin & da Silva 1998, Defran et al. 1999, Gubbins 2002, Mesnick & Ralls 2002, Flores & Bazzalo 2004, Martin & da Silva 2004b, Rayment 2009).

Elwen et al. (2006) noted that the relationship between body size and home range in odontocetes seems to break down in interspecies comparisons, and they suggest that ecological features and habitat types were the determining factors for home range size in different populations of dusky dolphins *Lagenorhynchus obscurus*.

Finally, it is important to mention that one of the major limitations of satellite tracking studies is the duration of the tag battery (Wells et al. 2017). In our study, we obtained a mean satellite tracking period of 107 d (±15.7) for 23 individuals. This does not cover a full annual hydrologic cycle. This means that our home range values should be considered a minimum. It also limited inferences about the temporal and ecological determinants affecting home range values. In addition, the heterogeneity in tag transmission times (24 to 336 d) introduced statistical difficulties when comparing the various sampling localities.

Based on our experience, we recommend (1) an increase in the number of tracked individuals for each aquatic system and (2) implementing a recapture procedure to exchange transmitters when the battery charge is low.

4.3. Effect of tagging

No fatal or injurious impacts or negative behavioral effects (such as erratic movements) were recorded among the 23 satellite-tagged individuals. Tag installation procedures followed established and approved recommendations for the SPOT-299A and

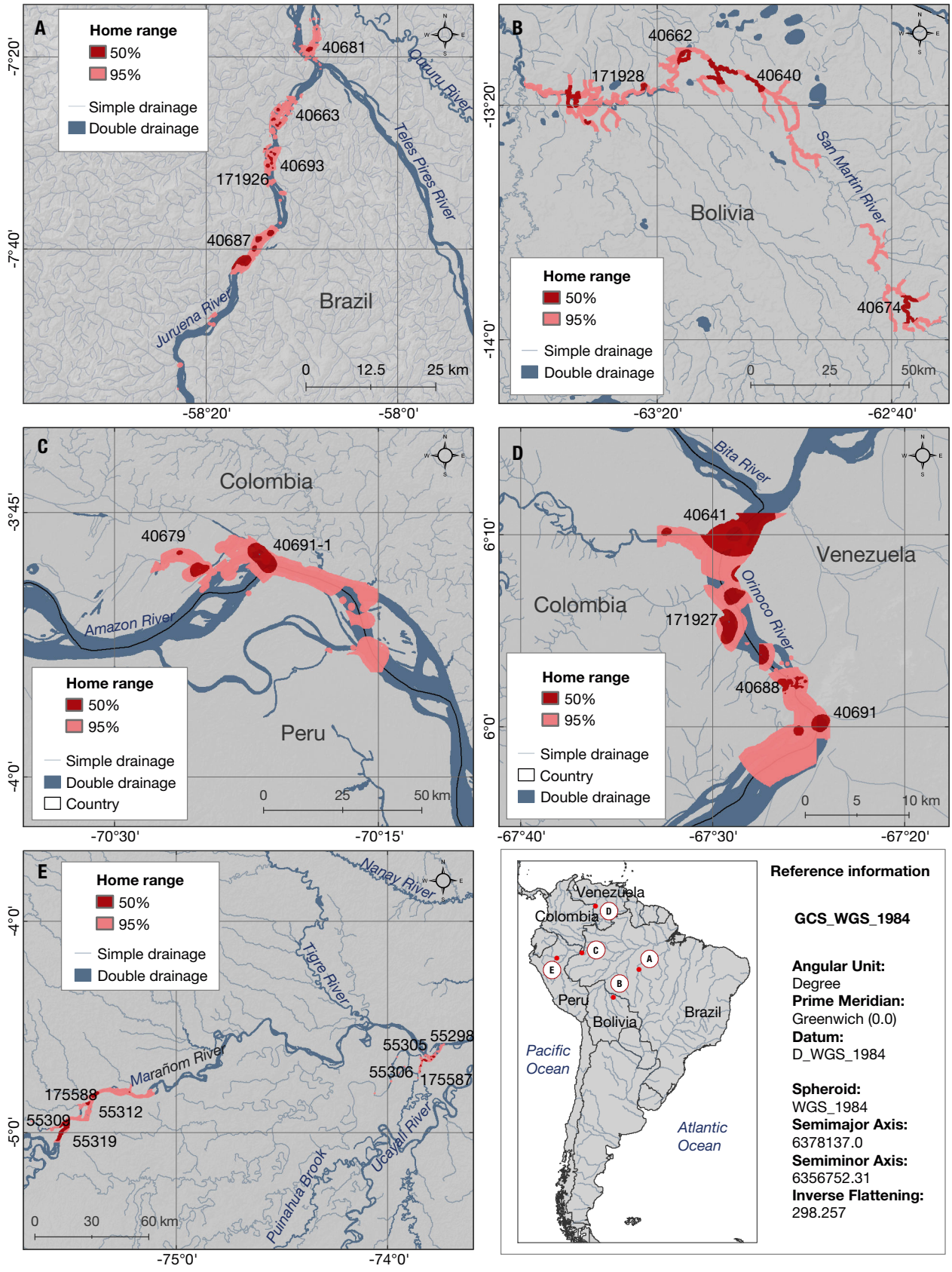

Fig. 2. Overall home range (95%) and core area of activity (50%) estimated using K_{95} and K_{50} utilization distribution (UD), respectively, for the 23 Amazon river dolphins tagged in the Amazon and Orinoco basins. Rivers: (A) Juruena, Brazil, (B) San Martín, Bolivia, (C) Amazon, Colombia, (D) Orinoco, Colombia, and (E) Marañón, Peru

SPOT6-F transmitters, including a single anchor point to the river dolphin's dorsal fin. The selected transmitter was one of the lightest devices on the market (62 g) and was fitted to the dorsal fin with a self-release mechanism. The manufacturer assured us that the transmitter would be released from the dolphin's fin no more than 13 mo after it was fitted in place.

Some individuals were seen by researchers and Colombian fishermen who participated in this study after the tag was released and they reported complete healing of the pierced area. These observations are consistent with those of Martin et al. (2006), who followed 38 radio-tagged dolphins in the Mamirauá Reserve in Brazil for more than 10 yr.

4.4. Implications for conservation

Our results highlight the complexity of dolphin habitat requirements, an aspect that makes these organisms especially vulnerable to basin-scale transformations. The extinction of the baiji *Lipotes vexillifer* in the Yangtze River, China, raises concerns about the potential impacts of large-scale infrastructure projects, as well as fishery bycatch (Reeves et al. 2003, Turvey et al. 2007, Trujillo et al. 2010). Our documentation of movements across the Colombian and Peruvian border (36.2 km) in the Amazon River and between Colombia and Venezuela (51.8 km) in the Orinoco River basin demonstrates the need to initiate transboundary conservation strategies. Range countries of river dolphins in South America that have been analyzed have different regulations in crucial aspects such as: (1) the use of fishing gear; (2) closure periods for fish capture and trade; and (3) conservation strategies for threatened aquatic vertebrates. These differences demand a more coordinated transboundary conservation approach (Trujillo et al. 2010).

Our results also indicate that Amazon river dolphins use a diverse range of aquatic ecosystems in at least 7 protected areas in 4 countries. It is important to mention that *I. geoffrensis* is not currently included as a priority species in any of these protected areas, except for the Parque Departamental, Area Natural de Manejo Integrado (ANMI) Iténez, Bolivia (Trujillo et al. 2010, Mosquera-Guerra et al. 2018).

5. CONCLUSIONS

The design of conservation strategies for Amazon river dolphins should consider the large heterogeneity of ecosystems in the Amazon and the Orinoco river basins and the different use of habitat types by dolphins, including main rivers, confluences, tributaries, and lakes. Reported minimum home ranges are extensive and include the use of protected areas and Ramsar sites. Long-distance transboundary movements were documented between Colombia and Peru in the Amazon, and Colombia and Venezuela in the Orinoco basin. Our results suggest that, to ensure that habitat requirements are met, transboundary management policies should be designed to prioritize the ecological integrity and connectivity of aquatic ecosystems used by river dolphins.

Acknowledgements. This program is part of the strategic plan set by the South American River Dolphin Initiative (SARDI), supported by World Wildlife Fund (WWF) in Brazil, Colombia, Peru, Ecuador, and Bolivia. Partial support for 2 tags in Peru was provided by the Rufford Foundation through RSG. Special gratitude to D. Amorocho, D. Willems, K. Berg, L. Sainz, J. Rivas, J. Surkin, R. Maldonado, D. Ember, V. Tellez, H. Yagui, N. Acuña, P. Colchao, M. Pajuelo, F. Nishio, and M. Wulms from WWF, and D. Parks from the Whitley Fund for Nature (WFN). F.M.G. received a doctoral scholarship from Colciencias (National Doctorate Scholarship 785 to 2017). E.C. received a doctoral scholarship from WWF-EFN. A. Echeverría and A. Salinas are acknowledged for their support during tagging campaigns in Bolivia. We acknowledge the fishing communities and the local and national authorities for participating in the river dolphin capture process.

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Editorial responsibility: Sascha Hooker, St. Andrews, UK
Reviewed by: B. Smith and 1 anonymous referee

Submitted: October 10, 2019
Accepted: May 11, 2021
Proofs received from author(s): July 19, 2021