Marine Mammal Science

Ecological factors influencing group sizes of river dolphins (*Inia geoffrensis* and *Sotalia fluviatilis*)

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ABSTRACT

Living in groups is usually driven by predation and competition for resources. River dolphins do not have natural predators but inhabit dynamic systems with predictable seasonal shifts. These ecological features may provide some insight into the forces driving group formation and help us to answer questions such as why river dolphins have some of the smallest group sizes of cetaceans, and why group sizes vary with time and place. We analyzed observations of group size for *Inia* and *Sotalia* over a 9 yr period. In the Amazon, largest group sizes occurred in main rivers and lakes, particularly during the low water season when resources are concentrated; smaller group sizes occurred in constricted waters (channels, tributaries, and confluences) that receive an influx of blackwaters that are poor in nutrients and sediments. In the Orinoco, the largest group sizes occurred during the transitional water season when the aquatic productivity increases. The largest group size of *Inia* occurred in the Orinoco location that contains the influx of two highly productive whitewater rivers. Flood pulses govern productivity and major biological factors of these river basins. Any threats to flood pulses will likely have an effect on the functionality of these ecosystems and the species living in them.

Key words: pink river dolphin, *Inia geoffrensis*, tucuxi, *Sotalia fluviatilis*, group sizes, Amazon, Orinoco, productivity, seasonality.

Group living likely evolved as a strategy to increase individual fitness by reducing the risk of predation and improving access to resources (Packer *et al*. 1990, Krause and Ruxton 2002, Gowans *et al.* 2007). Group living also has high costs. When group

sizes are larger, competition for resources may increase, and this competition may be further influenced by a combination of seasonal change and other environmental factors (Elgar 1989, Fortin and Fortin 2009). This mixture of costs and benefits may lead to optimal group sizes where the net benefits to group members are maximized (Krause and Ruxton 2002).

Many cetaceans form groups, although the stability varies between species. For instance, baleen whales often live in small, unstable groups (Clapham 2000), while odontocete social structures range from the very stable groups of killer whales (Bigg *et al.* 1990) to the variable group sizes and short-term associations of bottlenose dolphins' fission–fusion societies (Connor *et al.* 2000). Group sizes in cetaceans vary according to risk of predation and the availability of resources (Heithaus and Dill 2002). Typically, smaller group sizes occur close to inshore areas where resources are more predictable and the risk of predation is lower given that there are typically more places to hide; larger group sizes occur in open water where resources are not as predictable and the risk of predation increases (*e.g.*, Norris and Dohl 1979, Shane 1980, Heithaus and Dill 2002, Gygax 2002, Gowans *et al.* 2007). Strong seasonal cycles influence the habitat use of cetaceans and potentially their grouping behavior. For instance, some populations of bottlenose dolphins (*Tursiops* spp.) modify their habitat preferences as a result of seasonal changes in the distribution of resources and the abundance of predators (Shane 1980, Irvine *et al.* 1981, Heithaus and Dill 2002).

While factors affecting group size have been studied in oceanic dolphins (*e.g.*, Gowans *et al.* 2007), there has been less investigation of riverine species, where dolphins exist under very different environmental conditions. The Amazon and Orinoco river basins are very complex and dynamic systems with strong seasonal shifts causing fluctuations of 10–15 m in the water level over the course of a year. These changes affect dissolved oxygen concentration, fish migrations, habitat availability, productivity, and interactions between predators and their prey (Goulding 1980, 1989; Fernandes 1997; Lewis *et al.* 2000). For instance, during the low water season, the quality and quantity of habitat for both fish and dolphins are considerably reduced (with up to 5–10 times less area available during the low water season; Neiff 1996). Hence, flood pulses are a major force controlling biota in riverine floodplains (Junk *et al.* 1989). Consequently, we would expect that the extreme and predictable seasonal changes of the Amazon and Orinoco basins would be major factors influencing the formation of groups in river dolphins.

River dolphins are top predators in these two highly complex and dynamic river basins, and have no natural predators. There are three species of river dolphins in the Amazon and Orinoco river basins: *Inia geoffrensis*, *I. boliviensis*, and *Sotalia fluviatilis.* The pink river dolphin or boto, *I. geoffrensis*, has two subspecies: *I. geoffrensis geoffrensis* in the Amazon (Brazil, Colombia, Ecuador, Peru, and French Guiana) and *I. geoffrensis humboldtiana* in the Orinoco (Colombia and Venezuela). The bugeo, *I. boliviensis*, is distributed in the Amazon and Madeira upper basins (Bolivia) (da Silva 1994; Hamilton *et al.* 2001; Banguera-Hinestroza *et al.* 2002; Ruiz-Garcia *et al.* 2006, 2007, 2008; Ruiz-Garcia 2010) while the tucuxi, *S. fluviatilis*, is distributed in the Amazon (Brazil, Colombia, Ecuador, Peru, and French Guiana; Caballero *et al.* 2007) and in the lower and middle Orinoco basin (Venezuela, Gomez-Salazar *et al.* 2011*a*).

Inia and *Sotalia* have some of the smallest group sizes of cetaceans, ranging from one to eight for *Inia* (*e.g.*, McGuire and Winemiller 1998, Martin *et al.* 2004) and from one to six for *Sotalia* (*e.g.*, Martin *et al.* 2004). There are few studies that have investigated variation in group sizes of river dolphins with flood pulses and
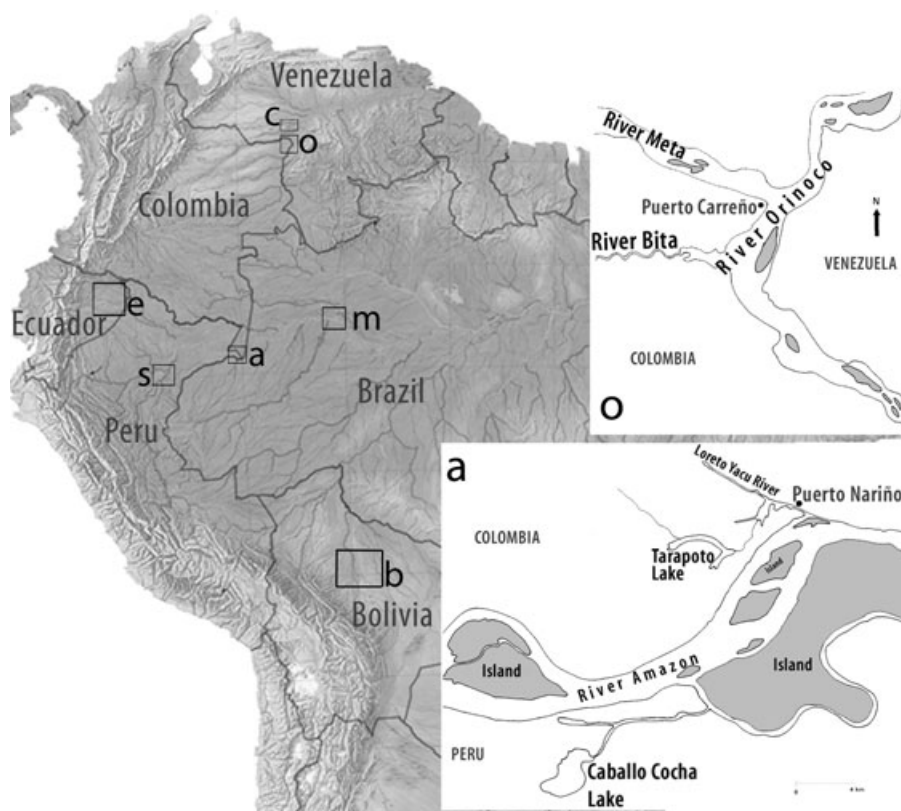
Figure 1. Map of study of study area showing locations where river dolphin research has been conducted. o = Orinoco and Meta rivers (260 km^2, this study), a = Amazon and Loreto Yacu rivers (140 km^2, this study; 170.1 km^2, Vidal *et al*. 1997), c = Cinaruco River (1.67 km^2, McGuire and Winemiller 1998), e = Tiputini, Yasuni, Lagartococha, Cuyabeno, Napo rivers (at least 300 km, Utreras *et al.* 2010), s = Samiria and Marañon rivers (35.6 km^2 and 288 km), b = Mamoré, Tijamuchi, Apere, Yacuma, Rapulo rivers (287 km, McGuire *et al*. 2010), m = Amazon and Japura rivers (220.2 km^2, Martin *et al*. 2004).

habitat type, and there are even fewer studies where sampling effort was included as a weighting factor (McGuire and Aliaga-Rossel 2010) (Fig. 1, Table 1).

Studies in the central Amazon (Brazil) have provided detailed results regarding habitat preferences of *Inia* and *Sotalia* over a period of 2 yr, by describing variation in density (Martin *et al*. 2004), as well as the seasonal movements and sex ratios of *Inia* in different habitat types over a period of 8 yr (Martin and da Silva 2004). Overall, these studies showed that *Inia* and *Sotalia* prefer confluences and areas within 150 m of the shore, and *Inia* adults are separated by sex during most of the year. Mean group sizes and SE were provided for different seasons and habitat type (see Table 1).

Studies in the northern Ecuadorian Amazon have been discontinuous and have been focused on distribution and encounter rates, instead of group sizes

Table 1. Estimates of group sizes of river dolphin populations in different locations of Asia and South America.

Location	Effort	Number of sightings	Mean group size	SD	Reference
Yangtze Rriver dolphin (*Lipotes vexillifer*)					
Yangtze River, China	November 1997–November 1999	18	2.1	0.87	Zhang *et al.* (2003)
Irrawaddy dolphin (*Orcaella brevirostris*)					
Sundarbans Delta, Bangladesh	4–24 March 2002	89	2.3	1.36	Smith *et al.* (2006)
Ganges River dolphin (*Platanista gangetica*)					
Sundarbans Delta, Bangladesh	4–24 March 2002	55	2.45	2.25	Smith *et al.* (2006)
Jamuna River, Bangladesh	22–25 April 1996	25	1.8	1.4	Smith *et al.* (1998)
Kushiyara River, Bangladesh and India	7–11 October 1995	9	3.8	2.8	Smith *et al.* (1998)
Pink river dolphin (*Inia*)					
Amazon River, Colombia	5–26 June 2002	97	2.9		Vidal *et al.* (1997)
Amazon and Japurá Rivers, Brazil	March 1999–April 2001	733	1.42	0.036 (SE)	Martin *et al.* (2004)
Amazon and Japurá Rivers, Brazil	June 1999	92	1.3	0.14 (SE)	
	October 1999		1.6	0.11 (SE)	
	March 2000		1	0 (SE)	
	July 2000		1.4	0.12 (SE)	
	April 2001		1	0 (SE)	
Tefe Lake, Brazil	June 1999	55	1.3	0.16 (SE)	Martin and da Silva (2004)
	October 1999		1.3	0.16 (SE)	
	March 2000		1.1	0.06 (SE)	Martin and da Silva (2004)
	July 2000		1.1	0.14 (SE)	
	April 2001		1.3	0.22 (SE)	

Location	Date	Sample size			Reference
Cinaruco River, Venezuela	November 1993–June 1994	489	2	1	McGuire and Winemiller (1998)
Amazon River, Colombia	December 1993–July 2005	4,419	3.4	3.1	This study.
Orinoco River, Colombia, Venezuela	July 1996–August 2003	1,725	5.3	4.5	This study.
Mamoré and Tijamuchi Rivers, Bolivia[a]	January 1998–September 1999	920[a]			Aliaga-Rossel (2002).
Rivers:			Rivers:		
Mamoré, Tijamuchi, Apere, Yacuma, Rapulo (Bolivia)	August–September 1998	492	2.1 3.3 2.3 1.8 2	1.34 2.96 0.98 0.75 0.81	Aliaga-Rossel et al. (2006)
Tucuxi (*Sotalia fluviatilis*)					
Amazon River, Colombia	5–26 June 2003	72	3.9		Vidal et al. (1997)
Amazon and Japura Rivers, Brazil	March 1999 – April 2001	504	2.24	0.065 (SE)	Martin et al. (2004)
Amazon River, Colombia	December 1993–July 2005	4,062	3.6	2.6	This study.

[a]Mean and SD were not reported.

(Utreras 1996, Utreras *et al*. 2010). Studies in the Peruvian Amazon (Pacaya-Samiria Natural Reserve) over a period of 9 yr focused mostly on encounter rates, habitat preferences, residence, density, and abundance estimates of *Inia* and *Sotalia* (*e.g.*, McGuire and Aliaga-Rosell 2010). Mean group sizes did not seem to vary according to season or habitat type (McGuire and Aliaga-Rosell 2010).

In the Orinoco basin, studies of the group sizes, distribution, habitat preferences, prey availability, and population structure of *Inia* dolphins were conducted in the Cinaruco River over a period of 8 mo (McGuire and Winemiller 1998). The largest group sizes were found in confluences during the rising water period; however, surveys were not conducted during the high water period.

Studies in the Bolivian Amazon over a period of 20 mo, focused on the distribution, abundance, encounter rates, and group sizes of *Inia* dolphins (Aliaga-Rossel 2002). These studies showed significant relationships between the distribution of group sizes and the habitat type and season (Aliaga-Rossel 2002); however, mean group sizes and SD were not provided. In a later study, conducted over a period of 2 mo, mean group sizes and SD were reported, which seemed to vary according to resource availability (Aliaga-Rossel *et al.* 2006). For instance, rivers with an influx of whitewaters in central Bolivia, which are rich in nutrients and prey, are believed to support large groups of *Inia* dolphins, while rivers with large human settlements and high boat traffic, which may disrupt the social structure of river dolphins, have smaller group sizes (Aliaga-Rossel *et al*. 2006).

Previous research on river dolphins has focused mainly on density estimates, encounter rates, residence patterns, and sighting frequency, (mostly of *Inia*), rather than variation in group sizes and the ecological factors influencing them. We examined group size for *Inia* and *Sotalia* in two locations within the Colombian Amazon and Orinoco river basins to determine how seasonal and environmental variation affects these species. We predicted that group sizes would change according to temporal and spatial factors, with bigger groups during the dry season when resources are concentrated and easily accessed, and in habitats that offer more availability of resources. Since areas close to riverbanks, as well as areas with aquatic macrophytes are highly important for many fish species, providing nursing areas, resources, and refuge from some predators (Henderson 1990, Winemiller and Jepsen 1998), and river dolphin densities are higher in areas closer to the riverbanks (Martin *et al*. 2004), we would also expect some variation in the group sizes of dolphins in relation to distance from shore and shore type.

METHODS

Field Surveys

Vessel-based surveys for river dolphins were conducted in two locations of the Colombian Amazon and Orinoco river basins from a 6 m boat with an outboard 25 hp engine and at an observation height of about 2 m (Fig. 1). The Amazon basin study area is located in the southern part of Colombia, and it comprises a section of about 60 linear km (approximately 140 km^2) including the Loretoyacu River, a small tributary of the Amazon River that leads to El Correo and Tarapoto Lakes, a section of the Amazon River that leads to Lake Caballo Cocha along the frontier with Peru, and another section that leads to the Atacuari River, another small tributary of the Amazon River (Fig. 1). The Amazon basin surveys were conducted

between December 1993 and July 2005. The Orinoco basin study area is located in the northeast of Colombia, and it comprises a section of about 120 linear km (approximately 260 km^2), including the Orinoco River that leads to sections of two tributaries: the Meta River in the north and the Bita River in the south (Fig. 1). Surveys of the Orinoco basin were conducted between July 1996 and August 2003. *Inia geoffrensis* occurs at both locations and *S. fluviatilis* only in the Amazon. Previous research conducted 13 yr ago in the Amazon study area estimated a population size of 346 *Inia* (CV = 0.12) and 409 *Sotalia* (CV = 0.13; Vidal *et al*. 1997). There are no estimates of *Inia* population sizes in the Orinoco, nor over their entire distribution.

Surveys followed standardized routes parallel to the riverbanks, maintaining a constant speed of 10 km/h (Table 2). Estimating group size is often difficult, so we conducted "closing mode" surveys in order to estimate the group size accurately (see Zerbini *et al*. 2007). When dolphins were encountered, we recorded species, location (using a Geographic Positioning System), group size, group composition, habitat type, shore type, and distance from shore. A group of river dolphins was defined as a set of animals that are seen together within 250 m from the boat, likely engaged in the same activities, and does not necessarily correspond to a social group (see McGuire and Winemiller 1998).

Although the dark-colored waters and the shy behavior of river dolphins make it hard to track and photograph individuals within groups, the typically small group sizes and short dives (which do not last more than 2 min) allowed us to obtain group sizes accurately within the 250 m range. This range was established given that individuals within groups of *Inia* are at most a maximum distance of 50 m from each other and individuals within groups of *Sotalia* are at most a maximum distance of 30 m. This is smaller than the 250 m used to define group membership. Therefore, it is unlikely that we are under representing *Inia* and *Sotalia* group sizes by much. Group composition was recorded as the number of adults/juveniles and calves. Calves were defined as animals <1 yr old, <1 m long, and generally dark gray. Calves are not included in further analyses. Several characteristics of the river course were used to identify six general habitat types: main river, tributary, channel, island, confluence, and lake (Table 3); and eight shore types (Table 4).

The distance of the group to the nearest shore of the river was calculated and classified into three categories: 0–50 m, 50–100 m, and ≥100 m. The distance from the boat to the dolphins, and from the group to the nearest shore, was estimated by eye, often validated using floating objects nearby whose range was determined with a laser range finder. Once group data were recorded, we resumed the survey effort immediately to avoid double counts of the same group of dolphins in each survey.

Four hydroclimatic seasons were identified for each year in the study area, according to the precipitation and water levels obtained from the environmental information system in Colombia (IDEAM; Fig. 2).

Data Analysis

Statistical analyses were conducted using Systat 12. When variables did not meet assumptions of parametric tests (Lilliefors test, $P < 0.05$; Levene's test, $P < 0.05$), nonparametric tests were used. Group size was examined according to habitat type, seasonality, shore type, and distance from shore. Mann–Whitney (MW) tests were

Table 2. Number of group sightings for each species by year and month. Blanks indicate no effort in that month and year.

Basin/ species/year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Amazon													
Inia	395	181	347	302	322	412	594	281	261	258	340	726	4,419
1990												402	402
1991	8		122	60		70	164						424
1993												23	23
1994	75		6			33	67	10			52	50	293
1996				16	99	70	75	34	83	62	62	67	568
1997	130	31	37				15	25				60	298
1998			18	64	49	48	57	98	79	66	91	41	611
1999	24	55	35	29	27	47	8	10			6	22	263
2000	54		57	19			3						133
2001	17	23	20	27	42	28	23		3	30	37	9	259
2002	21					15	13	19	6	12			86
2003	2	29	42	6	32	20	55	26	26	25	2	24	289
2004	19	43	10	81	66	81	85	59	64	63	90	28	689
2005	45				7		29						81
Sotalia	376	168	407	289	322	411	476	264	213	247	309	580	4,062
1990												339	339
1991	13		167	72		106	131						489
1993												22	22
1994	80		4			14	37	10			23	37	205
1996				17	146	67	52	27	30	35	42	33	449
1997	91	2	15				20	12				44	184
1998			9	60	33	30	48	56	43	42	77	31	429
1999	28	57	50	27	7	31	5	12			5	11	233
2000	49		73	21			1		14	47	27	9	241
2001	18	33	31	25	36	30	25	26	31	17	55	12	339
2002	34					13	22	65	32	43			209
2003	1	34	46	13	29	23	32	20	27	24	10	22	281
2004	17	42	12	54	61	97	74	36	36	39	70	20	558
2005	45				10		29						84
Orinoco													
Inia	107	86	168	108	118	117	188	176	197	185	172	103	1,725
1996							33	84	70	69	56	50	362
1997	28	30	19					46	57	77	99	53	409
1998	68	31	56	15	46	30	57						303
1999		12	58	56	13								139
2000									51				51
2001		5	15	10	20	30	36	11	19	39	17		202
2003	11	8	20	27	39	57	62	35					259
Total	878	435	922	699	762	940	1,258	721	671	690	821	1,409	10,206

used to evaluate whether group sizes of *Inia* differed according to the location, and whether the group sizes of *Inia* and *Sotalia* in the Amazon differed. Kruskal–Wallis (KW) tests were used to evaluate whether there were differences in the group sizes of dolphins according to the habitat type, shore type, or distance from the shore.

Table 3. Definitions of habitat types.

Habitat type	Definition	Locations surveyed
Main river	Whitewater rivers of Andean and Guyanese shield origin, typically turbid, brown-yellow in color with low transparency, basic pH, and sediment-rich (Sioli 1984). At least 400 m in width.	River Amazon, Orinoco, Meta.
Confluences	Intersection areas of the main channel with other channels or rivers. Confluences maintain connections during all hydrologic seasons and may or may not present a mix of white and blackwaters. Approximately 250 m width.	Confluence between the Amazon and Loretoyacu rivers.
Tributaries	Small and medium size rivers no more than 400 m in width. Water in tributaries is usually black and clear, originate from the flooded forest plains, with few suspended sediments and relatively acidic, high in tannins and particulate organic matter (Sioli 1984).	Loretoyacu and Bita Rivers.
Channels	Watercourses no more than 300 m wide and generally associated with island and main river systems. Navigability is limited depending on rainy seasons.	Channels from the river Amazon to the lake Caballo Cocha, between the El Correo and Tarapoto lakes.
Islands	Waters around land bodies in the watercourse of main rivers with vegetation that may appear or disappear due to hydrologic dynamics.	El Pañuelo, Chimborazo, Ventanas, Bugeo, Cacao, Mocagua, Patrullero, San Salvador, and Vamos Islands.

Table 4. Definition of shore types.

| Type of shore	Characteristics
Forest	Dense vegetation, mainly represented by high trees (>6 m).
Shrubs	Low vegetation (<6 m), usually in continuous patches along the shore, occasionally bordering the forest.
Flooded vegetation	Forest and shrubs swamped during the high water season.
Grass	Grass covering the shore.
Floating meadows	Floating vegetation mainly represented by aquatic plants (*i.e.*, *Eichornia* sp., *Paspallum* sp., *Pistia* sp.).
Steep bank	Shore is a steep bank usually with low, or without, vegetation.
Beach	Sand or mud banks on the main shore or islands, including those in the middle of water bodies.
Rocks	Large rocks on the shore. Occasionally related to rapids.
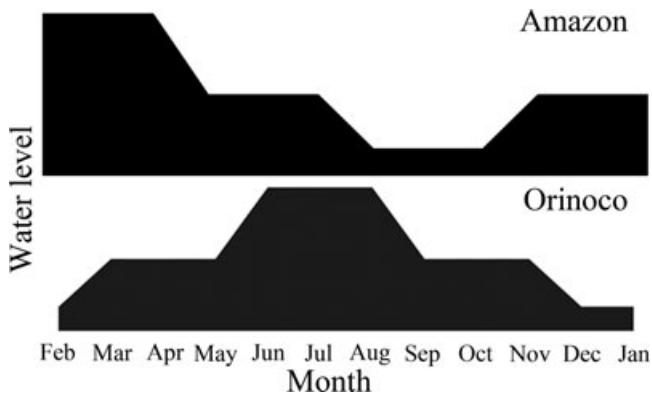
Figure 2. Seasons (high, low, and transitional water periods) in the Amazon and Orinoco locations. Data were provided by the local government hydroclimatic station (IDEAM).

RESULTS

Group sizes for *Inia* were larger in the Orinoco (range = 1–30, mean = 5.3, SD = 4.5) compared to the Amazon (range = 1–37, mean = 3.0, SD = 2.9; MW, $P < 0.05$, df = 1). In the Amazon, group sizes of *Sotalia* (range = 1–27, mean = 3.4, SD = 2.5) were larger than *Inia* (MW, $P < 0.05$, df = 1). When considering habitat types, group sizes in the Amazon for *Inia* were the largest in the island habitat (range = 1–18, mean = 3.7, SD = 2.9), lake (range = 1–37, mean = 3.2, SD = 3.4), and main river (range = 1–17, mean = 3.0, SD = 2.3; KW test, $P < 0.05$, df = 5). Similarly, the largest group sizes for *Sotalia* were found in the habitat types of main river (range = 1–23, mean = 3.6, SD = 2.4), lake (range = 1–27, mean = 3.5, SD = 2.9), and island (range = 1–19, mean = 3.5, SD = 2.5; KW test, $P < 0.05$, df = 5). In the Orinoco, larger mean group sizes of *Inia* were seen in the main river habitat (range = 1–30, mean = 5.5, SD = 4.7; KW test, $P < 0.05$, df = 2).

When considering seasonality (Fig. 3), the largest mean group sizes in the Amazon were observed in the lake habitat type during the low water season for *Inia* (range = 1–30, mean = 4.5, SD = 4.5) and *Sotalia* (range = 1–27, mean = 5.8, SD = 5.3). In the Orinoco, larger group sizes were found in the tributary habitat during the rising water season (range = 1–19, mean = 7, SD = 4.6), and smaller group sizes in the same habitat during the falling water season (range = 1–12, mean = 3.2, SD = 2.5).

Group sizes of *Inia* varied according to the shore type (Fig. 4). In the Amazon, the largest group sizes were found off beaches (range = 1–37, mean = 4.3, SD = 4.9) and steep banks (range = 1–30, mean = 4.1, SD = 3.5; Amazon, KW test, $P < 0.05$, df = 7). In the Orinoco, largest group sizes of *Inia* were also found off beaches (range = 1–24, mean = 5.4, SD = 4.5), floating meadows (range = 1–26, mean = 5.2, SD = 4.3), and forest (range = 1–22, mean = 5.0, SD = 4.3; KW tests, $P < 0.05$, df = 7). Group sizes of *Sotalia* did not change significantly according to the shore type (KW test, $P > 0.05$, df = 7). For neither *Inia* nor *Sotalia* were there significant differences in group size with distance from the shore (KW test, $P > 0.05$, df = 2). However, most group sightings were recorded within 50 m from the shore (40% for *Inia* in the Orinoco, 60% for *Sotalia*, and 66% for *Inia* in the Amazon).
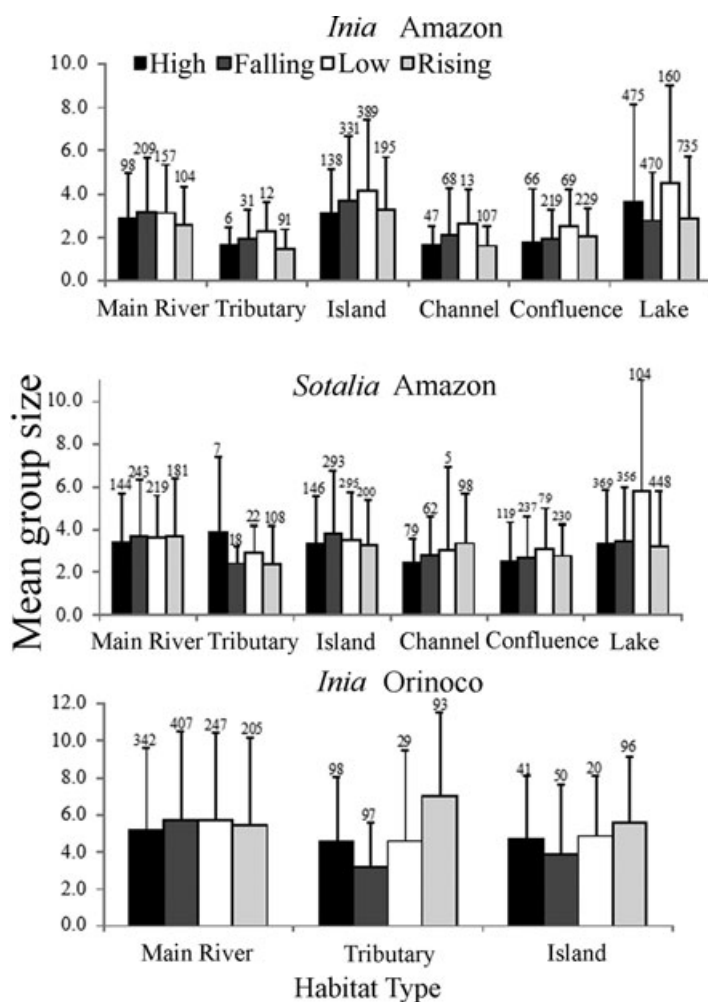
Figure 3. Mean group size (SD) by season and habitat type. Number of sightings is given above error bars.

DISCUSSION

Group sizes of river dolphins are often small, with two individuals being the most common group composition (Table 1). River dolphins have no natural predators. This lack of predation threat may partially explain why these dolphins have some of the smallest group sizes of cetaceans. Thus, for river dolphins, the distribution of resources and habitat availability are likely more important in determining group size (Smith and Reeves 2000). Given this pattern, group sizes of river dolphins were investigated in relation to environmental variables, such as seasonality and habitat type. The largest group sizes in the Amazon were found in lakes during low water season and in the Orinoco in the tributary during the rising water season. Group sizes for *Inia* were larger in the Orinoco compared to the Amazon, and group sizes
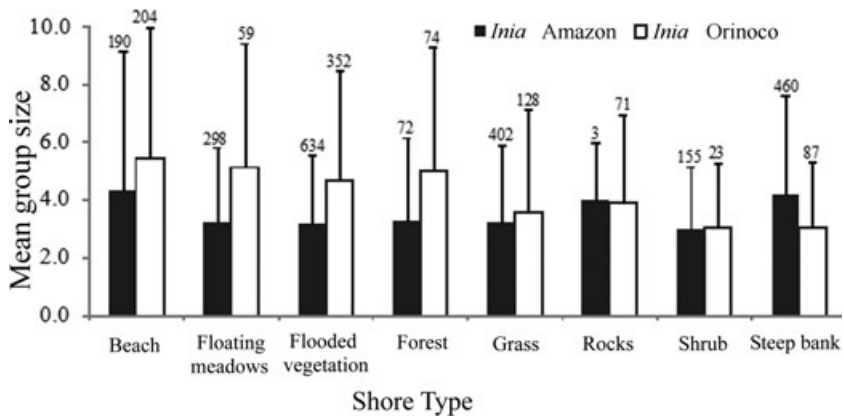
Figure 4. Mean group size (SD) by shore type. Number of sightings is given above error bars.

of *Sotalia* were larger than *Inia*. The largest group sizes were found off beaches and steep banks for *Inia* in the Amazon, and off beaches, floating meadows, and forest for *Inia* in the Orinoco. Group sizes did not change significantly as a function of shore type for *Sotalia*.

Environmental and Seasonal Variation

Group sizes of river dolphins, although typically small, can be large in habitat types with a high density of resources. The largest group sizes of river dolphins in the Amazon were found near islands, lakes, and main rivers. Fish availability is thought to drive movements of river dolphins between habitat types (Martin and da Silva 2004), and fish species concentrate in lakes, around islands, and close to the riverbanks in main rivers and tributaries, looking for resources and refuge provided by vegetation and slow currents (Goulding 1980). In the Orinoco, the largest mean group sizes were found in the main river (lakes were not surveyed in the Orinoco). Main rivers in both locations are highly productive whitewater rivers, which are very rich in nutrients and prey. Thus, productivity and availability of resources influence group sizes of river dolphins. Habitat quality also influences group sizes in carnivores (MacDonald 1983), and antelopes (*Ourebia ourebi*), which seem to form small group sizes in poor quality habitats (Arcese *et al*. 1995), as well as elephants (*Loxodonta africana*) in savanna habitats where smaller groups form in poor quality habitats, and larger groups form when water and food availability increase (Leuthold 1976, Moss 1988).

The most striking differences in group sizes of river dolphins were found when examining the interaction between annual seasonal changes and habitat type. The total aquatic productivity in the Amazon and Orinoco basins is strongly affected by extreme seasonal changes. During the rising and high water seasons, areas of the main channel covering about 7,000 km^2 in the Orinoco and 170,000 km^2 in the Amazon basins are inundated with water, which forms the floodplains (Hamilton and Lewis 1990), and the aquatic productivity increases (Barthem and Goulding 1997, Lewis *et al*. 2000). Freshwater floods dictate the seasonal movement of fish migrating from rivers into floodplains and forests to feed and reproduce (Henderson 1990, Barthem and Goulding 1997, Fernandes 1997). During the low water season, the water from

the floodplains drains into rivers; resources in rivers are therefore concentrated and easily accessed by predators, which may facilitate foraging and reduce competition between group members (Best and da Silva 1989, Hamilton and Lewis 1990, Junk *et al*. 2007). By the end of the low water season, the number of accessible aquatic habitat types is limited, and the fish populations are reduced due to predation, stranding, and depletion of dissolved oxygen (Goulding 1980, Goulding *et al*. 1996, Petermann 1997). Hence, we expect group sizes of dolphins to be largest when resources are concentrated and smallest when resources are dispersed.

Amazon

In the Amazon, as predicted, larger groups were found during the dry season when resources are concentrated and easily accessed. Similarly, larger group sizes of *Inia* dolphins in the Bolivian Amazon occurred during the falling and low water season, and groups were smallest during high water season (Aliaga-Rossel 2002). Group sizes were largest in lakes during the low water season. Lakes in this river basin are highly productive systems that offer a significant source of organic material supporting different trophic levels (Rai and Hill 1980). Previous studies show that Amazonian lakes have higher primary productivity compared to the Amazon River (Schmidt 1973, Fisher and Parsley 1979). This is due to many factors, including: (1) whitewaters from adjacent rivers, which are very high in nutrients, and penetrate lakes during the rising and high water season; (2) when the water level descends, the amount of light increases given the less-turbulent conditions, the phytoplankton and zooplankton increase, and there is nutrient regeneration, which is translated into higher primary productivity (Schmidt 1973, Fisher and Parsley 1979, Lewis *et al*. 2000). For example, the highest diversity of phytoplankton and concentration of nutrients in lakes occurs during the low water season according to a study conducted in an Amazonian lake in Brazil, also influenced by a whitewater river, the Solimões (Rodrigues-Ibañez 1997). Thus, lakes are providing refuge and resources for many fish species, which in turn provides optimal conditions to support large group sizes of dolphins. Similarly, the largest group sizes of *Inia* in the Bolivian Amazon were recorded in lakes, which have a greater biodiversity and abundance of fish than the main rivers (Aliaga-Rossel 2002).

Large group sizes of *Inia* were also recorded beside islands during the low water season. Riverine areas beside islands are characterized by low current speeds and high availability of resources, attracting a high biomass of fish, aquatic birds, turtles, and caimans that use the beaches for nesting (Petermann 1997, McGuire and Winemiller 1998, Correa 2008). For comparison purposes, the highest biotic complexity of plant species in the Parana River Basin is usually found on islands, where the water from the main river easily reaches the soil during the transitional and high water season (Casco *et al*. 2005).

Thus, as expected, large group sizes of river dolphins in the Amazon basin were found in habitats with high concentrations of resources and during the low water season when resources are concentrated and easily accessed.

In contrast, group sizes in channels, tributaries, and confluence waters were smaller and remained similar throughout the year. These areas are narrow in width with limited water depth and, therefore, may be used mainly for transit from lakes to rivers. Also, channels and tributaries mainly receive an influx of blackwaters, which are poorer in nutrients and sediments, and the influx of whitewaters occurs only during the rising and high water seasons.

Contrary to our results, large group sizes of *Inia* have been noted in confluences, which are considered habitats of high productivity that offer refuge, allow migrations of fish, and appear to be preferred habitat for river dolphins (*e.g.*, McGuire and Winemiller 1998, Aliaga-Rossel 2002, Martin *et al*. 2004). We suggest that the ecological importance of confluences depends on the resources that are contained within the rivers that form them, not just the presence of confluences.

Orinoco

Contrary to our predictions, larger groups were found in the transitional water season, and not during the dry season when resources are concentrated and easily accessed. Interestingly, other studies performed in close proximity to our location (Cinaruco River, Fig. 1) also found larger group sizes during the transitional water season (McGuire and Winemiller 1998, Fig. 1) when the aquatic productivity increases (Lewis *et al.* 2000).

Group sizes of *Inia* were the largest in the Orinoco and did not change as dynamically as in the Amazon. In fact, the largest mean group size of *Inia* dolphins ever recorded occurred during the rising water season in the tributary habitat (mean = 7, SD = 4.6). Whether this pattern is related to differences in the availability of resources is of interest. In terms of resources, both the Amazon and Orinoco locations are under the influence of highly productive whitewater rivers, but the Orinoco receives additional nutrients from the Andean mountains transported via the whitewater Meta River. As a comparison, larger group sizes of *Inia* in the Bolivian Amazon were also recorded in areas with an influx of whitewater rivers, while smaller group sizes were found in blackwater rivers (Aliaga-Rossel *et al.* 2006). Hence, the presence of two whitewater rivers in the Orinoco (*vs*. one in the Amazon) may increase the availability of nutrients in this location, which ultimately may increase the primary productivity and potentially the availability of resources.

Variation between Species

In the Amazon, variation in group sizes across seasons was greater for *Inia* than *Sotalia*. This could reflect the unique ability of *Inia* to actively search for food in restrictive aquatic habitats. *Sotalia* do not have the same morphological adaptations as *Inia* (*e.g*., flexible bodies, small dorsal fins, and large pectoral fins), making them unable to exploit the flooded forest and restricting them to habitats with significant water depth to avoid stranding (Martin and da Silva 2004). Thus, large group sizes of *Inia* in lakes during the high water season and near islands during the low water season may be related to the high productivity of these systems, but mostly, to the ability of *Inia* to exploit flooded areas alongside lakes when resources are dispersed within very shallow water depths. Similarly, group sizes changed more with shore type for *Inia* than for *Sotalia*. Different shore types may not play a role in group sizes of *Sotalia* because they prefer areas that are more open with higher water flow (Martin and da Silva 2004, Martin *et al*. 2004).

Broader Implications for River Dolphin Conservation

River dolphins inhabit large areas of the Amazon and Orinoco basins (6,869,000 km^2 and 953,598 km^2, respectively; Revenga *et al*. 1998, Goulding

et al. 2003); however, most of the research focused on the ecology of these species has been conducted in less than 1% of this range (Fig. 1). Due to the large size of the basin regions, it is unlikely that future surveys will be able to include the entire distribution. However, since environmental variables in this region have similar and predictable interannual patterns, our results could be useful in predicting the grouping behavior of river dolphins over the larger area. First, we expect some differences according to characteristics of each river basin. For instance, group sizes of river dolphins in the Amazon basin increase during the low water season when resources are concentrated, and in the Orinoco group sizes increase during the transitional water period when productivity is enhanced (see also McGuire and Winemiller 1998, Aliaga-Rossel 2002, Aliaga-Rossel *et al.* 2006). Second, we expect differences according to local productivity and habitat availability. For example, based on this study, we suggest that the ecological importance of confluences will depend on the local influx of resources and nutrients, rather than just the presence of the confluences. Third, in addition to ecological features, there are other aspects such as social structure, which influence group living. For example, male and female *Inia* have different habitat preferences (at least in central Brazil), with females and calves entering the flooded areas to look for resources and safety from male harassment (Martin and da Silva 2004). This temporal sex separation has been reported in sperm whales at sea as well as baleen whales, but not in other dolphin species (Martin and da Silva 2004). We are not aware of any social structure studies regarding *Sotalia* dolphins in freshwater systems.

The results of this study can lend insight into a number of ecological features driving the formation of groups in river dolphins, as well as direct the focus of further research and influence management actions. For instance, local communities and organizations are enhancing tourism based on dolphin watching in the Amazon and Orinoco locations that we studied. Although whale/dolphin watching has become a very valuable activity in many communities (Hoyt 2001), it may cause serious long-term problems for populations if it is not well regulated (Bejder *et al*. 1999, Reeves *et al*. 2003). Our results may provide some guidance for identifying areas of high conservation importance for river dolphins. River margins, confluences, and lakes are areas of high densities of river dolphins (Martin and da Silva 2004, Martin *et al*. 2004), and which have been proposed as critical habitats for river dolphins (Gomez-Salazar *et al*. 2011*b*). River margins and lakes also have the largest mean group sizes of river dolphins, and thus are preferred for dolphin watching. The critical habitats of river dolphins are primary targets for dolphin-watching activities and we know of no plans to regulate tourism in these areas.

Flood pulses are essential for maintaining productivity, and seem to be major factors governing the dolphins' behavior. If these are altered, there may be serious impacts on productivity, and other biological features such as group sizes of dolphins. Potential threats that destroy or greatly affect the flood pulses include the construction of dams and waterways, deforestation, and climate change. Each location has a different environmental dynamic, and for this reason conservation actions should be considered at local as well as basin-wide scales.

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