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River dolphins (*Inia geoffrensis* and *Sotalia fluviatilis*) in the Peruvian Amazon: habitat preferences and feeding behavior

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Abstract

To estimate river dolphin habitat preference through density, as well as which habitats were preferred for feeding in the Pacaya-Samiria National Reserve, surveys were conducted during the high- to low-water season transition, from 2016 to 2018, in the channels, lakes, and confluences of the Samiria River. Both the Amazon river dolphin and tucuxi dolphin showed a preference for the confluences. The wide channel (Amazon: 24.8 dolphins/km^2, tucuxi: 7.6 dolphins/km^2) and narrow channel (Amazon: 73.0 dolphins/km^2; tucuxi: 6.0 dolphins/km^2) also had high dolphin densities, especially for the Amazon river dolphins. In contrast with previous studies, the lakes had the lowest densities of dolphins for both species. High proportions of feeding behavior were observed in the confluence and wide channel habitats. The potentially larger presence of fish in these two habitats is likely the primary reason for the high dolphin densities. The high dolphin densities in the narrow channel, on the other hand, were associated with a low proportion of feeding behavior. Therefore, there are likely separate environmental factors attracting the dolphins, although additional data will be required to determine these factors. The results of this study will continue to help identify potential conservation and management actions by contributing to a better understanding of the ecology of river dolphins and their dependence on various habitats in one of the world's largest protected flooded forests.

Keywords:
Amazon river basin, density, habitat use, Pacaya-Samiria National Reserve, Amazon river dolphin, tucuxi

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Introduction

The Pacaya-Samiria National Reserve (hereafter Pacaya-Samiria) in the Peruvian Amazon is one of the largest areas of protected flooded forest in the world. It is characterized by high diversity and subject to extreme seasonal changes, creating variations in the quantity and quality of habitats (McGuire and Winemiller, 1998; McGuire and Aliaga-Rossel, 2007). Access to tributaries such as the Samiria River is seasonally dependent, as water levels recede during the transition from high- to low-water season (Gomez-Salazar *et al.*, 2012a). Moreover, the shallow channels/streams and the flooded forests of the Samiria River dry up before the tributaries. The seasonal changes in river water level cause seasonal fish migrations where the fish aggregate in main rivers in the low-water season and disperse throughout the flooded habitats in the high-water season (McGuire and Winemiller, 1998; Martin and da Silva, 2004). These movements of fish also change the distribution of their predators such as river dolphins (Martin and da Silva, 2004; Martin *et al.*, 2004; McGuire and Aliaga-Rossel, 2007; Reeves and Martin, 2009).

The Pacaya-Samiria freshwater protected area is comanaged with indigenous communities to ensure the sustainability of subsistence fishing and hunting (Bodmer *et al.*, 2017). It is also sheltered from many disturbances that the Amazon rainforest and the riverine ecosystem are facing such as deforestation, the construction of dams, water pollution, and overfishing/overhunting (Vidal, 1993; Vidal *et al*., 1997; Williams *et al*., 2016; Cartró-Sabaté *et al*., 2019). Within the Amazon, giant river otters and Amazonian manatees were decimated in the past by hunting (Recharte and Bodmer, 2009). River dolphins are generally not hunted but are impacted throughout the Amazon by droughts, bycatch, and oil spills (Gomez-Salazar *et al*., 2012a; Bodmer *et al*., 2017; Campbell *et al*., 2020). Oil extraction has been in operation within the bounds of the Pacaya-Samiria by various companies for over half a century (Yusta-García *et al*., 2017). Oil spills, which can cause numerous health problems in cetaceans (Godard-Codding and Collier, 2018), have been reported in the Pacaya-Samiria region, and new oil development projects have been planned in or near wetlands and the seasonally flooded forest of Pacaya-Samiria (Fraser, 2015; 2016). Nevertheless, relative to other areas in the Amazon River basin, Pacaya-Samiria can still be considered a refuge from many anthropogenic threats as there is low habitat modification, low species exploitation, smaller human population size, and low ecosystem degradation (Gomez-Salazar *et al*., 2012b). However, climate change is an additional factor that may still be of concern.

Over the past 20 years, there has been an increasing number of extreme flood and drought years impacting the ecosystem and human settlements (Bodmer *et al*., 2017; Barichivich *et al*., 2018). High flood years reduce available habitats for terrestrial biodiversity, while drought years disturb the local populations of aquatic animals such as river dolphins (Bodmer *et al*., 2017). The aquatic nature of these species makes them susceptible to dry-outs of rivers, lakes, and channels when droughts occur, and recent intensification of these phenomena has been linked to climate change occurring in the Amazon (Duffy *et al*., 2015). There is, however, a particularly notable increase in the number of flood years (Barichivich *et al*., 2018) leading to an increase in fish populations, which is beneficial to their predators such as river dolphins (Bodmer *et al*., 2017).

Local human populations within the Pacaya-Samiria have also adapted to these frequent flood years by profiting from the high fish stocks (Bodmer *et al*., 2017). However, with rapid changes between flood and drought years this could lead to unsustainable hunting and fishing as the environmental events affect aquatic and terrestrial species differently (Bodmer *et al*., 2017). Extreme flood years have reduced wild meat population sizes and subsequently indigenous Cocama communities have relied on fish for their sustenance (Bodmer *et al*., 2020). The drought years negatively impact the aquatic species. Following the 2010 drought, within the Pacaya-Samiria, river dolphin numbers rebounded only after multiple years of high flood levels (Bodmer *et al*., 2017).

As top predators, river dolphins are considered aquatic indicator species, in that they may be used as an indicator of ecosystem degradation and are useful proxies to monitor current or future changes in the river systems (Gomez-Salazar *et al*., 2012a; Bodmer *et al*., 2017), particularly in the context of climate change. Understanding the ecology of these animals and their dependence on various habitats is useful to identifying conservation and management actions (Martin and da Silva, 2004; Gomez-Salazar *et al*., 2012a, b). Additionally, identifying hydrological changes in response to climate change is important in assessing the dolphin population's vulnerability if these habitats change or disappear (Mosquera-Guerra *et al*., 2020).

Well-managed Freshwater Protected Areas, such as the Pacaya-Samiria, have high dolphin densities and the reserve is therefore considered an important conservation area for dolphin populations in the Amazon Basin (Gomez *et al*., 2012b). The Pacaya-Samiria is inhabited by two sympatric cetaceans, the Amazon river dolphin (*Inia geoffrensis*) and the tucuxi dolphin (*Sotalia fluviatilis*). Both species are classified as Endangered by the International Union for Conservation of Nature (IUCN), with a decreasing population trend (da Silva *et al*., 2018; 2020).

The Amazon river dolphin and the tucuxi dolphin can be found throughout various riverine habitats within the Amazon Basin. There are some emerging patterns in habitat preference for the two dolphin species. There appears to be agreement that both species prefer calmer waters, and areas of slower downstream current, due to disturbances such as confluences, floating vegetation, and meeting of waters (Martin *et al*., 2004; Gomez-Salazar *et al*., 2012b). Confluences are the often-turbulent junction of two streams of water, sometimes from two different rivers (Vidal *et al*., 1997; Martin *et al*., 2004; Gomez-Salazar *et al*., 2012b). Confluences are dolphin hotspots, having consistently been reported to contain high dolphin numbers (Martin *et al*., 2004; Gomez-Salazar *et al*., 2012b; Pavanato *et al*., 2019). It is hypothesized that this lower current habitat type is preferred due to the smaller energy requirements to remain in it, or due to fish abundance (Martin *et al*., 2004). Confluences likely have higher fish densities (McGuire and Winemiller, 1998), due to their high productivity and provision of shelter (Martin *et al*., 2004; Pavanato *et al*., 2019). In Colombia, lakes also appeared to have high densities of both dolphin species (Vidal *et al*., 1997; Gomez-Salazar *et al*., 2012*b*). Specifically, higher numbers of tucuxi have been reported in open lake waters rather than near banks and around islands (Vidal *et al*., 1997). In addition to lakes, the Amazon river dolphin has been observed more often in tributaries than near banks and islands of the main rivers (Vidal *et al*., 1997). Overall, there appear to be similar preferences of habitats between the two species (Martin *et al*., 2004).

This study was undertaken to complement the current information available on the ecology of the tucuxi and Amazon river dolphins, particularly their habitat preferences reflected in terms of dolphin densities, and habitat use. By habitat use, we mean the prevalence, or lack thereof, of observed feeding behavior across the habitats. We also provide recommendations on data collection and implications related to climate change.

Materials and method

Study area and time stratification

Passing mode transect sampling was conducted along the various habitats of the Samiria River in the Pacaya-Samiria (04°47' S, 74°23' W; Fig. 1). These were conducted twice a day (at morning starting at 09:00h and at afternoon starting at 14:00h), for a period of about eight weeks, in June and July, from 2016 to 2018. The transects were conducted in a downstream direction in a research boat: a 12 m covered launch with a 25 hp inboard engine at an average speed of 2 km/hour (see Bodmer *et al*.,

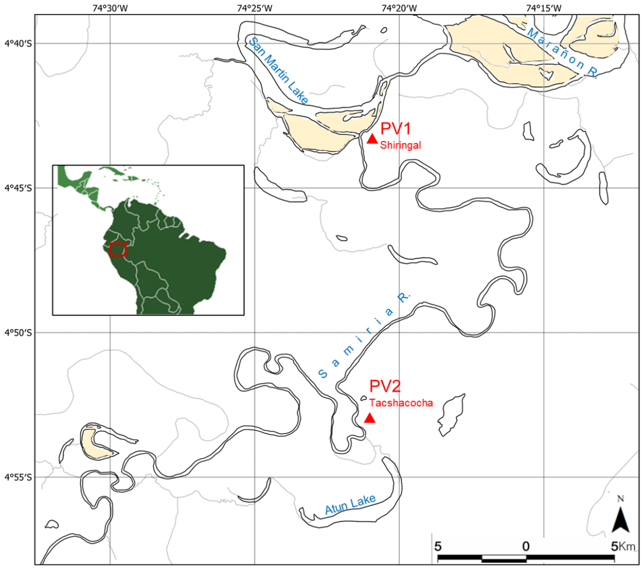

Figure 1. Map of Pacaya-Samiria National Reserve study sites. Map base shape files provided by Operation Wallacea. South America map: Wikipedia – Continent.

Table 1. Habitat type definitions adapted from Gomez-Salazar *et al.* (2012*b*).

Habitat	Definition
Tributary	Small and medium sized rivers no more than 400 m in width. Samiria River: ~120 m wide
(Oxbow) Lake	U-shaped lake. ~300-800 m wide. Separate from tributary
Confluence	Meeting of two streams of water. In this study, a point where a channel connected to a lake meets a tributary
Narrow Channel	A narrow, sheltered stream of water flowing from a lake into a tributary. PV2 only: ~30 m wide
Wide Channel	A stream of water flowing from a lake into a tributary < 200 m wide; shallower and narrower than the tributary but larger and less sheltered than the narrow channel. PV1 only: Two tributaries at ~90 m wide and ~120 m wide.

2017). Transects began or ended at least 300 m away from the residential boat to avoid any potential bias in dolphin observations from human presence, such as food scraps attracting fish. Two sites within Pacaya-Samiria were surveyed: '*Puesto Vigilancia*' (PV)1 (towards the edge of the reserve and the mouth of the Samiria River) and '*Puesto Vigilancia*' (PV)2 (further upriver, into the reserve) (Fig. 1).

Five main habitats were surveyed (see Table 1), with each PV station being the reference point (Fig. 1):

- Seven transects at PV1: four separate 5-km sections of the tributary (Samiria River), one lake transect (San Martin Lake), and two wide channel/lake transects;
- Six transects at PV2: four separate 5-km sections of the tributary (Samiria River), one lake transect (Atun Lake), and one narrow channel (or narrow channel/tributary) transect.

The water level drastically decreased across the survey season since these surveys were conducted during the transition from high- to low-water season [also known as falling water season (McGuire and Aliaga-Rossel, 2007)]. During the 2018 field season, this led to the residential boat having to move further downriver at PV1. This meant a tributary survey located 5-10 km upriver from the PV station was too far and was therefore traded for a survey located 5-10 km downriver from the PV station. Additionally, one of the wide channels became too shallow to survey, so the other wide channel off the lake was surveyed instead.

For each survey, start and end times and UTM coordinates (Garmin GPSMAP64), and weather conditions were recorded. During the surveys, the research boat team consisted of biologists, research assistants, and a local guide. The biologist and local guide ensured accurate data collection and safe navigation, and the five to eight research assistants allowed for a 360° view around the boat. This also allowed for the mitigation of double counting, through visual tracking of individuals.

All observations were by naked eye when a dolphin surfaced. For each sighting, the species, group size, estimated age class of individuals (calf, juvenile, adult), habitat, behavior, time, distance along the transect, and GPS location were recorded. Behaviors recorded included resting, traveling, playing, and feeding. When the dolphin species could be identified, the sighting was recorded. A group was established as any dolphin of the same species that appeared in the same general location (a subjective assessment) within the sighting period, to simplify the recording of the number of individuals. For this reason, group size, as an ecological element, was not a considered factor in this data analysis. Any transects where the distance traveled was not recorded or the habitat surveyed was unclear in the database were excluded as they could not be analyzed.

During data quality control, for surveys with multiple habitats, the GPS points of each group sighting were used to confirm the habitat in which the observation occurred, on GPS Geoplaner Online v2.8. To control for multiple habitats surveyed within a given 5-km transect, each habitat became a data line with the correct distance traveled assigned. The width of the tributary was measured in the field by traveling from edge to edge in a straight line and measuring the distance with a GPS unit. This was done every 500 m for 15 km and the average was taken. The other habitat widths were measured using Google Earth Pro. The lake transects were conducted approximately 100-200 m from the shoreline with the center region and shoreline of the lake both within an estimated reliable observation radius of ~150 m, for an approximate strip width of 300 m.

The impacts of habitat and day of year on density (dolphins/km^2) were evaluated using Generalized Linear Models (GLMs), with dolphins counted as the response variable and habitat (as a four-level factor) and Julian day (as a mean-centered numeric variable) as predictor variables. Area surveyed (km^2) was included as an offset, and Poisson error distributions were used in each model. For each dolphin species, the models were fitted for PV1 and PV2 separately because PV1 was only surveyed for a complete season in 2018, while data from PV2 were available across the three years. Additionally, similar GLMs were fitted to estimate whether dolphin density differed between PVs by using data from two overlapping habitats (tributary and lake) in one year (2018). In these models, PV (as a two-level factor) and mean-centered Julian day were used as the predictor variables, with other model elements similar to those described above. Day of year was included in these models to evaluate whether there was a difference across the field season as the water receded.

Table 2. Ethogram of the Amazon river dolphin (*Inia geoffrensis*) and the tucuxi dolphin (*Sotalia fluviatilis*). The primary activity for each behavioral category is denoted by a *.

Behavioral Category	Characteristic Activities
Resting	- *Low lying in one area. The melon and blowhole are often visible at the surface.
Traveling	- *Moving with intent in a certain direction – can be at speed - Swimming with no signs of other activity
Feeding/ Fishing	- *Individual or group showing evidence of deep diving (body sharply arched in a downward motion) - Dolphin identified feeding on fish - Fish being hunted at speed – evidence of fish being forced to surface up the bank - Pushing water at speed toward the edge of the river/ banks - Fish occasionally jumping out the water accompanied by dolphins moving stealthily at river margins - Visual evidence of jumping to catch fish
Playing	- *Jumping, flipping, and splashing - Producing whirlpools- flipper revolving round - Floating with belly up - Rolling over showing belly and pectoral fins - Diving rapidly under the boat, blowing bubbles under and around the boat - Squirting water out of the blow hole - Slapping with tail

Feeding Behavior

Following the behavioral categories detailed by Blackburn and Bodmer in 2002 (unpub. data), an ethogram is presented in Table 2. Recorded dolphin behavior was determined by establishing the first behavior observed in a given group of dolphins of the same species (*e.g.* if a dolphin was feeding and subsequently began the traveling behavior, the behavior recorded would be feeding). We did not spend additional time with observed dolphins to identify further behaviors. For each recorded sighting, the frequency of the behavior was one. Behaviors were classified as 'feeding' and 'non-feeding' in the analysis.

The proportion of feeding behavior was calculated by dividing the number of times feeding behavior was recorded by the total number of behaviors (feeding and non-feeding), for each habitat. The proportions were then compared using a test of equal proportions (prop.test) in R (RStudio Team, 2020). A Holm post hoc test was conducted to determine specifically which habitats differed in proportions of feeding behavior. The test was done for both dolphin species separately.

Results

Habitat Preference

The tucuxi and the Amazon river dolphins were found in all habitats of the study sites. Observations are displayed in Fig. 2 and Tables 3 and 4. There were fewer tucuxi dolphin sightings (n = 543) than Amazon river dolphin sightings (n = 1,976).

At the PV1 site, habitat was found to have a significant effect on the Amazon river dolphin density. With the Samiria River (a tributary) ($\bar{x}$ = 12.7 dolphins/km^2) as the base category in the GLM, the confluence had a higher density ($\bar{x}$ = 65.4 dolphins/km^2; $p < 0.001$) as did the wide channel ($\bar{x}$ = 24.8 dolphins/km^2; $p < 0.001$). The lake had fewer dolphins than the tributary ($\bar{x}$ = 6.0 dolphins/km^2; $p < 0.001$). At the PV1 site there were, in descending order, higher densities of Amazon river dolphins in the confluence, wide channel, and tributary, than in the lake category (Fig. 2). Julian day was a significant predictor of Amazon river dolphin density at PV1 with an approximate increase of 1.0 dolphin/day ($p < 0.001$).

At the PV2 site, habitat was found to have a significant effect on the Amazon river dolphin density. Again, with tributary ($\bar{x}$ = 10.6 dolphins/km^2) as the base category, the confluence had significantly more dolphins ($\bar{x}$ = 265.1 dolphins/km^2; $p < 0.001$). The narrow channel category also had a higher density ($\bar{x}$ = 73.0 dolphins/km^2) than the tributary ($p < 0.001$). The lake category ($\bar{x}$ = 4.0 dolphins/km^2) had a lower density than the tributary ($p < 0.001$). At the PV2 site, in descending order, there were higher densities of Amazon river dolphins in the confluence, narrow channel, and tributary, than the lake category (Fig. 2). Julian day was a significant predictor of density with a decrease of 1.0 dolphin/day ($p < 0.001$).

The tucuxi dolphins showed a pattern similar to that of the Amazon river dolphins. At PV1, the confluence category had the highest density ($\bar{x}$ = 18.9 dolphins/km^2; $p = 0.004$), followed by the wide channel ($\bar{x}$ = 7.6 dolphins/km^2; $p = 0.71$) and tributary ($\bar{x}$ = 7.2 dolphins/km^2), with the lake ($\bar{x}$ = 2.0 dolphins/km^2; $p < 0.001$) having the lowest density (Fig. 2). Julian day was a significant predictor of density with an increase of 1.0 dolphin/day ($p = 0.001$).

At the PV2 site, habitat had a significant effect on the tucuxi dolphin density. The confluence category had the highest density ($\bar{x}$ = 47.5 dolphins/km^2; $p < 0.001$; Fig. 2), followed by the narrow channel ($\bar{x}$ = 6.0 dolphins/km^2; $p < 0.001$). The lake ($\bar{x}$ = 0.3 dolphin/km^2) had a significantly lower density of dolphins than the tributary ($\bar{x}$ = 2.6 dolphins/km^2; $p < 0.001$). Julian day was a predictor of density with a decrease in density over time (1.0 dolphin/day; $p = 0.029$).

Although the narrow and wide channels cannot be directly compared due to confounding factors such as year and PV, the

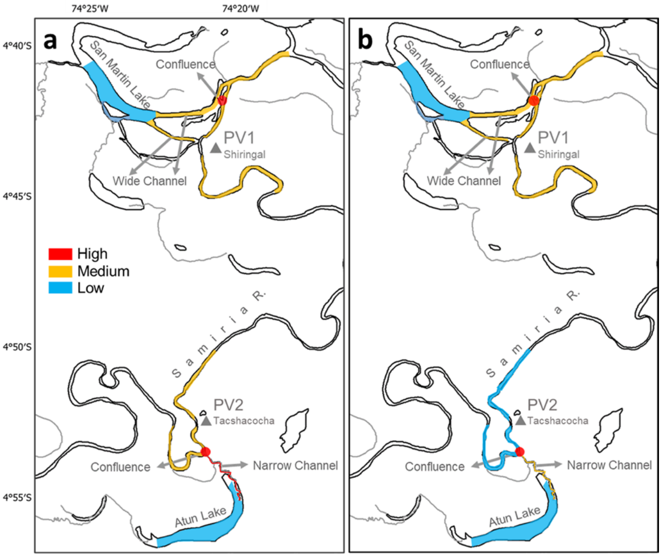

Figure 2. Surveyed habitats categorized as representing river dolphin density (dolphins/km^2). Summarized by three categories for (A) Amazon river dolphins (*Inia geoffrensis*): high (> 25), medium (10 ≤ 25), low (< 10) and (B) tucuxi dolphins (*Sotalia fluviatilis*): high (> 10), medium (5 ≤ 10), low (< 5). (See also Tables 3 and 4).

Table 3. Survey effort (km), total observed number of dolphins (N), mean encounter rate (E/L) and its coefficient of variation (CV), GLM model estimated densities as dolphins/km^2 (D), with standard error (SE) for the Amazon river dolphins (*Inia geoffrensis*) in each habitat at PV1 and PV2 sites. Densities with statistically significant differences from the tributary (for each PV) are denoted by a *.

	PV1					PV2				
	Tributary	**Lake**	**Confluence**	**WChannel**	**NChannel**	**Tributary**	**Lake**	**Confluence**	**WChannel**	**NChannel**
Km	266.1	85.1	7.0	40.4	-	354.5	149.7	5.6	-	140.7
N	433	162	31	130	-	510	167	200	-	343
E/L	1.6	1.9	4.4	3.0	-	1.4	1.3	35.7	-	2.4
CV	0.7	0.5	1.4	0.5	-	0.8	1.0	1.0	-	0.9
D	12.7	6.0*	65.4*	24.8*	-	10.6	4.0*	265.1*	-	73.0*
SE	1.1	1.1	1.2	1.1	-	1.0	1.1	1.1	-	1.1

narrow channel had on average a higher density of Amazon river dolphins (73.0 dolphins/km^2) than the wide channel (24.8 dolphins/km^2; Table 3). For the tucuxi dolphins, the wide channel had a marginally higher mean density (7.6 dolphins/km^2) than the narrow channel (6.0 dolphins/km^2; Table 4).

When comparing PV sites for Amazon river dolphin density, PV2 had a lower density in the tributary ($p < 0.001$), but PV was not a predictor of density in lakes ($p = 0.453$). Julian day was a predictor of density in the tributary, with an increase over time ($p < 0.001$), but not in the lake ($p = 0.226$). While there were lower density averages of tucuxi dolphins at PV2 for both the tributary and lake categories (Table 4, Fig. 2), PV was not a predictor of density for the tributary ($p = 0.830$) or the lake ($p = 0.164$), nor was Julian day a density predictor for either habitat ($p = 0.054$; $p = 0.177$).

Feeding Behavior

The Amazon river dolphin had different proportions of feeding behavior across the five different habitats ($\chi^2 = 60.852$, $p < 0.001$, df = 4, n = 1,147). The highest proportion of feeding behavior was recorded in the confluence habitat (87%), followed by the wide channel (66%) (Fig. 3). The narrow channel, tributary, and lake habitats all had about 50% of feeding behavior. A Holm post *hoc* test revealed the significant differences among the habitats. The confluence had a higher proportion of dolphins feeding than all the other habitats (lake: $p < 0.001$, narrow channel: $p < 0.001$, tributary: $p < 0.001$, wide channel: $p = 0.019$). The wide channel had a higher proportion of feeding behavior only when compared to the tributary ($p = 0.006$). All other habitats were not significantly different in the proportion of feeding behavior occurring by the Amazon river dolphins. The proportion of feeding behavior by the tucuxi dolphin did not differ across habitats ($\chi^2 = 5.417$, $p = 0.247$, df = 4, n = 280; Fig. 4).

Discussion

This study adds to the information available on the ecology of the tucuxi and Amazon river dolphins by exploring habitat preference and use during the high- to low-water season transition. Both species of dolphin display preferences for certain habitats within the Pacaya-Samiria. There are also differences in habitat use presented through feeding behavior.

The reasons why the dolphins prefer the channels and confluences over the tributary during this season are likely due to specific ecological characteristics of these habitats. Unlike the tributary, those habitats have a slower (based on field observation) or disrupted (in the case of the confluences, *e.g.* Martin *et al.*, 2004), downward current, which may be preferable to the dolphins. The confluence being the overall preferred habitat is unsurprising, as previous literature has consistently reported high dolphin numbers in confluences (*e.g.* Vidal *et al.*,

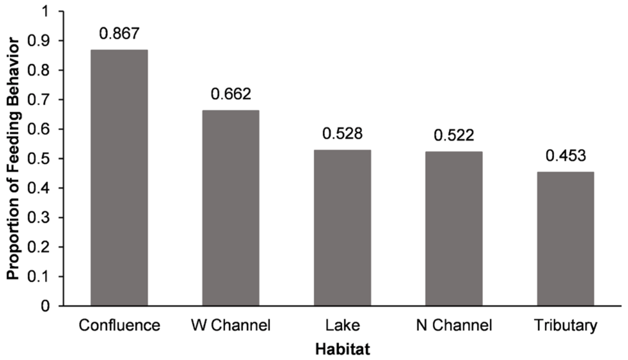

Figure 3. Proportion of feeding behavior observed for the Amazon river dolphin (*Inia geoffrensis*) across habitats, in the Pacaya-Samiria National Reserve. The confluence had a higher proportion of feeding behavior than all other habitats. The only other significant difference was between the wide channel and the tributary (α = 0.05).

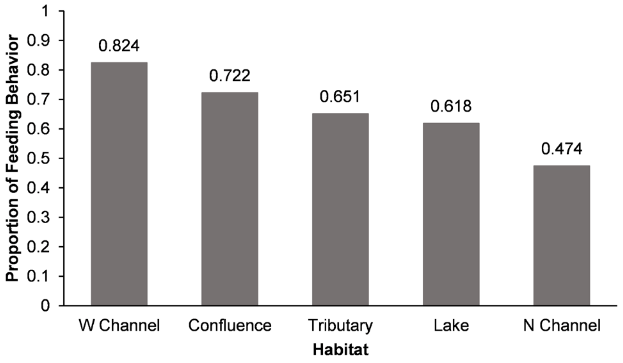

Figure 4. Proportion of feeding behavior observed for the tucuxi dolphins (*Sotalia fluviatilis*) across habitats, in the Pacaya-Samiria National Reserve.

1997; Martin *et al.*, 2004; Gomez-Salazar *et al.*, 2012*b*; Pavanato *et al.*, 2019). The confluences within this study do not always have dolphins present; however, when dolphins are present there are many, with often over five in one sighting, particularly for the Amazon dolphins. Furthermore, fish are very abundant in confluences because these are areas of high productivity (Martin *et al.*, 2004) – the often deep water in confluences is suspected to be desirable for the fish (McGuire and Winemiller, 1998). Of the habitats surveyed, the confluence was the one with the highest proportion of feeding behavior for the Amazon river dolphin, and it was the one with the second highest proportion for the tucuxi dolphin. Therefore, it is likely that fish attract dolphins to the confluences.

Behavior was recorded as a snapshot in time of the initial behavior observed during our passing mode surveys. Behavioral studies on river dolphins are difficult to conduct due to the environment; the dolphins spend a large portion of the time under the dark water surface where they are not visible. These dolphins can also change their behavioral state frequently. Future behavioral studies will need to consider sighting time when establishing behavioral states. Furthermore, social behavior, which is not well understood in these species, could be misidentified as other behaviors such as feeding, or playing; these behaviors can also occur in turn.

The PV2 confluence appears to attract more dolphins of both species than the PV1 confluence. This may be because the PV2 confluence is a perpendicular meeting of the waters, creating a large disturbance in the river flow, resulting in a circular current, while the PV1 confluence is better characterized as two water streams meeting and flowing together in the same direction. Despite both locations being confluences, specific characteristics may make one more desirable/productive than the other. For example: the larger current disturbance may result in a larger aggregation of prey.

The two other preferred habitats are the narrow channel and wide channel (for the Amazon river dolphin). These habitats have different properties from confluences; they have slow currents rather than a disrupted current. Similar to confluences, the wide channels had a higher proportion of feeding behavior. The combination of low energetic demand from a slow current and good feeding location likely contributes to the wide channels being a preferred habitat. Non-coincidentally, fishermen also prefer to use these low current habitats (Martin *et al.*, 2004). The narrow channel habitat had some of the lowest proportions of feeding behavior, so the high density of dolphins in the narrow channel is likely unrelated to prey. This habitat may be beneficial for other unexplored behaviors such as socialization.

The lake habitat had consistently lower dolphin density than the other habitats, for both species. These results were unexpected. Vidal *et al.* (2007) and Gomez-Salazar *et al.* (2012b) have reported lakes as being important habitats for these dolphins in Colombia. Low densities in the lake habitat could be related to the small sampled area within the lake. It is also possible that lakes surveyed in previous studies may be more accessible to dolphins than those off the Samiria River, particularly as the water level drops throughout the season.

We also explored Julian day as a possible predictor of density with relation to seasonality. Density changes across the season were expected, as the dolphins move from habitats such as flooded forests and shallow channels, into tributaries and main rivers such as the Marañón as the water level decreases (Martin and da Silva, 2004; Bodmer *et al.*, 2017). The dolphins appeared to move downstream from PV2 toward PV1 as time passed. Our density estimates are from a season where a larger congregation of dolphins is expected with the water level receding and the dolphins moving out of Pacaya-Samiria. In Brazil, seasonality affected the movements and densities of river dolphins: similar to the Pacaya-Samiria, as water levels decreased, access to various habitats was lost and dolphins moved into the main rivers (Martin *et al.*, 2004). Stronger trends may also be present between seasons.

In this study, year was not an explored variable, as PV1 was only surveyed in 2018. Long-term analysis of both research sites and a comparison across years, or the use of mark-recapture/resight and encounter histories such as in Mintzer *et al.* (2016) could provide a clearer insight into the seasonal movements and therefore changes in densities of these two species within Pacaya-Samiria. As extreme environmental events such as floods become more frequent, the seasonal movements by dolphins and timing of these movements from one year to the next may be less predictable (Bodmer *et al.*, 2017). The evaluation of dolphin habitat preference and movements across multiple seasons and years could also provide insight into the potential impacts of climate change on the two species.

Something worth noting with regard to the lake data is that, in 2017, the surveys in the lake stopped 35 days before the surveys conducted in all other habitats, due to low water levels. If this lack of access to the lake is an indication of a shrinking high-water season, it would impact the availability of habitats to dolphins. The water levels of 2016 through 2018 (Servicio de

Table 4. Survey effort (km), total observed number of dolphins (N), mean encounter rate (E/L) and its coefficient of variation (CV), GLM model estimated densities as dolphins/km^2 (D), with standard error (SE) for the tucuxi dolphins (Sotalia fluviatilis) in each habitat at PV1 and PV2 sites. Densities with statistically significant differences from the tributary (for each PV) are denoted by a *.

	PV1					PV2				
	Tributary	Lake	Confluence	WChannel	NChannel	Tributary	Lake	Confluence	WChannel	NChannel
Km	266.1	85.1	7.0	40.4	-	354.5	149.7	5.6	-	140.7
N	245	54	9	40	-	120	14	34	-	27
E/L	1.0	0.6	1.3	1.0	-	0.3	0.1	6.1	-	0.2
CV	0.9	1.0	3.0	0.9	-	2.0	2.9	2.2	-	2.4
D	7.2	2.0*	18.9*	7.6	-	2.6	0.3*	47.5*	-	6.0*
SE	1.1	1.2	1.4	1.2	-	1.1	1.3	1.2	-	1.2

Hidrografía, 2018) are not classified as intensive floods based on the distinction made by Bodmer *et al.* (2017). While the overall water level of the Amazon River in Iquitos did not surpass the "probable drought" level, as established by the Servicio de Hidrografía (2018) at 107.5 m above sea level over the study years, there may be sub-regional differences where certain rivers are more strongly affected by changing water levels. Looking at the dates in which various habitat types were surveyed may be an important step in determining whether accessibility to these habitats is changing as the climate changes, particularly with the uncertainty surrounding extreme flood and drought events in the Amazon. There is modeling work showing different outcomes as to how the extreme events of floods and droughts will continue, and these past few years may be an indication of a back and forth between the two extremes (Marengo and Espinoza, 2016). This alternation of high flood years followed by droughts is the greatest concern for the Amazonian environment (Bodmer *et al.*, 2017).

With this in mind, categorizing dolphin distribution into distinct habitats when they are in fact fluid habitats, particularly across seasons, years and even decades, may not actually be the most meaningful way to present information on these species. By establishing each species niche, we can better understand what environmental conditions these animals prefer and require. Having a more specific set of criteria to measure, particularly related to the physical environment, such as water temperature, depth, current speed, and primary production, may be more beneficial (MacLeod *et al.*, 2007). These environmental predictors can be collected alongside dolphin habitat observations to have a more comprehensive characterization of the system. Prey availability in various regions, through abundance of fish, would also be a beneficial aspect to consider. Additionally, a continued measure of recent drought history (*e.g.* a +1-year-lag on water levels or years-since-drought) may also be advantageous to include. Having such supplementary information at various specific locations throughout the Amazon might allow for better identification of key criteria attracting the two dolphin species. This can be particularly useful when faced with contrasting habitat results across multiple locations, such as the small dolphin numbers in the Pacaya-Samiria lakes in contrast to previous findings in other regions.

Conclusion

This study provides insight into how dolphins use the Pacaya-Samiria. Within the reserve, more Amazon river dolphins were observed than tucuxi dolphins. The confluence is the most relevant habitat for both species, being a location with suspected high fish abundance and therefore ideal for feeding. The narrow channel was also a preferred habitat for both species, and the wide channel for the Amazon river dolphins. The wide channel had a high prevalence of feeding behavior, like the confluences; however, the narrow channel had a low prevalence of feeding behavior, and is likely preferable due to some other unknown factor.

Amazonian rivers are complex systems difficult to survey. Furthermore, river dolphins are susceptible to dry-outs of rivers, lakes, and channels when droughts occur. Recent droughts linked to climate change occurring in the Amazon are expected to intensify (Duffy *et al*., 2015) and studies like this, on current habitat use of river dolphins, will shed light into potential scenarios of future change. Gathering additional environmental data is paramount to better understand what attracts and benefits these species, which are considered ecological indicators in large tropical rivers.

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