

RIVERINE HABITAT PREFERENCES OF BOTOS (*INIA GEOFFRENSIS*) AND TUCUXIS (*SOTALIA FLUVIATILIS*) IN THE CENTRAL AMAZON

A. R. MARTIN¹

NERC Sea Mammal Research Unit,
Gatty Marine Laboratory,
University of St Andrews, Fife KY16 8LB, United Kingdom
E-mail: arm@bas.ac.uk

V. M. F. DA SILVA

Laboratório de Mamíferos Aquáticos,
Instituto Nacional de Pesquisas da Amazônia,
CP 478, 69011-790 Manaus, Amazonas, Brazil

D. L. SALMON

NERC British Antarctic Survey,
High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom

ABSTRACT

The distribution and density of the Amazon's two contrasting endemic dolphins—boto, or Amazon river dolphin, *Inia geoffrensis*, and tucuxi, *Sotalia fluviatilis*—were examined on two adjoining large rivers in western Brazil. Using a 17-m river boat as a sightings platform, strip transects were used to cover areas within 150 m of the river margin and line transects were used in all other areas. Highest densities of both dolphins occurred near the margin, and lowest in the center of rivers. Seven different habitats were identified along river margins. The boto and the tucuxi differed in some elements of habitat choice, but they shared a preference for areas with diminished current and where two channels joined. Neither species favored the two most common edge types in this region of the Amazon—mud banks and flooded forest margins. Overall, the most preferred habitat type was the least common, and known as “meeting of the waters.” In these areas a channel of sediment-rich white water meets one carrying acidic black water; the resultant mixing produces particularly productive, and obviously attractive, conditions for dolphins. These results demonstrate that Amazonian dolphins selectively occur in areas known to be favored for gill net deployment by local fishermen, and may explain why entanglement is apparently a common cause of mortality.

Key words: boto, Amazon river dolphin, *Inia geoffrensis*, tucuxi, *Sotalia fluviatilis*, habitat preference, rivers, line transect surveys, strip transect surveys.

¹ Current address: NERC British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom.

The boto, a river dolphin of the family Iniidae, and the tucuxi, a small member of the family Delphinidae, are found sympatrically throughout the Amazon river basin (Best and da Silva 1989, 1993; da Silva and Best 1994). Although relatively little is known of these two contrasting small cetaceans, a striking consistency between many published observations is the assertion that neither species occurs randomly along waterways. They appear to cluster at particular physical features, especially where two channels meet (Magnusson *et al.* 1980, Best and da Silva 1989, Hurtado 1996, Leatherwood 1996, McGuire and Winemiller 1998). Such features are clearly important to the ecology of these dolphins throughout their range.

Little attempt has been made to quantify riverine habitat preference by the Amazon's two endemic dolphins. The margins of the main stem and tributaries of this river comprise a variety of contrasting habitats. Some are stable year-round, but many are modified or disappear altogether as the water level rises and falls during the annual flood cycle. The impact of fluctuating water levels on these dolphins is profound. It acts directly on them by allowing and preventing access to large areas of prey-rich habitat, and indirectly through its influence on the density, distribution, and migrations of prey (fish) populations.

In a separate paper (Martin and da Silva, in press), we investigated the seasonal use of various floodplain habitats by botos, treating the main rivers as just two habitat entities—center and edge. Here, we present an investigation of the distribution and density of both botos and tucuxis on large Amazonian rivers. The objective was to find and explain any quantifiable habitat preferences shown by either species at any time during the annual water level cycle.

Apart from the obvious benefit of improving our understanding of the ecology of these two dolphins, quantification of distribution across riverine habitats would be of particular use from a conservation perspective. It would show where these species are most vulnerable to human fishing activity—probably the greatest cause of mortality of dolphins in this area, and perhaps more widely. Additionally, it should result in more accurate abundance estimates by informing survey planning, especially in terms of sighting methodology and the most effective track design for a vessel in relation to river banks.

METHODS

The study was carried out within a 50-km radius of the junction of the large white water rivers: Amazon (named the Solimões in this region), and Japurá, near the town of Tefé, Amazonas State, Brazil ($64^{\circ}45'W$, $03^{\circ}35'S$). The Japurá is a major tributary that flows from Colombia. Both rivers have a width of about 1,000 m here, although at low water the emergence of sandbanks creates several smaller channels in some places.

The study comprised six multiday visual surveys carried out from a 16.8-m diesel powered river boat between March 1999 and April 2001. Surveys were carried out at or near high, low, and mid-water levels to allow an examination of dolphin behavior throughout the flooding cycle. Following Vidal *et al.* (1997), two survey methodologies were used—strip transects of 150 m width along the river margins, and line transects using distance sampling in the center of rivers, *i.e.*, between the marginal strips on each side. Line transects were carried out in a zig-zag pattern, crossing the river between the marginal strips at an angle of approximately 45° (Fig. 1). Line transects were not used near the margins for

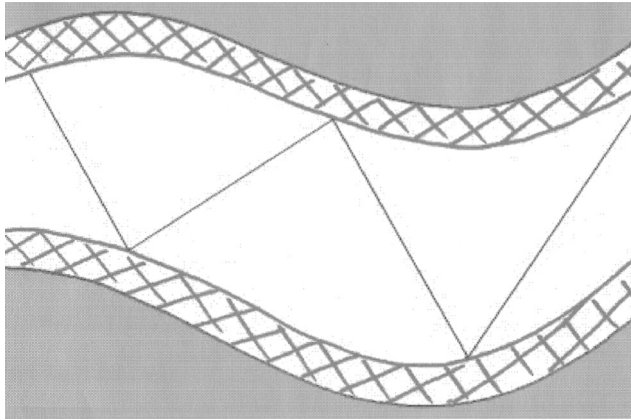


Figure 1. Schematic diagram of sighting methodologies employed. Areas within 150 m of the river margin (shown hatched) were surveyed using a strip transect, with the vessel track defining the outer limit of the transect. Areas in the center of the river were surveyed using line transects, the vessel track (shown) being a sequence of zig-zag straight lines between the marginal strips.

several reasons, including the difficulty of navigating and turning on a precise heading in shallow waters. For line transects we assumed that $g(0) = 1$, *i.e.*, that all dolphins on the trackline were seen. Both of the target species have short interbreath intervals (rarely >60 sec; unpublished data), and sighting work was only carried out in conditions of excellent visibility, so this assumption was probably valid in all but a small minority of cases at the very start of transects. For strip transects, we assumed that all animals within the strip were seen. For both sighting methodologies, observer effort (see below) was designed to meet the relevant objectives and assumptions, and the recorded sighting unit was a dolphin group at the surface. Extreme water turbidity prevented a dolphin being seen before it surfaced.

The interval between consecutive surveys of any segment of river was never less than 24 h, and usually several months. The results of each day's survey work were therefore assumed to be independent. The total trackline distance covered was 1,402 km in strip transect mode and 810 km in line transect mode.

Three primary observers were seated in a line at the front of a shaded platform above the wheelhouse, their eyes 6.3 m above water level. They recorded only sightings of animals as they broke the water surface to blow. For line transects, the central observer searched within an arc of 30° each side of the trackline, and used binoculars to detect targets far forward of the vessel. The left-hand and right-hand observers searched a 90° arc from the trackline to abeam on their respective side of the vessel, using binoculars only to investigate sightings first seen with the naked eye. Sightings made by the primary observers were referred to an auxiliary observer standing behind them for confirmation of species and group size. A recorder took sightings information from all observers, helped by an auxiliary when high densities of dolphins were encountered. Information recorded for each sighting was species, group size, angle from trackline at first observation (estimated using an angle-board situated in front of each observer), distance from vessel at first observation, and distance abeam when passing (when possible). Observations were

recorded as “primary” (sightings made ahead of the abeam line by the primary observers) or “secondary” (all others). Only primary sightings were used in the estimation of dolphin density. Primary observers were all experienced in searching for riverine dolphins, and received training in distance estimation calibrated with a laser range-finder until accurate to within 10% before each survey. Line transects were carried out at speeds of 14–20 km/h, and always downstream on rivers. Analysis of distance-sampling data was carried out using Program DISTANCE (version 4, release 1) developed and made available by the Research Unit for Wildlife Population Assessment, University of St Andrews, UK (Thomas *et al.* 2002).

Strip transects were carried out from the same platform, and with the vessel travelling along the strip edge to avoid disturbing dolphins in the strip as much as possible. During these surveys, the following details of all sightings of dolphins were recorded: species, group size, distance from margin, position (detailed latitude and longitude from a GPS device), and habitat type of the river margin at that location. A constant distance from the water edge was maintained by use of a laser range-finder. Sighting protocol was similar to that of line transects, except that all observers searched only on one side of the vessel and density estimates used sightings made from any observer including one dedicated to looking behind the vessel. Strip transects were normally carried out against the current, at speeds of 6.5–10.0 km/h.

Because botos often show very little of themselves when blowing, sighting work was carried out only when the water surface was calm, or almost calm. Surface conditions recognized were flat calm (denoted surface state 0), minimal ripples (0+), continuous ripples with a height of ~5 cm (1), continuous ripples with a height of ~10 cm (1+), wavelets of ~15 cm (state 2; conditions brought about by a wind speed of some 20 km/h in open-water habitat with no current), and wavelets >15 cm (2+). The effect of surface condition on density estimation was tested by treating surface condition as a stratification variable in the analysis by Program DISTANCE. No effect of surface state was detected for either species of dolphin ($P \gg 0.05$; see Buckland *et al.* 2001 for a discussion of relevant variance estimation), so the analyses below include sightings made in all conditions combined. All χ^2 tests discussed below relate to contingency tables.

Eight habitat types were recognized. Seven of these together formed the margins of the two rivers, and were arbitrarily deemed to characterize water out to 150 m from the edge. For the purposes of this study, each margin habitat was classified from “low current” (characterized by protection from, or disturbance of, riverine flow), to “high current” (unimpeded flow). The last was simply “river center,” *i.e.*, apparently featureless areas of water more than 150 m from any land or emergent vegetation, and by definition “high current.” The edge-type habitats were as follows:

Bank—The single most common edge type in the central Amazon, steep mud banks usually bordered *terra firme*, *i.e.*, land that is higher than maximum flood levels. This habitat provides no protection from currents, and was thus classified as “high current.”

Confluence—The mouth of a channel joining the main river. The channel could lead from a lake in the forest, a stream, or even simply another part of the same river. This habitat was usually in segments less than 500 m long, and rarely more than 800 m. Due to disturbance of the water flow, the production of eddies and counter-currents, confluences were classified as areas of “low current.”

Meeting of waters—In a small number of sites, at and downstream from confluences of black and white water channels, the contrasting waters ran parallel to

each other while slowly mixing. Black water is relatively acidic and high in tannins. It derives from forested floodplain areas. White water is basic, sediment-rich, and originates in the Andes (Sioli 1984). This was the least common habitat type encountered. Classified as "moderate current" because water flow was low at the confluence itself but increased with distance downstream.

Igapó—This name is given to areas of forest that have been flooded. *Igapó* only occurs at higher levels of water, and where it fringes a river it allows direct aquatic access to the forest. In terms of riverine habitat, this term was applied to river margins that bordered *igapó*. Classified as "high current."

Beach—Found only at lower water levels, shallow sandbanks occurred both on the margins of rivers and were even exposed in the river center in some places. Classified as "high current."

Bay—Known locally as "ressacas," bays are shallow and often dry out at low water. They are usually fringed with emergent or floating vegetation, where the current is much reduced, and are rarely more than 1 km long. Classified as "low current."

Floating vegetation—Extended areas (up to several km) of tangled mats of vegetation anchored to the river margin. Classified as "low current."

RESULTS

Group Size

Group size estimation was relatively simple for both species because most groups were small; 99% of boto groups were of one to four dolphins, and 98% of tucuxi groups were of one to six. The frequency distribution of group size was not significantly different between line transects and strip transects for either species (χ^2 , $P > 0.3$ in each case). For all surveys combined, the following values were obtained: Boto mean = 1.42, SE = 0.036, mode = 1, $n = 733$; tucuxi mean = 2.24, SE = 0.065, mode = 2, $n = 504$.

Longitudinal Distribution—River Margin Habitats

Results are given in Table 1. In both species of dolphin, the null hypothesis of equal distribution between habitat types across all surveys was rejected at $P \ll 0.001$ (boto: $\chi^2 = 141.5$, $df = 6$; tucuxi: $\chi^2 = 201.6$, $df = 6$), demonstrating very considerable habitat preferences. The relative distribution of botos between habitats also differed significantly from that of tucuxis ($\chi^2 = 67.2$, $df = 6$, $P \ll 0.001$), indicating that the Iniid and the Delphinid were making different choices.

Boto—The mean density of botos encountered along river margins across all surveys was 0.6 per km of river bank or 3.7 per km². Densities in each of the seven habitats varied from 0.4 per km (mud bank and *igapó* margins) to 3.9 (meeting of waters), a factor of 10 between the most- and least-favored habitats. All four of the remaining habitats—beach, floating vegetation, confluence, and bay—had very similar overall densities of botos, at 0.9–1.0 per linear km. The proportion of botos found in each edge type varied between surveys ($\chi^2 = 541$, $df = 30$, $P \ll 0.001$), but this is inevitable given that some habitats did not exist at some water levels (e.g., beach at high water and *igapó* at low water). Indications of real differences, even between surveys carried out at similar water levels, are evident in Table 1. The March 1999 and March/April 2001 surveys were executed at the same time of year and at water levels differing by only 0.6 m yet; for example, waterway confluences

Table 1. Distribution of botos and tucuxis along the margins of the rivers Japurá and Solimões, by habitat type of the adjacent margin. Data are from 150-m wide strip transects carried out during 6 multiday surveys between March 1999 and March 2001. Seven habitats were recognized, but not all were encountered in every survey due to water level changes.

Habitat type	Length (km)	Area (km ²)	No. botos	Botos per km	Botos per km ²	Rank	No. tucuxis	Tucuxis per km	Tucuxis per km ²	Rank
All Surveys Combined										
Confluence	39.1	6.6	40	1.0	6.1	4	68	1.7	10.3	1
Bank	594.2	102.4	258	0.4	2.5	7	135	0.2	1.3	7
Mtg. of waters	17.8	3.2	69	3.9	21.7	1	27	1.5	8.5	2
Igapó	411.1	63.9	181	0.4	2.8	6	221	0.5	3.5	5
Beach	60.1	12.1	53	0.9	4.4	5	31	0.5	2.6	6
Bay	26.9	4.2	26	1.0	6.2	3	27	1.0	6.4	4
Floating veg.	170.5	27.8	188	1.1	6.8	2	200	1.2	7.2	3
Σ or mean	1,319.7	220.2	815	0.6	3.7		709	0.5	3.2	
March 1999										
Confluence	10.0	1.7	13	1.3	7.8	2	23	2.3	13.9	1
Bank	42.5	7.3	0	0.0	0.0	6	1	0.0	0.1	5
Mtg. of waters	0.9	0.2	4	4.2	21.1	1	0	0.0	0.0	6
Igapó	92.2	14.6	24	0.3	1.6	5	91	1.0	6.2	3
Bay	5.9	1.0	3	0.5	3.1	4	13	2.2	13.5	2
Floating veg.	42.8	7.8	39	0.9	5.0	3	45	1.1	5.8	4
Σ or mean	194.3	32.6	83	0.4	2.6		173	0.9	5.3	
June 1999										
Confluence	3.2	0.5	2	0.6	4.1	6	10	3.1	20.7	1
Bank	25.4	4.3	38	1.5	8.8	4	6	0.2	1.4	5
Mtg. of waters	2.0	0.3	5	2.6	15.5	1	0	0.0	0.0	6
Igapó	91.7	14.8	72	0.8	4.9	3	45	0.5	3.0	3
Bay	3.9	0.6	6	1.5	9.4	2	1	0.3	1.6	4
Floating veg.	25.5	3.9	17	0.7	4.4	5	28	1.1	7.3	2
Σ or mean	151.7	24.4	140	0.9	5.7		90	0.6	3.7	
October 1999										
Confluence	4.7	0.9	7	1.5	7.4	2	2	0.4	2.1	1
Bank	133.3	27.3	88	0.7	3.2	4	44	0.3	1.6	3
Mtg. of waters	0.3	0.1	1	3.9	14.0	1	0	0.0	0.0	4
Beach	25.3	5.2	35	1.4	6.7	3	18	0.7	3.4	2
Bay	0.7	0.1	0	0.0	0.0	5	0	0.0	0.0	4
Σ or mean	164.3	33.6	131	0.8	3.9		64	0.4	1.9	
March 2000										
Confluence	9.3	1.7	10	1.1	5.8	2	14	1.5	8.1	1
Bank	192.3	30.5	36	0.2	1.2	5	27	0.1	0.9	5
Mtg. of waters	8.8	1.5	27	3.1	17.7	1	8	0.9	5.2	2
Igapó	96.1	14.6	8	0.1	0.5	6	3	0.0	0.2	6
Beach	34.1	6.8	15	0.4	2.2	3	13	0.4	1.9	4

Table 1. Continued.

Habitat type	Length (km)	Area (km ²)	No. botos	Botos per km	Botos per km ²	Rank	No. tucuxis	Tucuxis per km	Tucuxis per km ²	Rank
Bay	6.5	1.0	2	0.3	2.0	4	4	0.6	4.0	3
Σ or mean	347.1	56.1	98	0.3	1.8		69	0.2	1.2	
July 2000										
Confluence	6.1	0.9	6	1.0	6.5	4	7	1.1	7.6	2
Bank	63.9	10.7	27	0.4	2.5	6	7	0.1	0.7	6
Mtg. of waters	2.2	0.4	8	3.7	21.8	1	15	7.0	41.0	1
Igapó	82.0	12.4	49	0.6	3.9	5	51	0.6	4.1	4
Bay	3.8	0.6	5	1.3	8.7	2	2	0.5	3.5	5
Floating veg.	54.5	8.9	69	1.3	7.7	3	40	0.7	4.5	3
Σ or mean	212.5	33.9	164	0.8	4.8		122	0.6	3.6	
March/April 2001										
Confluence	5.8	0.9	2	0.3	2.3	7	12	2.1	13.9	1
Bank	136.9	22.3	69	0.5	3.1	6	50	0.4	2.2	6
Mtg. of waters	3.7	0.7	24	6.5	34.0	1	4	1.1	5.7	4
Igapó	49.2	7.5	28	0.6	3.7	5	31	0.6	4.1	5
Beach	0.7	0.1	3	4.1	27.6	2	0	0.0	0.0	7
Bay	6.0	0.9	10	1.7	11.0	3	7	1.2	7.7	3
Floating veg.	47.7	7.2	63	1.3	8.8	4	87	1.8	12.1	2
Σ or mean	250.0	39.6	199	0.8	5.0		191	0.8	4.8	

had boto densities varying by a factor of 4, and were ranked second of seven habitats in 1999, but seventh in 2001. In contrast, habitat "meeting of waters" ranked first in all six surveys.

Tucuxi—This species was found in slightly lower densities than botos along river margins, with a mean of 0.5 dolphins per km, or 3.2 per km². The most-favored habitats were waterway junctions (confluence and "meeting of waters"), and least-favored were mud banks. Floating vegetation and bays, both of which were often adjacent to confluences, held intermediate densities of tucuxis. As with botos, differences in habitat preferences were found between surveys overall ($\chi^2 = 521$, $df = 30$, $P \ll 0.001$) and between surveys at the same time of year. However, this species was broadly consistent in preferring confluences and avoiding mud banks year round.

Species comparison—A closer examination of the results for the two species shows that differences in the relative use of the seven recognized habitats masked considerable similarity in habitat choice. Over all surveys combined, the density of both species in all "low current" habitats (confluence, bay, and floating vegetation) and the rare "meeting of waters" habitat was higher than in any of the "high current" habitats (*igapó*, bank, and beach).

Distribution of Dolphins Across the River

The density of both species of dolphin was highest at the river margin and declined with distance from the margin. This trend was apparent even within the

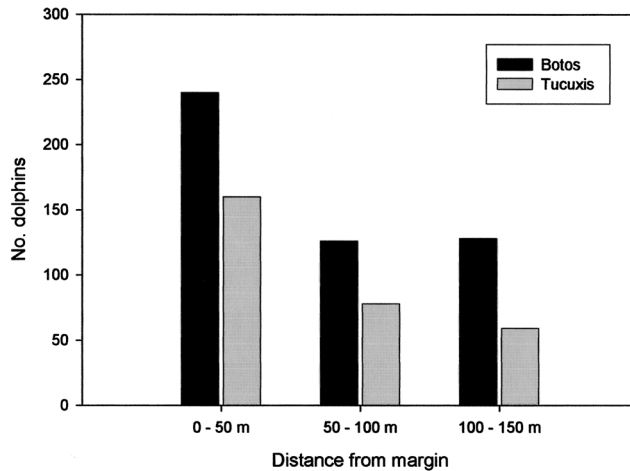


Figure 2. Distribution of botos and tucuxis with distance from river margin during all strip transects combined.

150-m survey strip, with 49% of botos and 54% of tucuxis occurring within 50 m of the edge (Fig. 2).

A variety of detection function models, with different truncation distances and bin sizes, were fitted to the mid-river line transect sightings data using program DISTANCE. On the basis of Akaike's Information Criterion (AIC) and Goodness-of-Fit (GOF) values, a Hazard Rate model fitted to a histogram with 45-m bins was adopted for both species, truncated at 405 m for botos (AIC = 557.2, GOF = 0.93) and 450 m for tucuxis (AIC = 638.5, GOF = 0.99). These also provided a good visual fit to the data (Fig. 3). Summary results of applying these models to the survey data are given in Table 2. The mean density of the two species varied between surveys, but the confidence intervals around the estimates were very wide because relatively few dolphins were encountered, and these differences were not statistically significant except between the October 1999 (low water) figure for botos and those of three other surveys. A mean density of 0.60 botos and 0.77 tucuxis per km² of central river habitat was derived if equal weight was given to all five surveys with line transect estimates. For both species, this was much lower than the density for any edge-type habitat along river margins.

From Tables 1 and 2, the percentage of botos occurring along the margins of a typical river of width 1,000 m varied seasonally between 59% and 93%. The lower bound rises to 70% without the low-water survey. The seasonal range for tucuxis was 40%–88% near the margins; in each survey a larger percentage of tucuxis than botos occurred mid-river.

DISCUSSION

Habitat Preferences

The relatively high density of botos in the center of rivers during the October 1999 survey was probably due to the fact that the water level was at its annual minimum during this period. This had three impacts, all of which were likely to

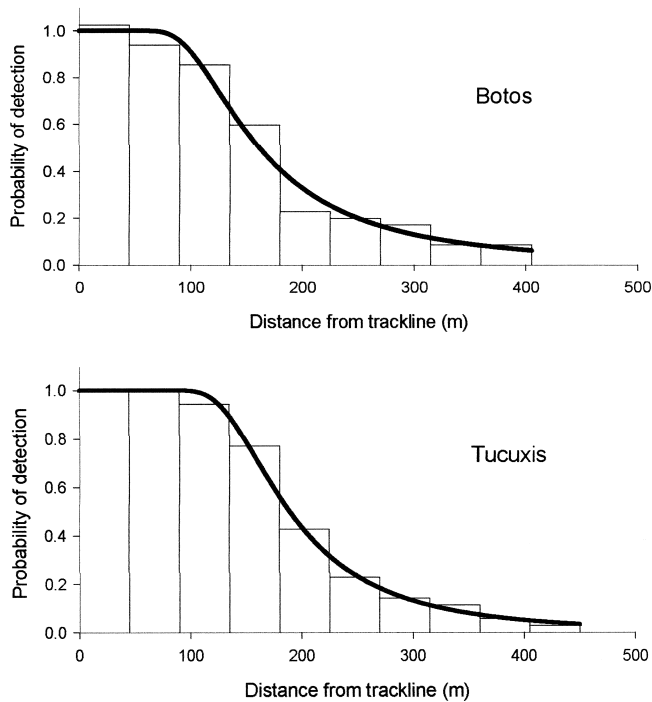


Figure 3. Probability of detection of botos and tucuxis with distance from the trackline during line transect surveys in the center of rivers. Histograms show the relative number of dolphins seen in contiguous 45-m “bins.” The curves represent the best-fit model as determined by program DISTANCE. For both species this was a Hazard Rate model, but truncated at 405 m for botos and 450 m for tucuxis.

increase dolphin densities in rivers. They are (1) a reduction in the surface area of river water, thereby concentrating dolphins, (2) the creation of shallow-water habitats in mid-river that were similar to river-edge habitats, and (3) the rendering of floodplain habitats too shallow for dolphins, thereby forcing them on to the main rivers (Martin and da Silva, unpublished data). The mid-river density of tucuxis was also numerically higher during this survey than all others, but the low encounter rate resulted in wide confidence intervals and the difference was not statistically significant. Both species forage in the extensive floodplain adjacent to the main rivers, especially during intermediate water levels, although a larger proportion of botos than tucuxis make use of these areas (Martin and da Silva, unpublished data). The impact of the flood cycle in terms of seasonal availability of habitats and prey is, therefore, broadly similar for these two dolphins.

The preference of both species for “low current” habitats was unequivocal. There are two obvious possible reasons for this. The first is that less energy is required to remain in a chosen position, and the second that such habitats are favored by fish. Confluences are chosen by fish migrating along the major rivers because they are areas of high productivity and offer underwater structure for refuge. Floating vegetation also provides refuge for a wide variety of small fish, including gymnotids, cichlids, and catfish (Crampton 1999). Botos are frequently seen

Table 2. Density of botos and tucuxis in the rivers Japurá and Solimões, excluding a strip of 150 m around the margins. Results are from line-transect analyses using program DISTANCE. For both species, the probability of seeing an animal with distance was assumed to follow a Hazard Rate model, with sightings truncated at 405 m and 450 m for botos and tucuxis, respectively. No line transects were carried out in March 1999.

Survey	June 1999	Oct 1999	March 2000	July 2000	April 2001
Effort (km track)	91.2	118	89.1	133.2	150.6
Water level (m)	15.4	3.9	8.6	13.8	12
Mean boto density (km⁻²)	0.25	1.60	0.36	0.63	0.17
% CV	54.0	22.8	54.7	50.1	46.2
df	42.3	94.6	65.5	44.7	95
Lower confidence limit	0.09	1.02	0.13	0.24	0.07
Upper confidence limit	0.71	2.5	1	1.63	0.4
Σ botos seen (trunc. data)	14	67	11	23	8
Mean tucuxi density (km⁻²)	0.49	1.28	0.84	0.95	0.30
% CV	65.5	37.6	47.8	37.3	54.4
df	52.6	89.6	42.2	108.4	90.3
Lower confidence limit	0.15	0.62	0.34	0.46	0.11
Upper confidence limit	1.62	2.64	2.11	1.94	0.84
Σ tucuxis seen (trunc. data)	18	56	31	56	25

feeding under these “floating meadows,” and stomachs of botos drowned in fishing nets often contain evidence of large numbers of fish typical of this habitat (da Silva 1983). The elevated energy cost of remaining in higher-current areas could be reason enough for dolphins to avoid them, unless they offered large rewards, such as better foraging. The available evidence indicates that this is not so, except in the very special case where black and white waters merge, producing a uniquely productive micro-environment (“meeting of waters”). Here, the sudden change in pH causes large carbon-based macromolecules to precipitate out and form a carbon- and mineral-rich sludge that supports detritivorous fishes and planktonic growth (Schmidt 1976).

On this basis, the low density of dolphins of both species in the center of rivers is predictable due to higher current speeds and relatively low fish density. The drop in density between the edge and center of rivers was greater for botos than tucuxis (Table 1, 2), and it is likely that the faster-swimming delphinid species is better able to function in areas of high water flow. Whereas botos outnumbered tucuxis overall along the river margins (Table 1), the delphinid dominated mid-river apart from during the low-water survey of October 1999, the only time of the year when almost all botos are on the main rivers (Martin and da Silva, unpublished data).

The habitat selectivity shown by both dolphin species resulted in considerable patchiness of animals along the margins of the rivers Japurá and Solimões. In this part of the central Amazon, 40% of botos, and 45% of tucuxis occurring along the river margins occupy just 19% of the river length, this being the combined contribution of “low current” habitats—confluences, bays, and floating vegetation, and the few “meeting of waters” areas. Observation of both species gave the clear impression that movements were, in general, far more directed in high current areas than those with low current, and it is likely that a substantial proportion of

dolphins in the less-preferred habitats were merely moving between more-favored areas.

In summary, these two contrasting cetaceans showed more similarities than differences in their choice of habitats on main rivers. Both occurred at higher densities near river margins than in open-water areas, and were very selective about which margin habitats to use. Relatively small areas with diminished current flow were favored, as were confluences of black and white water channels. Both species were found at lowest densities along the two most common riverine boundaries in the central Amazon—mud banks and the edge of flooded forest.

Broader Implications

The fact that such a high proportion of botos was found close to the bank at all times of year has obvious inferences for the design of future surveys for this river dolphin. We conclude that the most effective, and simplest, use of observer and vessel time would be to operate strip transects along the margins of rivers. The minority of dolphins mid-river could be accounted for by simple use of a correction factor without adding an unacceptable degree of error. Strip transects are easier to manage, require less observer training and the resultant data are much simpler to analyze. The situation is not so clear-cut for tucuxis, especially at lower water levels when rivers narrow and mid-river densities of this species are at their highest.

It is probably no coincidence that the habitat characteristics favored by Amazonian dolphins—high fish density and low current—are also those sought by Amazonian fishermen. The main fishing gear in the study area is a large-mesh, top-set monofilament gill net; dolphin entanglement in such gear is common, though as yet unquantified. Almost all carcasses of botos and tucuxis examined by our research team over many years showed unmistakable evidence of entanglement, and this is probably the most common cause of mortality. At present, there is no perception that either species has diminished in this region. However, gill nets deployed in the dolphins' favored habitats clearly have the potential to cause significant damage to these species at the population level, as they have to cetaceans worldwide (Northridge and Hofman 1999).

ACKNOWLEDGMENTS

We acknowledge the hard work and dedication of the riverboat survey observers, especially Admisson Martins Carvalho, and the boat crews. Galia Ely de Mattos contributed greatly to data handling and analysis. Jay Barlow kindly gave advice on the most appropriate survey methodology for large rivers.

This study was part of Projeto Boto, and a contribution to scientific research within the *Mamirauá* Sustainable Development Reserve. The staff and resources of Instituto Mamirauá were central to the successful conclusion of this study. We gratefully acknowledge funding from the Overseas Development Administration of the British Government (ODA, now DFID), World Conservation International (WCI/WCS), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Worldwide Fund for Nature (WWF), Instituto Nacional de Pesquisas da Amazônia (INPA), Instituto de Desenvolvimento Sustentável Mamirauá (IDSMA), Natural Environment Research Council (NERC), and the Darwin Initiative.

We thank Helene Marsh and an anonymous referee for their helpful reviews of this manuscript.

LITERATURE CITED

- BEST, R. C., AND V. M. F. DA SILVA. 1989. Amazon river dolphin, Boto. *Inia geoffrensis* (de Blainville, 1817). Pages 1–23 in S. H. Ridgway and R. J. Harrison, eds. Handbook of marine mammals. Volume 4. River dolphins and the larger toothed whales. Academic Press, London, United Kingdom.
- BEST, R. C., AND V. M. F. DA SILVA. 1993. *Inia geoffrensis*. The American Society of Mammalogists. Mammalian Species 426:1–8.
- BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS AND L. THOMAS. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford, United Kingdom.
- CRAMPTON, W. G. R. 1999. Os peixes da Reserva Mamirauá: Diversidade e história natural na planície alagável da Amazônia. Pages 10–36 in H. L. Queiroz and W. G. R. Crampton, eds. Estratégias para Manejo de Recursos Pesqueiros em Mamirauá. Sociedade Civil Mamirauá/CNPq, Brasília, Brazil.
- DA SILVA, V. M. F. 1983. Ecologia alimentar dos golfinhos da Amazônia. M.Sc. thesis, University of Amazonas, Manaus, Brazil. 118 pp.
- DA SILVA, V. M. F., AND R. C. BEST. 1994. Tucuxi—*Sotalia fluviatilis* (Gervais, 1853). Pages 43–69 in S. H. Ridgway and R. J. Harrison, eds. Handbook of marine mammals. Volume 5. The first book of dolphins. Academic Press, London, United Kingdom.
- HURTADO, L. A. C. 1996. Distribucion, uso del habitat, movimientos y organizacion social del bufeo colorado *Inia geoffrensis* (Cetacea: Iniidae) en el alto Rio Amazonas. Conservacion, Ecologia y Manejo de Recursos Naturales. M.Sc. Dissertation, Instituto Tecnológico y de Estudios Superiores de Monterrey—Campus Guayma, Monterrey, Mexico. 116 pp.
- LEATHERWOOD, J. S. 1996. Distributional ecology and conservation status of river dolphins (*Inia geoffrensis* and *Sotalia fluviatilis*) in portions of the Peruvian Amazon. Ph.D. thesis, Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX. 232 pp.
- MAGNUSON, W. E., R. C. BEST AND V. M. F. DA SILVA. 1980. Numbers and behavior of Amazonian dolphins, *Inia geoffrensis* and *Sotalia fluviatilis* in the Rio Solimões, Brasil. Aquatic Mammals 8:27–41.
- MARTIN A. R., AND V. M. F. DA SILVA. In press. River dolphins and flooded forest: Seasonal habitat use and sexual segregation of botos *Inia geoffrensis* in an extreme cetacean environment. Journal of Zoology, London.
- MCGUIRE, T. L., AND K. O. WINEMILLER. 1998. Occurrence patterns, habitat associations, and potential prey of the river dolphin, *Inia geoffrensis*, in the Cinaruco River, Venezuela. Biotropica 30:625–638.
- NORTHBRIDGE, S. P., AND R. J. HOFMAN. 1999. Marine mammal interactions with fisheries. Pages 99–119 in J. R. Twiss, Jr. and R. R. Reeves, eds. Conservation and management of marine mammals. Smithsonian Institution Press, Washington, DC.
- SCHMIDT, G. W. 1976. Primary production of phytoplankton in three types of Amazonian waters. IV. On the primary productivity of phytoplankton in a bay of the lower Rio Negro (Amazonas, Brazil). Amazoniana 5:517–528.
- SIOLI, H. 1984. The Amazon and its main affluents: Hydrography, morphology of the river courses, and river types. Pages 127–165 in H. Sioli, ed. The Amazon—Limnology and landscape ecology of a mighty tropical river and its basin. Junk, Dordrecht, The Netherlands.
- THOMAS, L., J. L. LAAKE, S. STRINDBERG, F. F. C. MARQUES, S. T. BUCKLAND, D. L. BORCHERS, D. R. ANDERSON, K. P. BURNHAM, S. L. HEDLEY AND J. H. POLLARD. 2002. Distance 4.0. Release 1. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. <http://www.ruwpa.st-and.ac.uk/distance/>
- VIDAL, O., J. BARLOW, L. A. HURTADO, J. TORRE, P. CENDÓN AND Z. OJEDA. 1997. Distribution and abundance of the Amazon river dolphin (*Inia geoffrensis*) and the tucuxi (*Sotalia fluviatilis*) in the upper Amazon River. Marine Mammal Science 13:427–445.

Received: 27 March 2003

Accepted: 17 October 2003