Number, seasonal movements, and residency characteristics of river dolphins in an Amazonian floodplain lake system

A.R. Martin and V.M.F. da Silva

Abstract: The size and structure of a community of Amazon river dolphins or botos, *Inia geoffrensis* (de Blainville, 1817), was investigated using boat surveys and long-term observations of recognisable animals. Year-round, some 260 botos occurred in or near the 225-km^2 Mamirauá várzea floodplain lake system, of which half were permanent residents by our definition. Seasonal variation in water levels influenced distribution between habitats but not the overall number of botos. Ninety percent of marked botos encountered within the lake system were permanent residents. There appeared to be a cline in site fidelity between those that always live in or near the system and those that visit at intervals of years. We estimated that 270 botos were "significant users" of the lake system (i.e., occurred within it for sufficient periods in a year to be observed at least once) and that many others visited for short periods. Individuals moved many tens to hundreds of kilometres along the rivers, but there was no broad-scale seasonal migration. The boto population of the central Amazon, at least, may be structured on the basis of floodplain lake systems, with extensive animal movement between systems. We estimate that 13 000 botos occur in the 11 240 km^2 Mamirauá Sustainable Development Reserve, which covers an estimated 11%–18% of várzea habitat in Brazil.

Résumé : Des inventaires par bateau et l'observation sur de longues périodes d'individus identifiables nous ont permis d'étudier la taille et la structure d'une communauté de dauphins de l'Amazone ou boutous, *Inia geoffrensis* (de Blainville, 1817). Au cours de l'année, quelque 260 boutous se retrouvent dans le système de 225 km^2 de lacs de la plaine d'inondation de la várzea de Mamirauá ou à proximité; la moitié sont, selon notre définition, des résidents permanents. La variation saisonnière du niveau de l'eau affecte la répartition des boutous dans les habitats, mais pas leur nombre total. Quatre-vingt-dix pour cent des boutous marqués rencontrés dans le système lacustre sont des résidants permanents. Il semble exister un gradient de fidélité au site, allant d'animaux qui vivent toujours dans le système ou à proximité à d'autres qui ne le visitent qu'à des intervalles de plusieurs années. Nous estimons que 270 boutous sont des utilisateurs significatifs du système lacustre (i.e. ils se retrouvent dans le système pour suffisamment de temps durant l'année pour être observés au moins une fois) et que plusieurs autres visitent le système pour de courtes périodes. Les individus se déplacent sur des distances de plusieurs dizaines à plusieurs centaines de kilomètre le long des rivières, mais il n'y a pas de migration saisonnière à grande échelle. Pour le moins, la population des boutous de l'Amazone central est probablement structurée en fonction des systèmes de lacs de la plaine d'inondation et il y a beaucoup de déplacements des animaux d'un système à l'autre. Nous estimons qu'il existe 13 000 boutous dans la Réserve de développement durable de Mamirauá qui couvre 11 240 km^2, soit environ 11 % – 18 % des habitats de várzea au Brésil.

[Traduit par la Rédaction]

Introduction

The Amazon river dolphin or boto, *Inia geoffrensis* (de Blainville, 1817), is a widespread and relatively numerous inhabitant of the Amazon and Orinoco river basins of South America (Best and da Silva 1989, 1993). The main stem of the Amazon is unobstructed by physical barriers such as rapids or dams for thousands of kilometres, and botos occur throughout its length except where the water becomes brackish as it nears the Atlantic Ocean. This continuity of distribution masks any population structure that may exist. The situation is made more difficult by the fact that the vast majority of botos cannot be readily distinguished by human eye and that their erratic surfacing behaviour renders photo-identification research techniques impractical even if theoretically possible (Trujillo 1994).

In much of the Amazon basin, floodplain lake systems fringe the main rivers, providing important habitat for a great variety of fish and their predators, including botos (Martin and da Silva 2004). Seasonally high densities of botos here indicate that lake systems are used preferentially, especially by females and their dependent offspring (Martin and da Silva 2004), and may provide some spatial structure

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to the boto population if individuals demonstrate fidelity to one or more such lake systems.

Wherever cetaceans occur in fresh water, their populations are subject to competition and damage from human activity (Reeves and Reijnders 2002). Knowledge of dolphin abundance and their site fidelity is of obvious value in assessing the importance of threats. In the Amazon, known threats to botos are all due to human use of their habitats and the surrounding land. They include incidental mortality in fishing gear, habitat fragmentation owing to the building of hydroelectric dams, and recently, in the area of this study, directed takes of botos for use as bait in catfish traps.

For 10 years, we have been marking botos at one lake system in the middle Amazon, and observing these individually recognisable animals through daily effort from boats and a moored raft. The facility to immediately distinguish botos (and to know their sex, age, and relationships) has transformed our ability to investigate numerous areas of biology, including patterns and scale of movement. This paper presents an analysis of the occurrence of individual botos in our study area within and between years. It addresses the question of population structure on a scale of tens of kilometres, as well as the concept of residency. It also presents an estimate of the number of botos occurring within and near the lake system on a day-to-day basis, and the total number of animals within the much larger Reserve of which the study area is a typical part.

Materials and methods

Study area

The study was carried out in the Mamirauá lake system and its environs centred at 64°45′W and 03°35′S, near the junction of the large white water rivers Solimões and Japurá, Brazil. Typically of lake systems in the floodplain of the central Amazon, Mamirauá is a mosaic of habitats (known as "várzea") that change seasonally with the annual flood cycle, including dense forest and lakes of various sizes connected by channels. The Mamirauá lake system is approximately 225 km^2 in extent, and parts of its main waterway are 30 km from the river Japurá to which the lake system is connected. For most of the year, botos are concentrated in lakes and channels that cover only a small proportion of this area, but at high water the area is almost entirely flooded and it effectively becomes an inland sea. The Mamirauá lake system is one of many that cover the 11 240 km^2 Mamirauá Sustainable Development Reserve. This conservation unit comprises an estimated 11%–18% of várzea habitat in Brazil (Pires 1974).

Marked botos

This paper is based largely on observations of 235 botos marked with freeze-branded characters during once-yearly capture programmes. With very few exceptions, botos were marked in late October or November, the time of year when water levels are at their lowest and most botos are at the river margins (Martin and da Silva 2004). Botos were captured using a seine technique and brought onto a shallowly shelving beach before being transferred to a floating laboratory that was located nearby. Full details of the procedures are given in da Silva and Martin (2000). Captures were made at two sites: one in bays at the mouth of the Mamirauá lake system and the other at the main waterway junction some 10 km inside the system. The sex ratio of marked botos was very close to parity (117 males : 118 females).

Observational effort

Observation teams were active in the study area on between 244 and 264 days in each of the 3 years from which data were contributed to this study, with a mean of 1385 h of effort per year. The observational platform was normally a 5-m aluminium skiff powered by a 15 horsepower outboard engine (1 horsepower = 746 W). Effort was not evenly distributed across the entire area for logistical reasons, but most accessible areas (determined by water level) were visited once per week, and the areas most used by botos were visited several times per week.

Density estimation

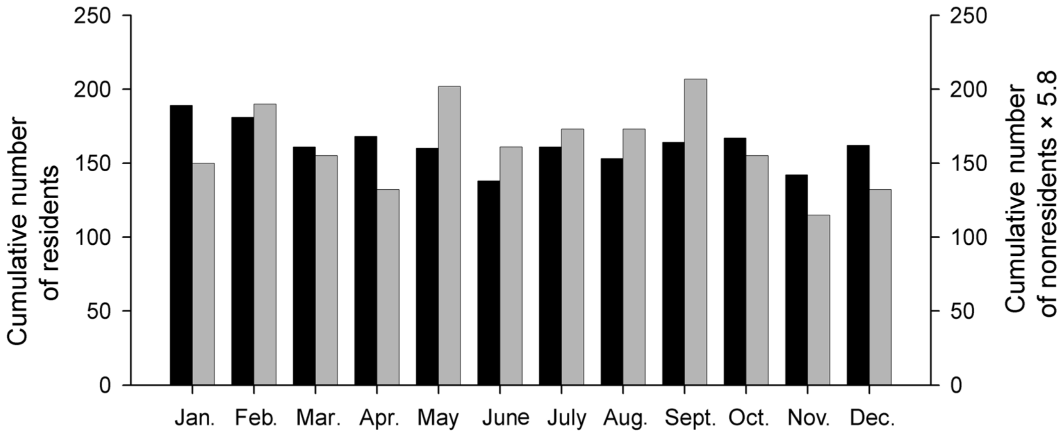
Estimates of boto density on rivers were made from a 16.8-m river boat using strip transects along the margins and line transects with distance sampling in all areas away from the margins. The total trackline length covered was 1402 km in strip transect mode and 810 km in line transect mode. Line transects were carried out in a zig-zag pattern, crossing the river between the marginal strips at an angle of approximately 45°. Resulting data were analysed using the 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). Full details of the methodology are given in Martin and da Silva (2004).

Regular surveys of botos within the lake system were made along a standard 30-km transect from the mouth of the system where it joins the river to the most distant part. These surveys produced a minimum count, and were always carried out along the same track and at the same time of day. The sighting platform was the 5-m skiff described above, with a complement of four trained people: two observers, a recorder, and a driver. One observer looked forward, using binoculars as much as possible to detect botos far ahead, and another to the rear. Some botos were overlooked with this technique, but the proportion seen and counted was perceived to be very high on the basis of test repeat counts made immediately after the first. We made the assumption only that the negative bias was similar between surveys.

Estimating the number or proportion of marked botos within a group

We refer to botos marked by us and the few bearing distinctive natural marks collectively as marked. The ratio of marked to unmarked botos within a group was estimated as follows. If the group size was exactly known, and the number of marked botos was also known, then these values were recorded. If not, then a series of visual samples was taken with replacement (i.e., not excluding marked botos seen before) at intervals of at least 60 s between samples to allow for mixing. During each sampling period the numbers of marked and unmarked botos surfacing within view of the boat was recorded. Each sample was completed after 10 s, or

Fig. 1. Cumulative numbers of marked botos (*Inia geoffrensis*) seen by month over the 3-year period, July 2000 to July 2003. Solid bars indicate residents, which are marked botos that were recorded in the study area in at least 7 months of any year (n = 1946); shaded bars indicate nonresidents, which are marked botos seen at least once in the study area but did not meet the residency criterion in any year (n = 338). For direct comparison between the groups to be made, the nonresident values were scaled up by the sample size ratio (5.8).



when there was a risk of two or more unmarked botos being confused by the observer, which ever was sooner. More samples were taken from the same group until the cumulative number of botos in all samples was approximately that of the estimated group size; therefore, the weighting of each group was proportional to the number of animals within the group.

Results

Numbers of botos using the Mamirauá lake system

Between 21 November 2001 and 2 November 2002 (i.e., the year between successive marking campaigns, with a stable number of marked botos in the population and ignoring mortality), 166 marked botos were seen within the study area, of which 132 were encountered at least once within the Mamirauá lake system itself. From subsequent recaptures, we estimated that 5% of the marked botos had insufficiently clear marks to allow unambiguous recognition. Inside the system within the same period, 56.6% of botos encountered were marked (n = 3470 encounters). The total number of botos of all ages using the lake system sufficiently often in the year to be recognised had they all been marked (hereinafter termed "significant users") can therefore be estimated as (132/0.566) × (100/95) = 245. The equivalent, independent, figures for the following year were 192 marked botos recognised in total, 144 within the system, 51.1% of 4116 encountered botos marked, and 297 significant users. The mean of the two estimates is 271.

Degree of residency

To investigate the degree of residency within and between years, the observational records of all marked botos seen within the study area over a 3-year period (August 2000 – July 2003) were examined. A "resident" was a boto that was recorded in at least 7 of 12 months in at least 1 of 3 years. "Permanent residents" met the criterion every year in which they were available to be identified, and "partial residents" met the criterion in one or more years but not in all. Marked botos that were seen at least once in the study area during the 3-year period but did not meet the residency criterion in any year were classified as "nonresidents". Of the 161 independent (post-weaning) botos identified during this period, 79 (49%) were classified on this basis as permanent residents, 13 (8%) as partial residents, and 69 (43%) as nonresidents. No resident was ever reported again after failing to be seen for an entire year, so it probably emigrated or died. The proportion of residents that were male (0.52) was higher than that of nonresidents (0.43), but not significantly so (χ^2 = 1.4, df = 1, p = 0.3).

The total number of botos of all ages meeting the criterion for permanent residents, N_{pr}, was estimated by assuming that the proportion of permanent residents was the same within the marked and unmarked populations of significant users, i.e., N_{pr} = (79/161) × 271 = 133. However, because permanent residents are probably more vulnerable to capture and marking than less frequent visitors to Mamirauá, 133 should be considered an upper bound on the true figure. Another implicit assumption in this calculation must be correct — that dependent calves have the same residency characteristics as their mothers.

The number of residents and of nonresidents identified within the study area in each month of the 3 years combined is shown in Fig. 1. The two histograms are not significantly different (χ^2 = 8.4, df = 11, p = 0.67), and when pooled, do not differ from a uniform distribution (χ^2 = 7.4, df = 11, p = 0.76), indicating that there is no clear seasonal influx or efflux of botos that occur within the area at some time of the year.

Ninety percent of sightings of marked botos within the lake system between November 2001 and November 2002 (n = 1732) were of residents or their dependent offspring.

Sampling differences with capture site

Seventy-two percent of 82 botos captured only within the lake system met the criterion of a resident compared with 36% of 56 botos captured only in bays at the entrance to the system. Thirteen of 16 botos (81%) captured twice within

Table 1. Estimated number of botos (*Inia geoffrensis*), and of marked botos, within the Mamirauá lake system zone of influence

	Water level (m)	Estimated mean no. per km of river	Percentage of marked botos on rivers	Estimated no. marked within 10 km of lake system[a]	Estimated no. in bays	Percentage marked in bays	Estimated no. of marked botos in bays[b]
June 1999	15.4	1.9	14.8	23.7	40	31	12.4
October 1999	3.9	2.2	23.5	43.8	40	41	16.4
March 2000	8.6	0.8	12.0	7.7	40	36	14.4
July 2000	13.8	1.8	13.5	20.7	40	32	12.8
March/April 2001	12.0	1.6	11.0	15.1	40	36	14.4

Note: The estimated mean number of botos per kilometre of river is based on a typical river width of 0.7 km during the low-water season (October when a constant number of marked botos were available to be seen (ignoring mortality).

[a]Value calculated as the estimated mean number of botos per kilometre of river × 84 × percentage of botos marked on rivers / 100.

[b]Value calculated as the estimated number of botos in bays × percentage of botos marked in bays / 100.

[c]Value calculated as the (minimum count of botos in the lake system + 20% for botos that were missed + estimated number of botos elsewhere in the

[d]Value calculated as the estimated mean number of botos per kilometre of river × 84 + estimated number of botos in bays + (minimum count of botos

[e]Value calculated as the (estimated mean number of botos per kilometre of river × 84 × percentage of botos marked on rivers / 100) + (estimated number estimated number of botos elsewhere in the lake system) × percentage of botos marked in the lake system / 100].

the system were residents compared with only 8 of 18 (44%) botos captured on two occasions in the bays.

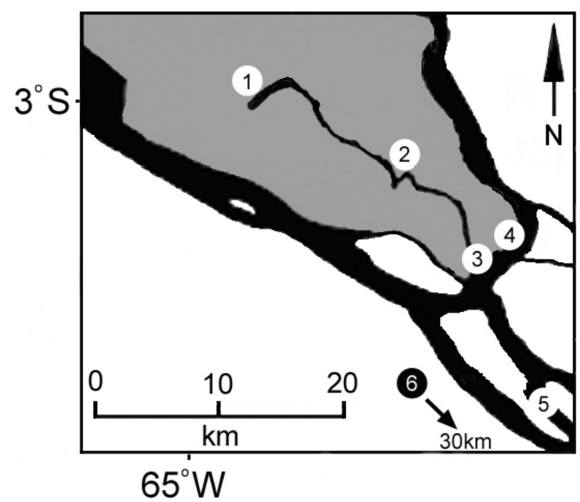
Numbers of botos in and near the study area through the year

The proportion of botos that were marked diminished rapidly with distance from the lake system (Fig. 2), and observations of marked botos were very infrequent beyond 10 km. None were recorded out of more than 200 observed in the region of Tefé, 30–35 km distant from the Reserve. We therefore arbitrarily define the area influenced by the lake system ("zone of influence") as the sum of three contiguous subzones: the system itself, bays at the entrance to the system, and rivers within 10 km of the system. The total number of botos within this zone was estimated seasonally using techniques appropriate for the various habitats within it. The study area is at the confluence of two rivers, so large waterways stretch in three directions from the main entrance to the Reserve. Islands approximately double the amount of boto habitat in the stretch of river where they occur by virtue of adding water margins (Martin et al. 2004). We estimated that the equivalent of 84 km of river habitat occur within 10 km of the Reserve, comprising 30 km defining its eastern border and a total of 54 km stretching in three directions as described above.

The number of animals within the zone of influence was estimated at various water levels between March 1999 and April 2001 (Table 1). The total number of botos within the lake system was calculated as the sum of three elements (i.e., those counted on the standard transect, those overlooked during the transect (estimated at 20% from marked animals known to be present), and those occurring in parts of the system (lakes, channels, and flooded forest) not covered by the standard transect). Based on repeated visits over 10 years, we allowed between 5 and 35 botos (according to season) for the latter, and estimated that approximately 40 animals occur in the bays at the mouth of the lake system year-round (Table 1).

Five multi-day river surveys were carried out between March 1999 and April 2001. The total trackline distance covered was 1402 km in strip transect mode and 810 km in line transect mode. Summary results of the strip transects and line transects are given in Tables 2 and 3. Mean densities of botos varied between 1.8 and 5.8 per km^2 along the river margins, and between 0.26 and 0.87 per km of river bank. Highest densities of botos on rivers were encountered at high and low water, and lowest at mid-rising water.

Fig. 2. Map of the study area showing rivers in black, the Mamirauá lake system in grey, and terra firme (i.e. land too high to be flooded) in white. Numbered sites and mean monthly percentages (in parentheses) of marked botos from November 2001 to November 2002 are as follows: 1, Mamirauá Lake (57.0%); 2, mid-channel (58.7%); 3, bays at the entrance to the lake system (36.7%); 4, river edge 2 km from the lake system entrance (12.5%); 5, river Solimões 8 km from the lake system entrance (10.3%); 6, Tefé Lake 30–35 km from the lake system (0%).



For line transect data from the centre of rivers, a variety of detection function models with different truncation distances and bin sizes were fitted to the sightings data using the program DISTANCE. On the basis of the Akaike's information criterion (AIC) and χ^2 goodness-of-fit values, a hazard-rate model fitted to a histogram with 45-m bins and truncated at 405 m was adopted (AIC = 557.2, χ^2 goodness-of-fit = 0.93). This also provided a good visual fit to the data (Fig. 3).

The results from these five independent surveys at varying water levels are brought together in Table 1, which shows (defined as the sum of three subzones: the system itself, bays at its entrance, and main rivers within 10 km) during the survey dates.

Minimum count in lake system	Add 20% for botos missed	Estimated no. elsewhere in lake system	Percentage of marked botos in lake system	Estimated no. of marked botos in lake system[c]	Total no. in zone of influence[d]	Estimated no. marked in zone of influence[e]
28	5.6	35	45.9	31	268	68
34	6.8	5	50.3	23	272	83
100	20	20	65	91	244	113
38	7.6	35	49.1	40	274	73
51	10.2	35	65	63	273	92

1999) and 1.0 km during all other times. The percentage marked in each subzone is based on data collected from November 2001 to November 2002

lake system) × percentage of botos marked in the lake system / 100.
in the lake system + 20% for botos that were missed + estimated number of botos elsewhere in the lake system).
of botos in bays × percentage of botos marked in bays / 100) + [(minimum count of botos in the lake system + 20% for botos that were missed +

Table 2. Summary results of strip surveys for botos carried out along the margins of the rivers Japurá and Solimões.

	Total distance covered (km)	Area within strips (km^2)	Number seen	Mean number per km of margin	Mean number per km^2	Water level (m)
June 1999	161.3	24.4	140	0.87	5.75	15.4
October 1999	172.3	33.7	131	0.76	3.89	3.9
March 2000	374.1	56.1	99	0.26	1.76	8.6
July 2000	227.3	33.9	164	0.72	4.84	13.8
March/April 2001	263.4	39.5	199	0.76	5.04	12.0

that the estimated number of botos within the zone of influence varied seasonally from 244 to 274.

The number of marked animals within the zone of influence was estimated on five occasions by multiplying the estimated number of botos in each subzone by the mean proportion of marked animals seen there during the appropriate season in the year 2001/2002. Between 68 and 113 marked botos were estimated to be within the zone (Table 1), with highest numbers in March 2000 when the water was at mid-level and rising. This compares with a minimum of 186 known to be alive during the year (166 seen during the year, and an additional 20 seen only in the following year), i.e., between an estimated 37% and 61% of marked botos were within the zone of influence at any one time.

Numbers of Mamirauá-marked botos in the nearest lake systems to Mamirauá were estimated during bimonthly small-boat surveys. The small Jacaré system 4–15 km from Mamirauá held between 2 and 4 marked animals (average 10% of 20–40 in total), and Jarauá, some 15–35 km distant, similarly held an estimated 2–4 (average 3% of 50–125 total animals).

Boto movements

Seasonal population-level movements in and out of the Mamirauá lake system were apparent from regular density estimates and confirmed by changes in the proportion of botos that were marked. Figure 4 shows the monthly proportions of marked animals in each of three habitats (i.e., lake system, bays at the entrance to the system, and river close to the main system entrance (<2 km)) from November 2001 to November 2002. The proportion marked was highest inside the system, lower in the bays, and lower still on the river. There was a significant negative correlation between the monthly proportion of marked botos in the lake system and on the rivers nearby (Pearson's coefficient = –0.606, p = 0.037). On a monthly basis within the lake system, less than half the animals encountered between high and low water were marked, but the proportion rose to approximately two-thirds between November and March (i.e., from the start of rising waters to mid-rising when numbers within the lake system are at their peak; Fig. 4). This must be due to the influx of botos being disproportionately of marked animals, i.e., returnees, since there were too few within the system at low water for any egress to have an impact.

Discussion

Numbers of botos using the Mamirauá lake system and their degree of residency

The results of this study point to approximately 350–450 botos using the Mamirauá lake system to some extent during the year, of which about 250–300 do so for more than a short visit and half that number treat it as their main area of residence. Some of the marked botos that were seen only outside the lake system probably occurred within it for a short period during the year, as did an unknown number of unmarked animals. We are unable to estimate the number of these visitors, but we believe that to have avoided detection the marked ones stayed in the lake system for no more than a few weeks, and in most cases much less time than this.

Because of the seasonal water level cycle, no boto spends its entire year within this lake system (Martin and da Silva

Table 3. Summary results of line transect surveys for botos carried out in the middle reaches of the rivers Japurá and Solimões.

		Density (number/km^2)								
	Survey effort (km of track)	Mean	% CV	df	Lower confidence limit	Upper confidence limit	Number of groups wthin 405 m of the track	Group size (mean ± SE)	Number within 315 m of the track	Water level (m)
June 1999	91.2	0.23	54.9	44.8	0.08	0.66	11	1.3±0.14	14	15.4
October 1999	118	1.75	23.9	115.5	1.1	2.79	45	1.6±0.11	67	3.9
March 2000	89.1	0.35	54.2	64.2	0.13	0.95	11	1±0	11	8.6
July 2000	133.2	0.55	43.2	61.3	0.24	1.25	17	1.4±0.12	23	13.77
April 2001	150.6	0.16	47.6	95	0.07	0.39	8	1±0	8	12.0

Note: Results are based on a hazard-rate model fitted to the sighting data and truncated at 405 m from the trackline (see Fig. 3).

2004), but the sighting records for individually recognisable animals (Martin and da Silva 2004; A.R. Martin and V.M.F. da Silva, unpublished data) demonstrate that some probably travel no farther than the area near the system entrance. At the other end of the spectrum, some well-marked individuals of both sexes were encountered in Mamirauá briefly at intervals of several years and, because they would have been recognised if seen, probably remained well away from the study area during the interim.

The densities of botos within this lake system (Martin and da Silva 2004) and others within 40 km (A.R. Martin and V.M.F. da Silva, unpublished data) are extremely high for periods of the year, and routinely higher than that of the large rivers which collectively form the greatest area of habitat available to this species (Martin and da Silva 2004). This preference for lake systems has resulted in some botos showing high levels of site fidelity for one particular system, and our data are consistent with most doing so. However, although the vast majority of botos within Mamirauá on any particular day are permanent residents by our definition, it is clear that fewer than half of the botos visiting the Reserve during a typical year would consider it “home”. They are either more closely associated with another lake system or are river-dwelling itinerants. The substantial proportion of Mamirauá residents that are apparently outside the lake system at any one time would likely have the behavioural characteristics of nonresidents at any other system they visit. The fact that 20 marked botos known to be alive during the main study year were not seen during the year, and an additional 34 were not seen within the lake system, demonstrates that a substantial proportion of these Mamirauá-marked animals are just intermittent visitors to the study area. This is likely because most captures were made in the bays at the entrance to the lake system in November when most botos were on the rivers or their margins (Martin and da Silva 2004). At this time of year the proportion of marked botos in these areas is low (Fig. 4), reflecting a disproportionate ingress of unmarked (and therefore more likely visiting) botos.

Because the sex ratio of botos occurring in the lake system is biased towards females, and males are numerically dominant on the rivers (Martin and da Silva 2004), the equal sex ratio of permanent residents was not anticipated. The definition of residency adopted here (observed in 7 or more months of a 12-month period) does not exclude the possibility that males are the more itinerant sex, but there is no clear support for this hypothesis within these data. It is more likely that males show a similar degree of site fidelity to the study area as females, but simply spend less time within the lake system itself and more on the rivers close to the system.

Despite the short distance between the three neighbouring lake systems and Mamirauá, only a small proportion of Mamirauá-marked botos was encountered within them. There is no evidence to indicate that a substantial number of Mamirauá-marked dolphins spend significant amounts of time in adjacent systems.

The discovery that as many as 100 botos apparently treat the Mamirauá lake system as their main centre of residence is not surprising. Várzea lake systems are recognised for the density and diversity of their fish fauna, and these fish are patchily distributed both temporally and spatially within complex habitats (Goulding 1980; Junk et al. 1997). A boto

Fig. 3. Probability of detection of botos with distance from the trackline during line transect surveys in the centre of rivers. Histogram shows the relative number of botos seen in contiguous 45-m "bins". The curve represents the best-fit model as determined by the program DISTANCE with the hazard-rate model truncated at 405 m.

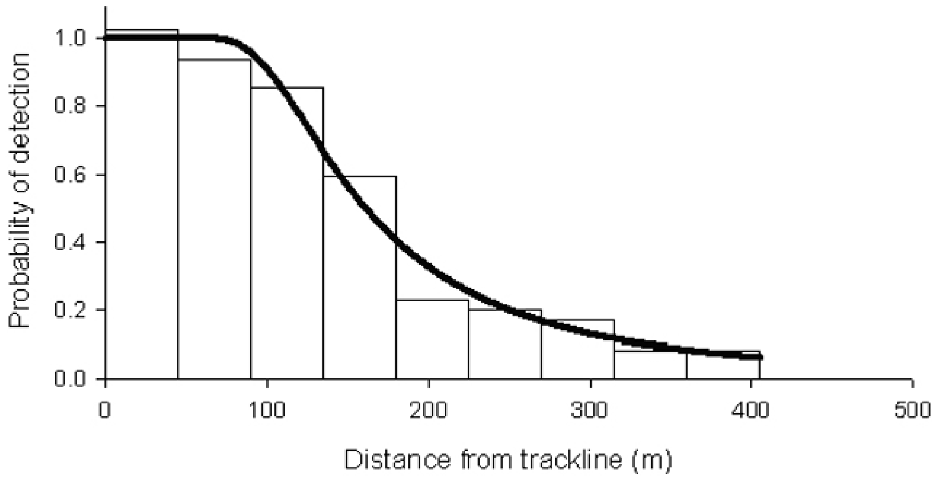
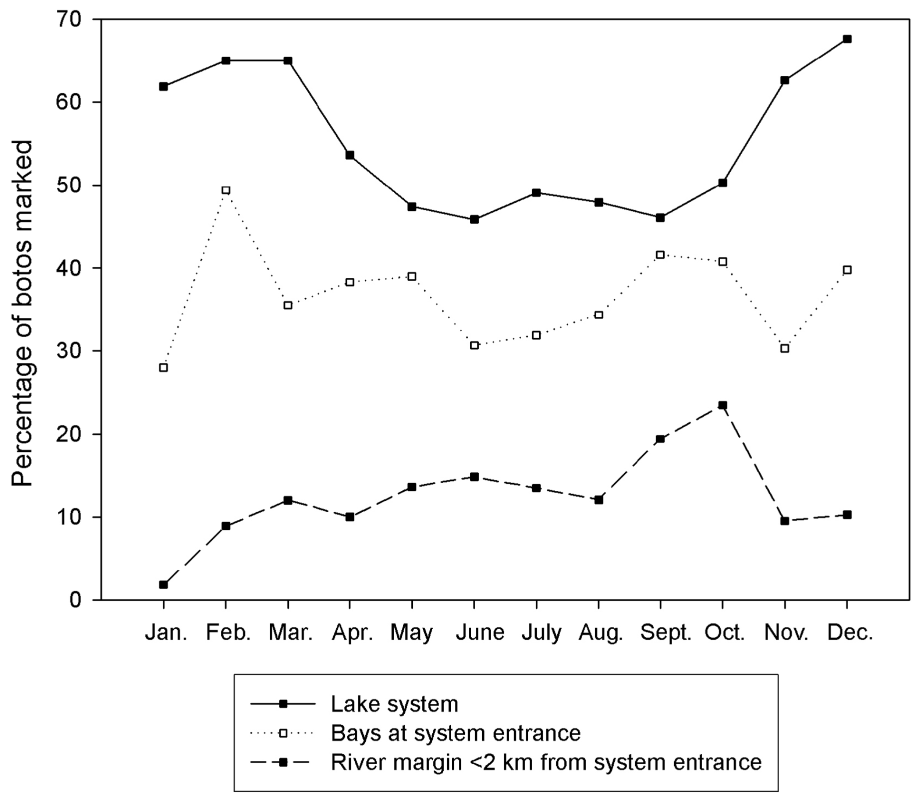


Fig 4. Monthly percentage of encountered botos that were marked in three key habitat zones. These data were collected between November 2001 and November 2002 (because the sample of marked botos did not change during this time), but are arranged as a conventional calendar year.



that has previous experience of an area could therefore benefit nutritionally compared with a naïve animal.

The site fidelity found in this study demonstrates that the boto population in the central Amazon is at least partly spatially structured, and that the structure is probably based on floodplain lake systems. Nevertheless, there is clearly a lot of movement along the rivers, and no suggestion of any isolation between residents of different systems. The implications of these results for the genetic structure of this population are clear: there is considerable potential for genetic exchange between areas, including lake systems, separated by hundreds of kilometres of unobstructed river.

The lack of a seasonal pattern in the number of either residents or nonresidents seen in the study area (Fig. 1) indicates that there is no clear distinction in this regard between the two groups and no strong seasonal migration in any Mamirauá users. The criterion used here to distinguish the groups is an arbitrary one and it is possible, indeed likely, that there is a cline in the degree of residency from those that never leave the Mamirauá system and its immediate environs to those that visit once in their lifetime. Certainly, we have no evidence of two or more distinct populations of botos (characterised by differences in site fidelity, ecology, and behaviour), as described for killer whales, *Orcinus orca* (L., 1758), off western North America (Baird 2000). Nevertheless, some level of seasonal movements is suggested by the resighting of a small number of individuals that are recorded in or near Mamirauá very infrequently, and always at the same time of year (A.R. Martin and V.M.F. da Silva, unpublished data).

Movements

The negative correlation between the monthly proportion of marked botos in the lake system and on the river within 2 km (Fig. 4) is consistent with other evidence (e.g., the rapid fall in the proportion of marked animals with distance from Mamirauá), indicating that many residents travel little distance when forced on to the river at low water. Nevertheless, anecdotal reports of marked animals up to 1000 km away are sufficiently regular to suggest that animals known from Mamirauá do travel considerable distances. That such movements are not permanent, in most cases at least, is indicated by the fact that the marked botos seen at the greatest distances have all subsequently been encountered within the study area.

Given the low percentage of marked animals seen on rivers outside the zone of influence (1.3%), most of those absent from Mamirauá were presumably spread thinly over a large area. There is insufficient evidence to indicate the distribution of these botos; however for illustrative purposes, 100 km of river would likely hold no more than 2–5 Mamirauá-marked botos (calculated as 1.3% of the mean number of animals per kilometre of river from our seasonal surveys plus 25% for islands).

Numbers of botos in the study area and local region

The five independent seasonal estimates of the number of botos occurring within the zone of influence (i.e., up to 10 km from Mamirauá) are remarkably consistent at between 244 and 274. This apparent consistency belies the fact that they include sampling error and a number of estimates. Nonetheless, there is certainly no evidence of substantial seasonal changes in boto numbers in this area, and an average of 260 ± 50 appears to be a reasonable year-round estimate. It is probably just a coincidence that this figure closely matches the number of significant users of the Mamirauá lake system. A substantial degree of movement of botos in and out of the zone is demonstrated by the fact that on any particular day a large number of marked animals, including many residents, are outside. Yet individual sighting histories demonstrate that almost all return after periods of days, weeks, or even years (A.R. Martin and V.M.F. da Silva, unpublished data).

From direct counts and density estimates based on visual surveys (Table 1), we derived a year-round total of some 260 botos in 225 km^2 of várzea floodplain habitat and 84 linear km of adjacent river, giving an average 1.16 botos per km^2 of várzea or 0.84 per km^2 in total. The Mamirauá Sustainable Development Reserve in its entirety covers 11 240 km^2 of várzea bounded by the same rivers as the study area. By extrapolation, we therefore estimate that some 13 000 botos occur in the Reserve or on its adjacent rivers on a day-to-day basis, and that substantially more use the Reserve for varying periods of time through the year.

The density of botos in this part of the central Amazon is high for a cetacean, and the abundance of this dolphin in the Mamirauá Reserve alone is probably greater than that of the two other river dolphin species living exclusively in fresh water combined (i.e., baiji (*Lipotes vexillifer* Miller, 1918) and Indian river dolphin (*Platanista gangetica* (Roxburgh, 1801))). There can be little doubt that the principal reason for this exceptional status is that, in contrast to the other major rivers in which river dolphins occur, the Amazon is as yet little damaged by human activity. Should they choose to do so, the botos at the focus of this study could swim to the headwaters of the Amazon, and to its mouth, without encountering any dam or irrigation barrier. The productive várzea habitat which helps to support the high boto density is ecologically intact. The status and ecology of botos today is probably little different to that pertaining before the region was settled by Europeans. It is, nonetheless, important to recall that the entire geomorphology of the Amazon is geologically recent. Várzea lake systems are a product of the Pleistocene and Holocene (Ayres 1993) and, consequently, appeared late in the evolutionary development of iniid dolphins (Hamilton et al. 2001). The genus *Inia* has clearly adapted very successfully to habitat changes on a geological timescale, but the demise of river dolphins elsewhere demonstrates that they are unlikely to do so in the face of the rapid changes currently being brought about by humans in the Amazon basin.

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