

# The lesser of two evils: seasonal migrations of Amazonian manatees in the Western Amazon

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## Keywords

*Trichechus inunguis*; habitat selection; remote sensing; geographical information system; Sirenia; migration.

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## Abstract

We investigated the paradox of why Amazonian manatees *Trichechus inunguis* undergo seasonal migrations to a habitat where they apparently fast. Ten males were tracked using VHF telemetry between 1994 and 2006 in the Mamirauá and Amanã Sustainable Development Reserves, constituting the only long-term dataset on Amazonian manatee movements in the wild. Their habitat was characterized by analysing aquatic space and macrophyte coverage dynamics associated with the annual flood-pulse cycle of the River Solimões. Habitat information came from fieldwork, two hydrographs, a three-dimensional model of the water bodies and classifications of Landsat-TM/ETM<sup>+</sup> images. We show that during high-water season (mid-May to end-June), males stay in *várzea* lakes in association with macrophytes, which they select. We then show that, during low-water (October–November), the drastic reduction in aquatic space in the *várzea* leads to the risk of their habitat drying out and increases the manatees' vulnerability to predators such as caimans, jaguars and humans. This explains why males migrate to Ria Amanã. Based on data on illegal hunting, we argue that this habitat variability influences females to migrate too. We then use published knowledge of the environment's dynamics to argue that when water levels are high, the habitats that can support the largest manatee populations are the *várzeas* of white-water rivers, and we conjecture that rias are the species' main low-water refuges throughout Western Amazonia. Finally, we warn that the species may be at greater risk than previously thought, because migration and low-water levels make manatees particularly vulnerable to hunters. Moreover, because the flooding regime of Amazonian rivers is strongly related to large-scale climatic phenomena, there might be a perilous connection between climate change and the future prospects for the species. Our experience reveals that the success of research and conservation of wild Amazonian manatees depends on close working relationships with local inhabitants.

## Introduction

Migration is an adaptation to environments in which habitat quality in different regions changes asynchronously in space and/or time (Dingle & Drake, 2007). This implies that habitat quality in the destination will be better than that at the origin, but not necessarily that it must be good. Here, we show that Amazonian manatees that live in the region of the Mamirauá and Amanã Sustainable Development Reserves (RDSM and RDSA, respectively) are subject to challenging habitat conditions during part of the year, and that they migrate into an area that is their best option under difficult circumstances.

We studied the influence of seasonal habitat variation on the migration of the Amazonian manatee *Trichechus inunguis*, which is the only member of the order Sirenia that lives exclusively in freshwater (Bertram & Bertram, 1973). Its distribution spans the Amazon basin, from Ecuador (Timm, Albuja & Clauson, 1986) and Peru (Reeves *et al.*, 1996) to the Atlantic coast of Brazil (Best, 1984). Phylogenetic studies suggest that manatees from the mid-Solimões, mid- and low-Amazonas form a single panmictic population (Cantanhede *et al.*, 2005).

Amazonian manatees are herbivores that in the RDSM and RDSA have been reported to feed on 63 species of

aquatic macrophytes (annual freshwater plants) (Guterres & Marmontel, 2008). Adults reach up to 3 m in length and 450 kg in weight (Caldwell & Caldwell, 1985), and consume about 8% of their body weight in aquatic macrophytes per day (Rosas, 1994). Because of strong habitat seasonality (see 'Materials and methods'), Amazonian manatees face an annual period of food shortage, which may last 7 months, during which they apparently fast (Best, 1983).

The first tracking of an Amazonian manatee was carried out by Montgomery, Best & Yamakoshi (1981). A juvenile male was captured in the wild, kept in captivity for 20 months (approximately half its life) and then released during the rising-water period in a *várzea* (a floodplain of a river with nutrient-rich and high-silt content water) near Manaus (a different region from where it had been captured). The manatee was tracked for 20 days, during which it spent most of its time feeding on aquatic macrophytes, and moved at a similar rate by day and by night.

The Amazonian manatee's migration was first reported by Marmontel *et al.* (2002), who tracked five adult males during a period of four and a half years. This showed that individuals migrated each year between *várzea* lakes, where they spent the high-water period, and Ria Amanã (a ria is long narrow lake formed by the partial submergence of a river valley), where they spent the low-water period (see 'Materials and methods'). Here, we extend the initial sample to 10 radio-tagged manatees to show (1) new migratory routes and (2) that the migration pattern remains consistent. We also indicate associations between Amazonian manatee

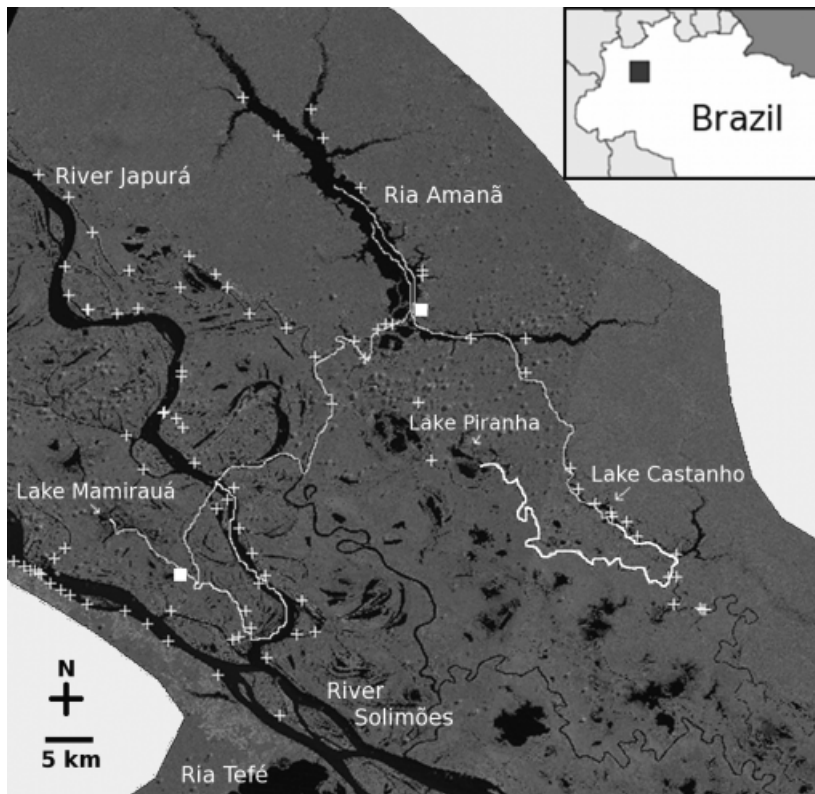
migratory movements and (3) availability of preferred food and (4) aquatic space reduction and predator aggregation. On that basis, we propose that the migratory behaviour, which is paradoxical insofar as animals travel to a place where, seemingly, they cannot eat, is a balance of feeding and predator avoidance. Finally, in the light of our results, we discuss the next steps for the species' conservation.

## Materials and methods

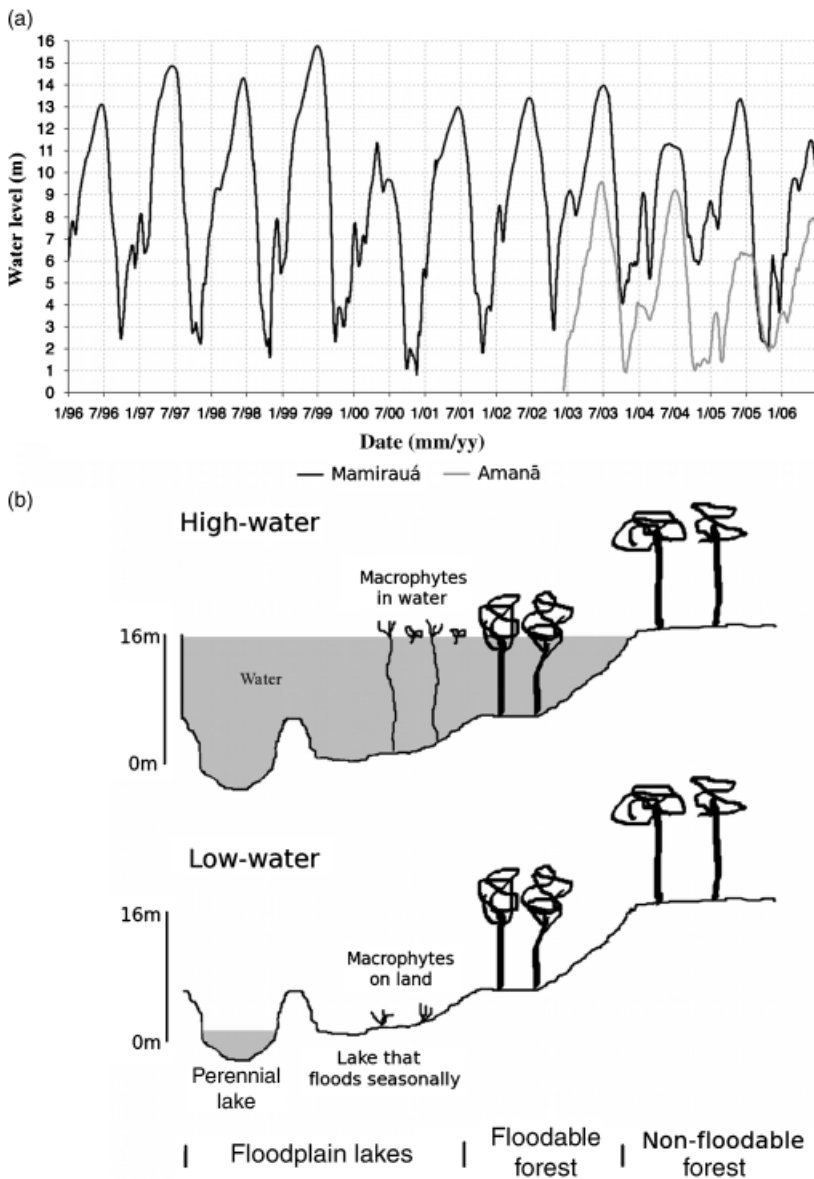
### Study site

The study region comprises just over 1 million hectares and lies within RDSM and RDSA, mid-River Solimões region, Amazonas, Brazil (Fig. 1). The region was chosen because there were previous data on radio-tracked manatees (Marmontel *et al.*, 2002), and the RDSM infrastructure facilitated fieldwork and the development of relationships with local communities. Its 120 km longitudinal extent (W65°03'43.60"–W63°51'49.80") encompassed all locations of the tracked manatees, and its 70 km latitudinal extent (S02°14'39.34"–S03°37'45.74) is bounded by *várzea* and by the Ria Amanã.

In the *várzea* study region, water levels fluctuate annually over a range of 16 m, while in Ria Amanã annual variation is about 10 m (Fig. 2a). This variation in water level is caused by a flood pulse in the River Solimões, and this pulse is the principal determinant of the extent and depth of flooding (Fig. 2b) and of the water's physical chemistry (Junk, Bayley



**Figure 1** Study region showing in: small quadrant, location in relation to South America; large quadrant, band 4 of Landsat-TM image overlaid by migration routes of male Amazonian manatees *Trichechus inunguis*. Thin white lines are routes reported by Marmontel *et al.*, (2002), thicker white lines are routes of manatees tracked later; thicker lines end at Lake Castanho so as not to mask previously detected routes, but all routes lead to or depart from Ria Amanã. Also shown are location of gauges (white squares) and of local human communities (white crosses).



**Figure 2** (a) Water-level variation as a result of River Solimões’s flood pulse measured by gauges positioned in the channel of Lake Mamirauá and in Ria Amaná (see Fig. 1). The gauges are not inter-calibrated, so hydrographs are only comparable with respect to time and water-level variation. (b) Habitats vary depending on flooding duration and flood pulse phase. When water levels are high, lakes, rivers and flooded forest are all passable for the manatee. When levels are low, lakes may lose connectivity.

& Sparks, 1989). As a result of this large variation in water level, and because of the irregular geomorphology of many lakes and channels, water depth is the principal determinant of the connectivity between water bodies. The differences of geomorphology and of water level variation explain, for example, why although Lake Mamirauá and Ria Amaná have similar depths during high-water, the former might become isolated during low-water while the latter remains deeper, connected to adjacent water bodies and with more aquatic space (Arraut, 2008). Based on this habitat seasonality, we distinguish between periods of lowering-water (July–August), low-water (September–November), rising-water (December–April) and high-water (May–June), defined on the basis of the water level and its speed of vertical change (Arraut, 2008).

### Manatee tracking

From 1994 to 2006 (excepting 2004), 10 males were radio-tracked with an Advanced Telemetry Systems (ATS) transmitter (Advanced Telemetry Systems Inc., Isanti, MN, USA) on the 164 MHz band using a three-element Yagi antenna. They were caught under government permit by research teams, sometimes aided by local hunters, mostly using a wide mesh net. Attempts were made to locate each individual once a day. Although hunting of Brazilian native fauna is illegal (Castello-Branco & Gomes, 1967), hunters eventually killed six out of our 10 tracked Amazonian manatees. We also captured three females, but we lost track of two on the following day and one was found dead 2 days later (Table 1). On some occasions, individuals were tracked

**Table 1** Information about tracked Amazonian manatees

ID	Gender	Capture		Tracking period	Seasonal ranges	N_locs used for range estimate	95% kernel range size (ha)
		Location	Water season				
1	M	L. Mamirauá	High	4 years	A B	36 18	1289 518
2	M	L. Mamirauá	High	3 years 4 months	A B	170 150	794 1952
3	M	L. Mamirauá	High	4 years 4 months	A B	58 50	727 1031
4	M	R. Amanã	Lowering	1 year 4 month	A B	92 61	394 2664
5	M	R. Amanã	Low	5 months	A B	9 6	3474 234
6	M	P. do Castanho	Low	3 years	A	85	308
7	M	L. Mamirauá	High	2 years 2 months	A	156	250
8	M	R. Amanã	Lowering	3 months	B	55	1186
9	M	R. Amanã	Lowering	3 months	B	43	2117
10	M	R. Amanã	Low	6 months	B	19	748
11	F	P. do Castanho	Lowering	Not tracked	–	–	–
12	F	P. do Castanho	Lowering	Not tracked	–	–	–
13	F	R. Amanã	Low	Not tracked	–	–	–

Number of locations used to calculate each of the seasonal home ranges is shown. Letter 'A' identifies high-water ranges in várzea lakes and letter 'B' identifies lowering-water ranges in River Japurá and low-water ranges in Ria Amanã (see 'Habitat Analysis' section).

L., lake; P., paranã; M, male; F, female; ID, individual identification.

but no GPS coordinate was associated to the location (Table 1); in these instances, the geographical location is recorded as the name of the place (lake or part of lake) where the individuals were active and, for analysis, subsequently given coordinates at the centre of that location. As a result, for this subsample of the data, all locations of all manatees that had been recorded as being from that place were allocated the same coordinates. Thus, for example, individual seven was located 168 times, and these sites are allocated, for analysis, to only 12 GPS positions.

### Estimation of manatee locations

We triangulated using the Best bi-angulation algorithm of the software LOCATION OF A SIGNAL (LOAS) 4.0b (ESS, 2006). Magnetic bearing corrections were calculated using the software DECLINAÇÃO MAGNÉTICA 2.0 (LEEE, 2003). Field experiments in which manatee tracking conditions were simulated at distances up to 2 km gave a mean positional error of 140 m (Arraut, 2008); we used a tracking resolution of 300 m, which was much smaller than either the range size or the dimensions of the habitat fragments.

### Migration detection and home-range calculations

We first separated ranging from migratory movements using the dispersal detector algorithm in the software RANGES8 (Kenward *et al.*, 2008). We detected that all the eight manatees that we tracked for more than one flood-pulse period had migrated. Then, because in the scale of our analysis the habitat showed annual seasonality, (e.g. macro-

phyte cover and flooding were similar in high-water periods of different years), we pooled locations of each individual in the same geographic area and flood-pulse period. Home ranges were estimated using 95% kernels with fixed-smoothing parameter (Kenward *et al.*, 2008). This model was especially appropriate because of variability in positional accuracy and owing to the small number of locations in some ranges (mean = 59, range = 6–170,  $n = 15$ ): kernels with fixed smoothing can give maximum range area estimates with as few as 12–15 locations (Kenward, 2001) (all but one animal had at least 12 locations); fixed smoothing also generates better overall surface estimates than adaptive smoothing (Seaman & Powell, 1996). Five individuals had two seasonal home ranges, whereas for the five other individuals, we could only calculate one home range.

### Habitat characterization

To analyse the spatial-temporal corollaries of manatee movement we considered: (1) water-level variation, measured daily from gauges with 1 cm interval positioned at Lake Mamirauá (since 1992) and Ria Amanã (since 2001); (2) the bottom topography and depths of water bodies, based on a bathymetric model from the field survey and geographical information system modelling; (3) the growth cycle and spatial distribution of macrophytes combined with the flooding dynamics in the area, from classifications of 11 Landsat-TM and ETM+ images acquired between 1995 and 2005 (three of the high-water, four of the lowering-water, two of the low-water and two of the rising-water). The total of 5 months of fieldwork was distributed throughout all four flood-pulse periods.

Frequent cloud cover over the Amazon limited the availability of good-quality satellite images. Previous studies, however, suggest that on a broad scale, the environment shows annual seasonality with regard to the flooding extent, water physical chemistry and macrophyte cover dynamics (Junk *et al.*, 1989; Junk & Piedade, 1993; Barbosa, 2005; Arraut, 2008). Thus, when images from the same dates as the tracking data were not available, we used images from a different year but same flood pulse period.

In the classifications, we distinguished six habitat classes: (1) macrophytes on water; (2) flooded forest; (3) open-water; (4) macrophytes on non-flooded land; (5) non-flooded forest; (6) non-flooded land. The first three occurred during high-water and the last three, plus open-water, during the low-water. Classification assessment was based on a confusion matrix (Congalton & Green, 2008), which indicated accuracies above 90%. Further details of the habitat characterization process are given in Arraut (2008).

## Habitat analysis

Habitat analysis addressed three questions:

*Question 1:* Selective use of habitat

Are males selective in their use of habitats, and specifically of aquatic macrophytes?

*Question 2:* Proportion of forage within home ranges during high-water

During the high-water, was there proportionally more forage in manatee home ranges within *várzea* lakes than if they had remained in River Japurá or Ria Amanã?

*Question 3:* Seasonal reduction in flooded area within home ranges

Did the proportional seasonal reduction in the aquatic area within home ranges differ between manatees in *várzea* lakes and those in River Japurá or Ria Amanã?

Selective use of habitat (question 1) was assessed using compositional analysis (CA) on log ratios of used and available habitats (Aebischer, Robertson & Kenward, 1993). To answer questions 2 and 3, we separated the 15 home ranges occupied by the 10 manatees into two categories: ranges in *várzea* lakes during the high-water (category A) and ranges in River Japurá during the lowering-water or in Ria Amanã during the low-water (category B). Ranges in River Japurá and Ria Amanã were grouped into one category because the objective was to discover, with quantitative evidence, why male manatees remained in *várzea* lakes during high-water, and why they did not remain there during low-water (i.e. why they migrated); this grouping also increased sample size for statistical analyses.

We carried out analyses of variance (ANOVA) by means of general linear models (GLM) using MINITAB v15.1.1 (Minitab, 2007). For question 2, the response variable in the GLM was the 'proportion of the home range covered by aquatic macrophytes' (arcsine root transformed), and for question 3, it was the 'proportional seasonal reduction in the flooded area' (arcsine root transformed). Although there

were too few ranges to test for inclusion of multiple predictor variables, we included individual identification (ID) and location number in each home range (N\_locs) in the GLMs with category variable A/B to exclude the possibility that relationships with the response variable depended on differences between individuals and sampling characteristics.

## Results

### Seasonal habitat use and migration

Males remained in *várzea* lakes from the middle of the rising to the beginning of the lowering-water period (approximately from February to the beginning of August), when flooding facilitated unconstrained access to all lakes, rivers and flooded forest. During the lowering-water, they left *várzea* lakes and migrated to Ria Amanã, where they stayed during the low-water. Then, during the rising-water, males migrated back to *várzea* lakes, thus closing the annual migratory cycle. The three females captured were either at (during low-water) or migrating to (during lowering-water) Ria Amanã, thus, moving in accordance with what was observed for the radio-tracked males.

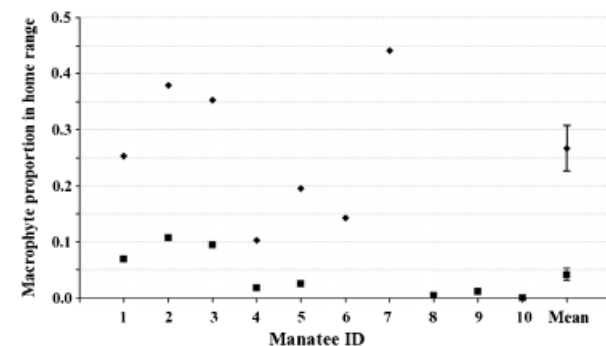
### Habitat analysis

#### Selective use of habitat

CA revealed aquatic macrophytes as the only preferred habitat class during high-water, and ranked the three habitat classes: (2) macrophytes, (1) open-water and (0) flooded forest [ $F(2, 5 \text{ d.f.}) = 7.56, P = 0.04$ ].

#### Proportion of forage within home ranges during high-water

During high-water, home ranges in *várzea* lakes (category A) encompassed almost sevenfold the area of aquatic macrophytes that occurred within home ranges in River Japurá or Ria Amanã (A: mean = 0.27, SE = 0.13; B:



**Figure 3** Macrophyte proportion in the home ranges of individuals was greater when in *várzea* lakes (◆) than when in River Japurá or Ria Amanã (■). ID, individual identification.

mean = 0.04, SE = 0.04) (Fig. 3). In the GLM, the category A/B variable explained the most variance in the response variable, and continued to do so with the inclusion of ID and N\_locs (Table 2). Model residuals showed no trend, indicating that the model was appropriate. Thus, the proportion of the home range classified as macrophyte habitat was greatest for males while they were in *várzea* lakes.

### Seasonal reduction in flooded area within home ranges

Reduction in the flooded area in *várzea* lakes was over 4.5 times greater than in River Japurá or Ria Amanã (A: mean = 0.98, SE = 0.01; B: mean = 0.21, SE = 0.07) (Fig. 4). In the GLM, variable A/B explained most of the variance in the response variable, and continued to do so with inclusion of ID and N\_locs (Table 3). Analysis of full model residuals showed no particular trend, indicating the model was appropriate. Areas within high-water ranges practically dried out during low-water, while areas where manatees had low-water ranges suffered much smaller reduction in the aquatic space.

After leaving Mamirauá while the water was lowering in 1996, individuals one, two and three remained for a few days in an area of River Japurá. They then disappeared during the low-water, only to return in the next rising-water. On the other hand, individuals captured at Paran  do Castanho during the lowering-water were moving in the direction of

**Table 2** General linear model results: *F* statistic and *P* values for response variable 'macrophyte proportion in the home ranges' for full and reduced models

Explanatory variables	A/B	N_locs	ID
Variable alone	38.48 <sup>a</sup>	0.51 <sup>d</sup>	0.73 <sup>d</sup>
A/B with each	–	31.20 <sup>b</sup>	67.50 <sup>b</sup>
A/B with both	–	121.36 <sup>c</sup>	

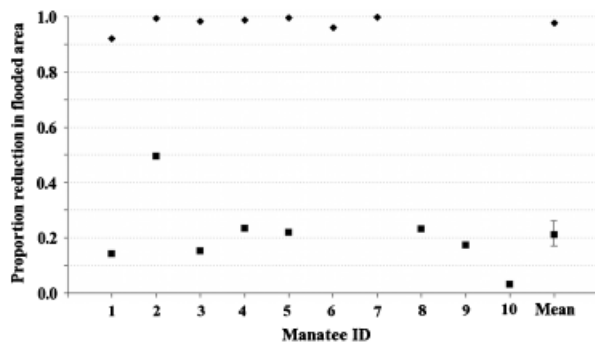
<sup>a</sup>*P* < 0.001.

<sup>b</sup>*P* = 0.001.

<sup>c</sup>*P* = 0.002.

<sup>d</sup>*P* not significant.

ID, individual identification.



**Figure 4** Proportion reduction in flooded area (from high- to low-water) was much greater for ranges in *várzea* lakes (◆) than for those in River Japurá or Ria Amanã (■). ID, individual identification.

**Table 3** General linear model results: *F* statistic and *P* values of the A/B variable 'proportion reduction in flooded area' for the full and reduced models

Explanatory variables	A/B	N_locs	ID
Variable alone	227.37 <sup>a</sup>	0.93 <sup>c</sup>	0.40 <sup>c</sup>
A/B with each	–	238.94 <sup>a</sup>	165.14 <sup>a</sup>
A/B with both	–	138.70 <sup>b</sup>	

<sup>a</sup>*P* < 0.001.

<sup>b</sup>*P* = 0.001.

<sup>c</sup>*P* not significant.

ID, individual identification.

Ria Amanã, and all those captured and/or tracked during low-water were within Ria Amanã (*n* = 9). This suggests that manatees aggregate in Ria Amanã during low-water.

## Discussion

*Várzea* species are adapted to the seasonality of the environment (Junk *et al.*, 1989). In the RDSM region, river dolphins *Inia geoffrensis* spend the high-water in *várzea* lakes and in flooded forest, but during low-water, they are in the main channels of Rivers Solimões and Japurá (Martin & da Silva, 2004). Male Amazonian manatees also lived in *várzea* lakes during high-water, but in the low-water migrated to Ria Amanã.

The *várzea* lakes used during high-water offered forage in greater abundance [Results (1) and (2); Fig. 3, Table 2] and diversity (Junk *et al.*, 1989; Arraut, 2008; Guterres & Marmontel, 2008), and less water current than rivers and paranás (channels that connect rivers). When the water level dropped and the flooded area significantly contracted, restricting their home ranges [Result (3), Fig. 4, Table 3], male manatees migrated to Ria Amanã where they spent the low-water season. There, apart from more space, they encounter reduced risk from predators like: caimans *Melanosuchus niger* and *Caiman crocodilus* (Nunes Pereira, 1947), jaguars *Panthera onca* (Bertram & Bertram, 1973) and humans *Homo sapiens sapiens* (Domning, 1982a; Marmontel, 2008). During the low-water period, caimans aggregate in whichever water bodies remain in the *várzea* (E. M. Arraut & M. Marmontel, pers. obs.), jaguars frequent the water margins (Ramalho, 2006) and humans come to gather the fish that aggregate there. Conversely, local hunters assert that the manatees in Ria Amanã are more difficult to kill (Calvimontes, 2009).

Further information from interviews with local hunters indicates that female manatees have seasonal movement patterns similar to those of males. Sixty-four manatees were killed in Lake Castanho, Ria Amanã and the migration route between them during 2002–2004 (Calvimontes, 2009). These manatees were killed in Lake Castanho only between the rising- and the mid-lowering-water seasons and in Ria Amanã, only between the lowering- and the beginning of the rising-water seasons. Of the 35 that had their sex determined, there were 13 males and 22 females. All four manatees killed in upper-Amanã at the beginning of the

rising-water were females, including two that were calves (Calvimontes, 2009). From estimated birth dates of 24 neonate Amazonian manatees, Best (1982) suggested that calves are normally born during the period of rising-water. As gestation is 12–14 months (Rosas, 1994), mating is expected to occur during low-water or the start of rising-water. Therefore, Ria Amanã may be both a mating and calving ground for Amazonian manatees.

### Do manatees that live in the *várzeas* of other white-water rivers move similarly as those in the mid-Solimões region?

In the Amazon, immense white-water rivers such as the Solimões, Amazonas, Purús and Madeira form *várzeas* and have rias annexed to their *várzeas*. They are also typified by flood pulses, and seasonal macrophytes (Junk & Furch, 1993) (Fig. 5). The habitats available to manatees in these other regions of the Amazon, thus, seem similar to that which we have described in our study region.

Evidence for the occurrence of manatees in these areas Acuña (1641), who reported them as abundant enough to be easily seen throughout the Rivers Solimões and Amazonas, and Domning (1982a), who analysed the records of manatees hunted (legally at the time) that were documented in Manaus between 1785 and 1983. Based on such information, as well as on how the large-scale movements of manatees in our study region coincide closely with the flood pulse, we conjecture that the habitats that can sustain the largest populations of *T. inunguis* during the high-water are the *várzeas* of large white-water rivers.

On the other hand, during low-water, when most of the *várzea* dries out, rias remain the main places where aquatic space (Hess *et al.*, 2003) with minimal current can be found. We thus conjecture that rias are the main low-water refuges of manatees that live in the floodplains of these major white-water rivers; these floodplains comprise the great majority of the manatees' known geographical range.

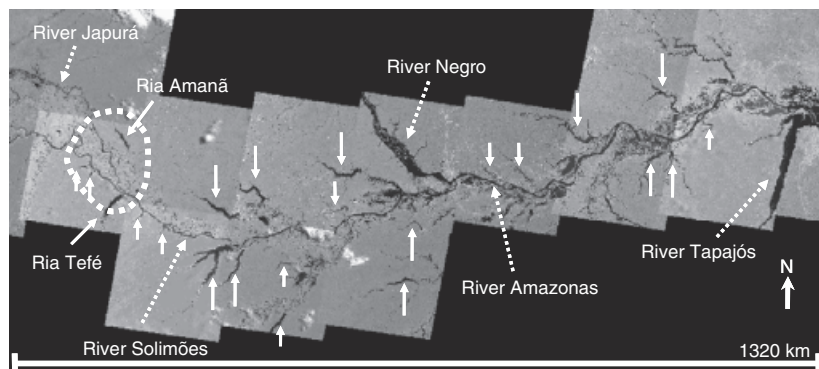
### Evolutionary ecology of the Amazonian manatees' migration

Seasonal migrations have been well documented in other aquatic mammals, and the ecological processes that drive

migration often seem to be related to habitat variability. The Florida manatee *Trichechus manatus latirostris* (Deutsch *et al.*, 2003) and the dugong *Dugong dugon* (Sheppard *et al.*, 2006) migrate to warmer waters in autumn, and back to their summer areas in spring. In these two species, the evolution of migration can be explained as a means of optimizing forage when it is available and avoiding harsh environmental conditions during the rest of the year. We have demonstrated comparable seasonal movements for Amazonian manatees, although in their case the 'seasons' are determined by variation in water level and the limiting factors are space and predation.

*Trichechus inunguis* is thought to be the most derived species of manatee, having evolved from ancestral trichechids that colonized the Western Amazon in the Pliocene (2–6 million years ago) (Domning, 1982b). Geological evidence suggests that the *várzea* of River Solimões achieved its present form in the Holocene (<10 000 years), and that terraces on its sides were formed a bit earlier, in the last 47 300 years (Rossetti, Toledo & Góes, 2005). Because rias are formed by the excavation of such terraces by ancient rivers, they must be younger than the terraces. Thus, the use of Ria Amanã as a breeding and calving ground, and migration to it, must be a relatively recent phenomenon in the species' evolutionary history and, if our conjecture is correct, this also applies to the use of other rias. The geological history of the Western Amazon thus indicates that Amazonian manatees have changed their spatial behaviour in response to changes in the habitat that occurred within the last few tens of thousands of years.

The fact that manatees living from the mouth of the River Amazon and those occurring throughout Amazonia to the west are part of a single panmictic population (Cantanhede *et al.*, 2005) indicates that any differences in the movements of individuals in these widely separated areas are probably a result of behavioural plasticity in response to local habitat conditions. This raises the question: what are the movement patterns of the manatees living near the mouth of River Amazon (Domning, 1981), where water level varies daily (ANA, 2009) because of the Atlantic tides and where there are no rias? How do these differences in the spatial-temporal dynamics of their habitats affect manatee reproductive ecology? For example, if manatees find forage and living space in the same area throughout the year, we would not



**Figure 5** Rias (shown by arrows), which are numerous and of various sizes, occur throughout the margins of Rivers Solimões and Amazonas and are conjectured to be the Amazonian manatee's main low-water refuges. Study-region limits indicated by dashed-line polygon. Landsat-TM mosaic of the central Amazon *várzea*. Source: Shimabukuro, Novo & Mertes (2002).

expect them to migrate. Answers to these questions await further research.

### Conservation implications

Migrating Amazonian manatees pass through narrow channels where hunters can wait within harpoon range. Because human settlements are numerous and widespread (Fig. 1), and local inhabitants relish manatee meat, and are aware of the timing of their migration, manatees have to pass through perilous bottlenecks to arrive at the relative safety of Ria Amanã. Then, in the beginning of the rising-water, water levels rise sufficiently to flood the few beaches where macrophytes have been growing close to the mouth of Ria Amanã. The manatees aggregate at these beaches, hungry after several months of fasting and again become vulnerable to hunters. Hence, the migration to, and prolonged occupation of, Ria Amanã present clear risks to contemporary manatees. Nevertheless, the fact that manatees migrate to Ria Amanã, and that, as argued above, this migratory behaviour is probably not genetically determined, suggests that staying in *várzea* lakes during the low-water has been (at least until recently) even more perilous. The lowering- and low-water seasons are, thus, periods when Amazonian manatees living in the mid-Solimões region have to choose between the lesser of two evils.

Any climate changes that lead to more intense droughts, and thus to a reduction in the aquatic space during the low-water period, would increase the exposure of Amazonian manatees to hunters. A connection between climate change and an increase in the frequency of droughts in the Amazon is predicted under all scenarios of all 23 IPCC climatic models (Malhi *et al.*, 2008), and relationships between large-scale climatic phenomena, such as the El Niño Southern Oscillation and the Tropical North Atlantic Ocean Temperatures, and the levels of major Amazonian rivers, were determined by Richey, Nobre & Deser (1989), Schongart & Junk (2007) and Marengo *et al.* (2008*a,b*). A situation that might become more frequent is exemplified by the drought of 2005, estimated to be the most intense in the last 40 years, when the Amazon River and its major tributaries were left with only a fraction of their normal volume (Marengo *et al.*, 2008*a,b*). During this drought, enormous quantities of fish died, clogging rivers and poisoning the water, and people living in small communities had to walk several kilometres to find water and food (Giles, 2006). Amazonian manatees also suffered. Local people informed us of the killings of at least five manatees in Ria Tefé, and colleagues working in River Purús informed us of at least 12 that were killed in Ria Jari (B. Marioni, E. V. Mullen & F. Rossoni, pers. comm.).

In order to protect the manatees better now, and to safeguard them in the face of climate change, it is important to research their status in other regions, and to complement such research with education. Our experience indicates that to be effective, any conservation programme needs to learn from, educate and bring benefits to local populations, because local people are necessary actors in conserving the manatees and

their environment. Our conjecture that rias are the manatee's main low-water refuge can serve as a starting point in the search for manatees in other regions of the Amazon.

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### References

- Acuña, C. (1641). *Novo descobrimento do Grande Rio Amazonas/Critóbal de Acuña, 1641*. Rio de Janeiro: Agir.
- Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313–1325.
- ANA. (2009). Hidroweb – Hydrological Information System, Brazilian National Agency of the Waters. Available at <http://hidroweb.ana.gov.br/> (accessed 10 February 2009).
- Arraut, E. (2008). *Migração do Peixe-boi Amazônico: uma abordagem por sensoriamento remoto, radiotelemetria e geoprocessamento*. PhD thesis, Instituto Nacional de Pesquisas Espaciais (National Institute for Space Research), São José dos Campos.
- Barbosa, C.C.F. (2005). *Sensoriamento Remoto da dinâmica da circulação da água do sistema planície de Curuai/Rio Amazonas*. São José dos Campos: Instituto Nacional de Pesquisas Espaciais.
- Bertram, G.C.L. & Bertram, C.K.R. (1973). The modern Sirenia: their distribution and status. *Biol. J. Linn. Soc.* **5**, 297–338.
- Best, R.C. (1982). Seasonal breeding in the Amazonian manatee, *Trichechus inunguis* (Mammalia, Sirenia). *Biotropica* **14**, 76–78.
- Best, R.C. (1983). Apparent dry-season fasting in Amazonian Manatees (Mammalia: Sirenia). *Biotropica* **15**, 61–64.
- Best, R.C. (1984). The aquatic mammals and reptiles of the Amazon. In *The Amazon limnology and landscape ecology of a mighty tropical river and its basins*: 371–412. Sioly, H. (Ed.). Dordrecht: Dr Junk W. Publishers.
- Caldwell, D.K. & Caldwell, M.C. (1985). Manatees *Trichechus manatus* (Linnaeus, 1758); *Trichechus senegalensis*



- (Link, 1795) and *Trichechus inunguis* (Natterer, 1883). In *Handbook of marine mammals*: 33–66. Ridgway, S.H. & Harisson, R. (Eds). London: Academic Press.
- Calvimontes, J. (2009). *Etnoconocimiento, uso y conservación del manatí amazónico Trichechus inunguis en la Reserva de Desarrollo Sostenible Amanã, Brasil*. Lima: Universidad Nacional Agraria La Molina.
- Cantanhede, A., Da Silva, V., Farias, I., Hrbek, T., Lazzarini, S. & Alves-Gomes, J. (2005). Phylogeography and population genetics of the endangered Amazonian manatee, *Trichechus inunguis* Natterer, 1883 (Mammalia, Sirenia). *Mol. Ecol.* **14**, 401–413.
- Castello-Branco, H. & Gomes, S.F. (1967). *Lei de proteção da fauna silvestre (Law for the protection of native fauna)*. Brasília: C. C. Presidência da República, Subchefia de Assuntos Jurídicos.
- Congalton, R.G. & Green, K. (2008). *Assessing the accuracy of remotely sensed data: principles and practices*, 2nd edn. Boca Raton: CRC Press, Taylor & Francis Group.
- Deutsch, C., Reid, J., Bonde, R., Easton, D., Kochman, H. & O'Shea, T. (2003). Seasonal movements, migratory behavior, and site fidelity of West Indian manatees along the Atlantic coast of the United States. *Wildl. Monogr.* **151**, 1–77.
- Dingle, H. & Drake, V. (2007). What is migration? *Bioscience* **57**, 113–121.
- Domning, D. (1981). Distribution and status of manatees *Trichechus* spp. near the mouth of the Amazon River, Brazil. *Biol. Conserv.* **19**, 85–97.
- Domning, D. (1982a). Commercial exploitation of manatees *Trichechus* in Brazil c. 1785–1973. *Biol. Conserv.* **22**, 101–126.
- Domning, D. (1982b). Evolution of manatees: a speculative history. *J. Paleontol.* **56**, 599–619.
- ESS. (2006). *Location of a Signal (LOAS)*. Heymagas: Ecological Software Solutions LLC.
- Giles, J. (2006). The outlook for Amazonia is dry. In *Nature news*: 726–727. Campbell, P. & Lincoln, T. (Eds). London: Nature Publishing Group.
- Guterres, M. & Marmontel, M. (2008). *Anatomia e Morfologia de plantas aquáticas da Amazônia utilizadas como potencial alimento pelo peixe-boi amazônico*. Belém: Instituto de Desenvolvimento Sustentável Mamirauá.
- Hess, L.L., Melack, J.M., Novo, E., Barbosa, C.C.F. & Gastil, M. (2003). Dual-season mapping of wetland inundation and vegetation for the central Amazon basin. *Remote Sens. Environ.* **87**, 404–428.
- Junk, W.J., Bayley, P.B. & Sparks, R.E. (1989). The flood pulse concept in river–floodplain systems. In *Proceedings of the International Large River Symposium (LARS)*: 110–127. Dodge, D.P. (Ed.). Toronto: Canadian Special Publication of Fisheries and Aquatic Sciences.
- Junk, W.J. & Furch, K. (1993). A general review of tropical South American floodplains. *Wetl. Ecol. Mgmt.* **2**, 231–238.
- Junk, W.J. & Piedade, M.T.F. (1993). Biomass and primary-production of herbaceous plant communities in the Amazon floodplain. *Hydrobiologia* **263**, 155–162.
- Kenward, R.E. (2001). *A manual for wildlife radio tagging*. London: Academic Press.
- Kenward, R.E., Walls, S.S., South, A.B. & Casey, N. (2008). *Ranges8 for the analysis of tracking and location data*. Wareham: Anatrack Ltd.
- LEEE. (2003). *Declinação Magnética 2.0*. Santa Catarina: Laboratório de Eficiência Energética em Edificações.
- Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W. & Nobre, C.A. (2008). Climate change, deforestation, and the fate of the Amazon. *Science* **319**, 169–172.
- Marengo, J.A., Nobre, C.A., Tomasella, J., Cardoso, M.F. & Oyama, M.D. (2008a). Hydro-climatic and ecological behaviour of the drought of Amazonia in 2005. *Philos. Trans. Roy. Soc. Lond. Ser. B Biol. Sci.* **363**, 1773–1778.
- Marengo, J.A., Nobre, C.A., Tomasella, J., Oyama, M.D., Oliveira, G.S., Oliveira, R., Alves, L.M. & Brown, I.F. (2008b). The drought of Amazonia in 2005. *J. Clim.* **21**, 495–516.
- Marmontel, M. (2008). *Trichechus inunguis*. Available at <http://www.iucnredlist.org> (accessed 19 February 2009).
- Marmontel, M., Guterres, M., Meirelles, A.C., Calvimontes, J. & Rosas, F.C.W. (2002). Lago Amanã: destino estival de manatíes amazônicos en la Amazonia occidental brasileña.: 40. Reunion de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur (RT), 10 Congreso Sociedad Latinoamericana de Especialistas en Mamíferos Acuáticos (SOLAMAC), Valdivia, Chile.
- Martin, A.R. & da Silva, V.M.F. (2004). River dolphins and flooded forest: seasonal habitat use and sexual segregation of botos (*Inia geoffrensis*) in an extreme cetacean environment. *J. Zool. (Lond.)* **263**, 295–305.
- Minitab. (2007). *Minitab*. State College: Minitab Inc.
- Montgomery, G.G., Best, R.C. & Yamakoshi, M. (1981). A radio-tracking study of the Amazonian manatee *Trichechus inunguis* (Mammalia: Sirenia). *Biotropica* **13**, 81–85.
- Nunes Pereira, M. (1947). *O peixe-boi da Amazônia*. Manaus: Imprensa Oficial.
- Ramalho, E.E. (2006). *Uso do hábitat e dieta da Onça-pintada (Panthera onca) em uma área de várzea, Reserva de Desenvolvimento Sustentável Mamirauá, Amazônia Central, Brasil*. Masters thesis, Instituto Nacional de Pesquisas da Amazônia (National Institute for Research in Amazonia), Manaus.
- Reeves, R.R., Leatherwood, S., Jefferson, T.A. & Curry, B.E. (1996). Amazonian manatees, *Trichechus inunguis*, in Peru: distribution, exploitation, and conservation status. *Inter-ciência* **21**, 246–254.
- Richey, J.E., Nobre, C. & Deser, C. (1989). Amazon river discharge and climate variability: 1903 to 1985. *Science* **246**, 101–103.

- Rosas, F.C.W. (1994). Biology, conservation and status of the Amazonian manatee *Trichechus inunguis*. *Mammal. Rev.* **24**, 49–59.
- Rossetti, D.F., Toledo, P.M. & Góes, A.M. (2005). New geological framework for Western Amazonia (Brazil) and implications for biogeography and evolution. *Quat. Res.* **63**, 78–89.
- Schongart, J. & Junk, W.J. (2007). Forecasting the flood-pulse in Central Amazonia by ENSO-indices. *J. Hydrol.* **335**, 124–132.
- Seaman, D.E. & Powell, R.A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*. **77**, 2075–2085.
- Sheppard, J., Preen, A., Marsh, H., Lawler, I., Whiting, S. & Jones, R. (2006). Movement heterogeneity of dugongs, *Dugong dugon* (Müller), over large spatial scales. *J. Exp. Mar. Biol. Ecol.* **334**, 64–83.
- Shimabukuro, Y., Novo, E.M.L.M. & Mertes, L.K. (2002). Amazonas river mainstream floodplain Landsat TM digital mosaic. *Int. J. Remote Sens.* **23**, 57–69.
- Timm, R., Albuja, V. & Clauson, B. (1986). Ecology, distribution, harvest, and conservation of the Amazonian manatee *Trichechus inunguis* in Ecuador. *Biotropica* **18**, 150–156.