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.

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+ 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 Amana (a ria is a 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 RDHA, 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°11'14"–S03°13'45.74") is bounded by várzea and by the Ria Amana.

In the várzea study region, water levels fluctuate annually over a range of 16 m, while in Ria Amana 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...
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 Amana 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).

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...
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.

### Table 1 Information about tracked Amazonian manatees

<table>
<thead>
<tr>
<th>ID</th>
<th>Gender</th>
<th>Capture Location</th>
<th>Water season</th>
<th>Tracking period</th>
<th>Seasonal ranges</th>
<th>N_locs used for range estimate</th>
<th>95% kernel range size (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>M</td>
<td>L. Mamirauã</td>
<td>High</td>
<td>4 years</td>
<td>A</td>
<td>36</td>
<td>1289</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>B</td>
<td>18</td>
<td>518</td>
</tr>
<tr>
<td>2</td>
<td>M</td>
<td>L. Mamirauã</td>
<td>High</td>
<td>3 years 4 months</td>
<td>A</td>
<td>170</td>
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<td>1932</td>
</tr>
<tr>
<td>3</td>
<td>M</td>
<td>L. Mamirauã</td>
<td>High</td>
<td>4 years 4 months</td>
<td>A</td>
<td>58</td>
<td>727</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>1031</td>
</tr>
<tr>
<td>4</td>
<td>M</td>
<td>R. Amanã</td>
<td>Lowering</td>
<td>1 year 4 month</td>
<td>A</td>
<td>92</td>
<td>394</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>B</td>
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<td>2664</td>
</tr>
<tr>
<td>5</td>
<td>M</td>
<td>R. Amanã</td>
<td>Low</td>
<td>5 months</td>
<td>A</td>
<td>9</td>
<td>3474</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>B</td>
<td>6</td>
<td>234</td>
</tr>
<tr>
<td>6</td>
<td>M</td>
<td>P. do Castanho</td>
<td>Low</td>
<td>3 years</td>
<td>A</td>
<td>85</td>
<td>308</td>
</tr>
<tr>
<td>7</td>
<td>M</td>
<td>L. Mamirauã</td>
<td>High</td>
<td>2 years 2 months</td>
<td>A</td>
<td>156</td>
<td>250</td>
</tr>
<tr>
<td>8</td>
<td>M</td>
<td>R. Amanã</td>
<td>Lowering</td>
<td>3 months</td>
<td>B</td>
<td>55</td>
<td>1186</td>
</tr>
<tr>
<td>9</td>
<td>M</td>
<td>R. Amanã</td>
<td>Lowering</td>
<td>3 months</td>
<td>B</td>
<td>43</td>
<td>2117</td>
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<tr>
<td>10</td>
<td>M</td>
<td>R. Amanã</td>
<td>Low</td>
<td>6 months</td>
<td>B</td>
<td>19</td>
<td>748</td>
</tr>
<tr>
<td>11</td>
<td>F</td>
<td>P. do Castanho</td>
<td>Lowering</td>
<td>Not tracked</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>12</td>
<td>F</td>
<td>P. do Castanho</td>
<td>Lowering</td>
<td>Not tracked</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>13</td>
<td>F</td>
<td>R. Amanã</td>
<td>Low</td>
<td>Not tracked</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

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., paraná; M, male; F, female; ID, individual identification.

### 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 MAGNETICA 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. macrophyte 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 Mamirauã (since 1992) and Ria Amanaã (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 Amana?

**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 Amana?

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 low-water (category B). Ranges in River Japurá and Ria Amana 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.

#### 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 Amana (A: mean = 0.27, SE = 0.13; B:

![Figure 3](image-url)  
**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 Paraná do Castanho during the lowering-water were moving in the direction of Ria Amanaã.

**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

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>A/B</th>
<th>N_locs</th>
<th>ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variable alone</td>
<td>38.48*</td>
<td>0.51*</td>
<td>0.73*</td>
</tr>
<tr>
<td>A/B with each</td>
<td>–</td>
<td>31.20*</td>
<td>67.50*</td>
</tr>
<tr>
<td>A/B with both</td>
<td>–</td>
<td>121.36*</td>
<td></td>
</tr>
</tbody>
</table>

*aP<0.001.  
bP=0.001.  
cP=0.002.  
dP 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.

**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 Amanaã.

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 paranãs (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 Amanaã 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 Amanaã 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

**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

<table>
<thead>
<tr>
<th>Explanatory variables</th>
<th>A/B</th>
<th>N_locs</th>
<th>ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variable alone</td>
<td>227.37*</td>
<td>0.93*</td>
<td>0.40*</td>
</tr>
<tr>
<td>A/B with each</td>
<td>–</td>
<td>238.94*</td>
<td>165.14*</td>
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<tr>
<td>A/B with both</td>
<td>–</td>
<td>138.70*</td>
<td></td>
</tr>
</tbody>
</table>

*aP<0.001.  
bP=0.001.  
cP 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.
Seasonal migration of Amazonian manatees

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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 (<10000 years), and that terraces on its sides were formed a bit earlier, in the last 47300 years (Rossetti, Toledo & Gões, 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...
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-Solimães 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 (Majli 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. (2008a,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., 2008a,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 Tefã, and colleagues working in River Purús informed us of at least 12 that were killed in Ria Jari (B. Marioni, Eric M. 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**


