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Habitat analysis and exclusive bank feeding of the Antillean manatee (*Trichechus manatus manatus* L. 1758) in the Coswine Swamps of French Guiana, South America

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A study was conducted to analyse the habitat of the Antillean manatee (*Trichechus manatus manatus* L. 1758) in the Coswine Swamps of northwest French Guiana, South America.

Water parameters were similar to those described in other studies: water depth varied from 2.5 m to more than 20 m; water temperature was between 24.5 °C and 30.3 °C and pH varied between 5.5 and 6.9. Salinity was low (0.0‰ to 1.3‰) with 86.9% of all samples taken in fresh water.

No submerged aquatic vegetation was found in the study area. A botanical survey along the banks revealed that most plants seem to be potential forage for manatees. Red Mangrove is very abundant throughout the area. It is suggested, therefore, that manatees graze on the bank vegetation, where feeding traces were found, or leave the area to feed.

The Coswine Swamps provide a suitable manatee habitat and are able to support a large manatee population. Food supply is sufficient, brackish and fresh water are available, and the site is free from human disturbance. Further studies should be carried out to assess the population size, travel routes and foraging patterns, as well as acquire detailed information about the other manatee habitats in French Guiana.

KEY WORDS: *Trichechus manatus manatus*, habitat analysis, water quality, feeding behaviour, submerged aquatic vegetation, bank vegetation, botanical survey, mangrove, French Guiana.

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INTRODUCTION

The Antillean manatee (*Trichechus manatus manatus* Linnaeus 1758), a subspecies of the West Indian manatee, is restricted to the tropical and sub-tropical New World Atlantic (Husar 1977). All manatee species are classified as endangered by the Red Data Book of the World Conservation Union (Hilton-Taylor 2000). In French Guiana, the manatee is totally protected by two ministerial decrees of 1986 and 1995.

The status of the West Indian manatee has been relatively well studied throughout its distribution range (see e.g. Lefebvre et al. 1989, Caribbean Environment Programme 1995). Nevertheless, specific information on the manatee population in French Guiana is virtually absent. Interviews among fishermen and residents in French Guiana revealed that manatees might be less abundant than they were 20 years ago, although they are still present and widespread. Furthermore, the study indicated the presence of a small but stable manatee population in the estuaries of the rivers Maroni and Oyapock and in the swamps near Sinnamary (de Thoisy et al. 2003) (cf. Fig. 1).

Habitat loss is one of the major problems for conservation of manatees (Reynolds 1999). Therefore the habitat requirements of manatees, and in particular their feeding resources, should be investigated. However, only a few studies have concentrated on this issue and – to our knowledge – none of these on the Antillean manatee. Bengtson (1983) and Hartman (1979) described the habitat of the Florida manatee (*Trichechus manatus latirostis* Harlan 1823), but a direct comparison with the Antillean manatee must be made with caution because the two subspecies differ in behaviour. While the Florida manatee has a distinct seasonality and aggregates around thermal outflows during winter, such behaviour is not reported for the Antillean manatee (Axis Arroyo et al. 1998, Reynolds 1999).

Manatee foraging behaviour

Manatees are known to eat a wide variety of aquatic and semi-aquatic macrophytes (Bertram & Bertram Ricardo 1964, Campbell & Irvine 1977). They favour submergent to floating and floating to emergent vegetation and show a preference for luscious, non-woody, soft plants (ALLSOPP 1969). Plants are chosen according to their palatability, digestibility and nutritional value (HEINSOHN & BIRCH 1972), but availability is the most important factor and influences the seasonal distribution of manatees (AXIS ARROYO et al. 1998). Thus, manatee feeding behaviour varies widely due to regional and seasonal changes. Manatees in the northern part of the Gulf of Mexico principally graze on submerged or floating vegetation (HARTMAN 1979, PACKARD 1984, POWELL & RATHBUN 1984), while in the absence of such forage along the coasts of South America and in the north of Florida, manatees mainly feed on shoreline vegetation such as mangroves (*Avicennia*, *Rhizophora*, *Languncularia*) or other terrestrial plants (*Montrichardia*, *Pachira*, different *Poaceae*, *Rhabdadenia*, *Spartina*) (BEST 1981, DOMNING 1981, MOU SUE et al. 1990, ZOODSMA 1991, SMETHURST & NIETSCHMANN 1999). Seasonal changes due to low temperature or dry/rainy seasons also influence the feeding behaviour of manatees. In their northern distribution range, feeding is limited to a few hours per day due to cold temperatures (HARTMAN 1979). In the estuaries along the coast of South America, manatees selectively graze during the rainy season when food availability is increased due to a higher water level. During the dry season, leaves of mangroves become important (O'SHEA et al. 1988, BOROBIA & LODI 1992). Manatees normally feed under or just above the water surface, but they can push their body up to 30 cm out of the water to graze on bank vegetation (BERTRAM & BERTRAM RICARDO 1964, HAIGH 1991, ZOODSMA 1991) or on plants hanging over the water (MOU SUE et al. 1990).

Objectives

After an initial assessment of the actual status of manatees in French Guiana (DE THOISY et al. 2001, 2003), this study focuses on the analysis and characterisation of a manatee habitat in the northwest of French Guiana and on the available forage.

The main questions are:

— Is the range of water temperature, pH and salinity acceptable for manatees?
— Which potential manatee food plants can be found in the Coswine Swamps?
— Within the Coswine Swamps, are there any areas preferred by manatees?

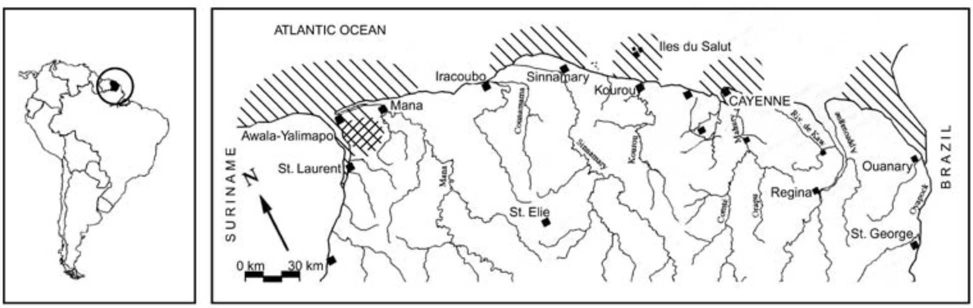

Fig. 1. — Map of South America and costal French Guiana with main rivers. Left shading indicates areas with regular manatee sightings (DE THOISY et al. 2003) and right shading the study area.

MATERIAL AND METHODS

The study area

Among the areas where manatees can be observed in French Guiana (cf. Fig. 1), most sightings are reported from the Coswine Swamps (DE THOISY et al. 2003). The Coswine Swamps (total area ca 160 km²; 5°34' to 5°41'N, 53°53' to 54°00'E) are located in the northwest of French Guiana near the Guianan-Surinamese border. Situated in the southeast of the River Maroni estuary, the Coswine Swamps link up with the Maroni via numerous creeks. The climate is tropical, with the wet season lasting from mid-November to mid-August and the dry season occurring between mid-August and mid-November. Occasionally there is a short dry season in March and maximum precipitation occurs in mid-May. During the study period, the maximal lunar tide was 4.09 m (20.VIII) and the minimum 0.98 m (20.VIII), calculated at the closest point to the estuary (SERVICE HYDROGRAPHIQUE ET OCÉANOGRAPHIQUE DE LA MARINE 2004). The main soil type in the study area is composed of recent marine deposits with little organic matter. The vegetation types are mangroves, swamp or marsh forests and herbaceous swamps. The fauna in the Coswine Swamps is relatively undisturbed, as a large part of the area is only accessible by boat. To protect this very valuable area, national and regional authorities have created different conservation zones: the nature reserve "Réserve naturelle de l'Amana", the Ramsar zone "Basse Mana" and a ZNIEFF ("Zone of National Ecological, Faunal and Floral Interest").

Water parameters

Water depths, temperature, salinity and pH were sampled in each of the 18 creeks at no less than two sites, 1500 m apart. At each site, three 100 m line transects were established along the left and right banks and in the middle of a creek, and three samples were taken at the beginning, in the middle and at the end of each transect. Sampling was carried out once at each site between 02.VI.2001 and 14.IX.2001. Measurements were taken from a boat, no more than 1 hr before and after the daily high tide, at a depth of 50 cm below the water surface, and they were pooled for each site. All parameters were recorded with the Universal Pocket MultiLine P4 (WTW, Schondorf, Germany). The pH was measured with a SenTix 97/T electrode (accuracy 0.01 ± 1 digit), the temperature and salinity with a TetraCon 325® cell (accuracy ± 0.2 with 25-30 °C for salinity and 0.1 K ± 1 digit for temperature). Water depth was determined by calculating the sum of the actual depth (measured with a rope attached to a rake, as described below) plus the maximal wet season water height. The seasonal maximal water height was clearly visible as a horizontal line on the trunks of the shoreline trees.

Submerged Aquatic Vegetation (SAV)

Sampling for SAV was carried out during a boat survey of all 18 creeks from 21.VI.2001 to 25.VI.2001. In every creek shorter than 1 km, one SAV sample was taken, while in all the other creeks at least two sites were investigated.

The SAV was collected with a double-headed garden rake similar to the one used by DEPPE & LATHROP (1992): a 1.35 m long shaft with 32 tines, each 10 cm long and 0.3 cm wide and spaced 1.5 cm apart. A diving weight of 500 g was fixed to one end of the rake. A rope attached to the shaft allowed sampling to a maximum depth of 20 m. To collect the SAV, the rake was dragged on the bottom of the creek for a distance of approximately 2 m, turned to an upright position and then hoisted from the water so the plants could be deposited in the hull. The quantity of the collected macrophytes was estimated in five steps according to the Kohler scale (KOHLER 1978).

Table 1.

Abundance classes used for vegetation samples in the Coswine Swamps, French Guiana, and its corresponding Braun-Blanquet-scale and percentages.

Abundance classes	Braun-Blanquet scale	Percentage
0.1	r	<< 1
0.5	+	< 1
5	1, 2	1-10
25	2, 3	11-50
75	4 and 5	> 50

Possible forage on the banks

The vegetation surveys for potential manatee food plants were made during the same period and at the same locations as the water parameter recordings. All vascular plants on the two banks were noted during low tide, along the 100 × 1 m transect, and between the water surface and 50 cm above the maximal wet season water level (50 cm represents the maximum height manatees can reach to graze on bank vegetation). The abundance of each plant species was estimated with a modified Braun-Blanquet scale (MBB, cf. Table 1). If possible, the plants were identified immediately, otherwise samples were collected and plants identified in the Herbier de Cayenne. The Shannon index was used to estimate the plant diversity (DIERSCHKE 1994). All calculations were made using Excel 2000.

RESULTS

Aquatic parameters

Maximal water depth ranged from 2.5 m to more than 20 m, but was less than 4.0 m (6.3%) at only four sites. At 16.1% of the stations, water depth was not measured because currents were too strong to be able to suspend the rope vertically. Width of the creeks varied between 3 and ca 400 m. The mean water temperature for the whole study area was 28.4 °C (min: 26.2 °C, max: 30.1 °C). Salinity ranged from 0.0‰ to 1.3‰ for the whole study area, but 86.9% of the samples were taken in fresh water. The farthest inland record of brackish water (salinity of 0.7‰) was approximately 15 km from the sea. The points where brackish water was recorded were rather randomly distributed over the whole area. The pH ranged from 5.6 to 6.8 for the whole study area.

Submerged Aquatic Vegetation (SAV) and bank vegetation

Fifty-five locations in the Coswine Swamps were investigated for SAV. Despite repeated attempts, no SAV were found, not even in shallow waters alongside the bank.

The bank vegetation was sampled along 62 transects resulting in 124 vegetation surveys. In total, 77 terrestrial plant species were recorded. A single sighting of a patch (diameter approximately 1 m) of floating *Eichhornia crassipes* was also recorded. Table 2 shows the 15 most common plants, together representing 76.9% of all species occurring on the bank, but only 19.4% of all recorded species. In total, 31 plants were recorded only once (40.3%) and 31 plants (40.3%) were found two to nine times in the study area.

In 11 cases (9.0% of all transects), only Red Mangrove (*Rhizophora racemosa*) occurred, but the median number of species per transect was 4.5 (min: 1, max: 17). *R. racemosa* was only absent in 6.6% of all samples. The two most diverse transects comprised 17 species (1.6% of all transects). The floral diversity (Shannon-Index) of the transects ranged from 0.000 (min) to 3.170 (max), with a median of 0.980. Among the 15 most common plants, only one (*Machaerium lunatum*) is mechanically defended against manatee grazing, while 8 plants contain toxic substances (cf. Table 2).

Feeding traces and manatee observations

During the study, one manatee was observed feeding on *Rhizophora* sp. along the shoreline. Evidence of manatee feeding on bank vegetation was found

Table 2.

The 15 most common plants along the banks of the Coswine Swamps, French Guiana. Toxic substances of leaves according to Hegnauer (1963, 1964, 1966, 1986, 1989) and Hegnauer & Hegnauer (2001).

Plant family	Plant	Life form	Substance	aP	F (%)	rP_{15} (%)
Rhizophoraceae	*Rhizophora racemosa* G.F.W. Meyer	tree	tannins	114	93.4	21.6
Mimosaceae	*Zygia cataractae* (Kunth) L. Rico	shrub		54	44.3	10.2
Papilionaceae	*Machaerium lunatum* (Linnaeus f.) Ducke	thorny shrub		51	41.8	9.6
Bombacaeae	*Pachira aquatica* J.B. Aublet	tree		43	35.2	8.1
Araceae	*Montrichardia arborescens* (Linnaeus) Schott	herbaceous	saponiens	41	33.6	7.8
Pteridaceae	*Acrostichum aureum* C. Linnaeus	fern	flavonoids	37	30.3	7.0
Papilionaceae	*Dalbergia monetaria* Linnaeus f.	liana	flavonoids	39	32.0	7.4
Apocynaceae	*Rhabdadenia biflora* (N.J. Jacquin) Müller-Argoviensis	liana		39	32.0	7.4
Combretaceae	*Laguncularia racemosa* (Linnaeus) C.F. Gaertner	tree	tannins	24	19.7	4.5
Bignoniaceae	*Clytostoma binatum* (Thunberg) Sandwith	liana		17	13.9	3.2
Liliaceae	*Crinum erubescens* Solander in W. Aiton	small shrub	alkaloids	16	13.1	3.0
Hippocrateaceae	*Hippocratea volubilis* Linnaeus	liana	alkaloids	16	13.1	3.0
Papilionaceae	*Pterocarpus officinalis* N.J. Jacquin	tree		14	11.5	2.6
Rhizophoraceae	*Rhizophora mangle* Linnaeus	tree	tannins	14	11.5	2.6
Malvaceae	*Pavonia paludicola* Nicolson	small shrub		10	8.2	1.9
			Total	529	434	100

aP: absolute presence of a plant within all samples taken; F: frequency of a species in all samples; rP_{15}: relative presence within the 15 most represented plants.

at two sites in the study area. These observations were made independently of the sampling protocols described above. The first evidence of feeding was seen on a small *Rhizophora racemosa* shrub, where the leaves were cropped off and only the branches were left. The second grazed patch was found on a very flat bank, where manatees feed on *Montrichardia arborescens* and *Scleria pterota*. The latter was nearly completely grazed with only about 5 cm of the grass remaining, while on *M. arborescens,* only the leaves were eaten and the stems were avoided. The absence of any herbivores likely to graze on these plants and the similarity of the observed feeding patterns, in particular on *M. arborescens,* to those described in the literature (Dekker 1974), makes it very likely that these feeding traces can be attributed to manatees.

Patterns within the study area

Water parameters were rather homogeneous throughout the study area, but one distribution pattern of shoreline vegetation was remarkable. The Red Mangrove, *Rhizophora* sp., and a fern, *Acrostichum aureum*, dominated the northeastern part of the Coswine Swamps. These stands were very homogeneous and *Rhizophora* sp. reached at least abundance class 25 on the MBB scale, but in most cases (73.7%), *R. racemosa* had a minimal cover of 50% (MBB 75). On the relatively flat banks, *Crinum erubescens* and the small grass, *Kyllinga brevifolia,* were common. In eight cases, the spiny *Machaerium lunatum* shrub was found (cover between 5 and 25 on the MBB scale) and *Zygia cataractae* (maximal cover < 10%) was present in 21.1% of the samples. The species number was relatively low (median: 3) and 76.3% of the 38 samples in this region had fewer species than the mean for the whole area (4.5 species per transect). This reveals a vegetation largely dominated by *Rhizophora* sp., but otherwise very uniform. The rest of the study area was, with a few exceptions, more heterogeneous than this northeastern part: species diversity was higher and 39.3% of the samples had more than 4.5 species.

DISCUSSION

Aquatic parameters

Water parameters are comparable to those observed in similar studies in Mexico (Axis Arroyo et al. 1998, Morales-Vela et al. 2000). Virtually all creeks are accessible both at low and high lunar tide, at least during the rain season, and temperature and pH are within an adequate range for manatees. Despite the fact that measurements of water parameters were limited to a relatively short period in this study, and therefore seasonal influences on the water parameter were not recorded, it seems that aquatic parameters do not limit the distribution of manatees.

Salinity in the study area was very low. This was unexpected since the vegetation was dominated by *Rhizophora*; a plant that typically occurs in brackish estuaries (West 1983) and salt water areas (Pires & Prance 1985). To limit the bias of salinity measurements, sampling of the aquatic parameters was restricted to 1 hr before and after the daily peak tide. Unexpectedly low salinity values could have been caused by rainwater or outflow of swamp water at the beginning of low tide. One possible explanation for the low quantities of salt water could be the period of sampling. At the beginning of the study, daily precipitation was still high and could have prevented sea water from flowing into the swamps. In general, French Guianan estuaries are influxed with salt water during the dry season and with brackish water during the wet season (Lointier & Prost 1986). During the dry season, salt water flows upstream in the River Maroni (adjacent to the Coswine Swamps) with the rising tide to the southern end of the study area. However, in the wet season, marine waters entering the mouth of Maroni only reach the northern limit of the study area (Jounneau & Pujos 1988). Indeed, brackish water tended to be recorded more often in the north of the study area, near the sea.

Submerged aquatic vegetation (SAV)

No SAV was detected in the Coswine Swamps. SAV sampling with a rake is a common method for macrophyte cartography (Meilinger & Schneider 2000), but rare, small plants with stem length less than 8 cm (e.g. *Isoetes macrospora*, *Carex lasiocarpa*) or plants with robust stems (*Thypa latifolia* or *Scirpus acutus*) can be missed (Marshall & Lee 1994, Caspers 2000). In addition, plants that only occurred between two sites would not have been recorded. However, this potential sampling bias can be regarded as negligible since manatees need to consume at least 4-9% of their body weight each day (Bengtson 1983) and it seems unlikely that manatees search for such small plants if other food resources are abundant. Furthermore, the low maximal transparency of 0.6 m (pers. obs.) limited the occurrence of SAV to a narrow zone between the fringe and a water depth of about 2 m (Havens 2003). However, even repeated measurements within these areas did not reveal any SAV.

Forage and feeding traces

Since no SAV was found, the manatee's main food resource in the Coswine Swamps seems to be shoreline vegetation. *Rhizophora* was the most common plant genus recorded and was particular dominant in the northeastern part of the Coswine Swamps.

Manatees normally feed on submerged aquatic vegetation, but are very adaptive in the absence of such vegetation. Feeding on bank vegetation is fairly common for manatees in different habitats (cf. chapter *Manatee foraging behaviour*), but is not reported from Guyana where manatees are described as feeding exclusively on aquatic and semi-aquatic plants (Haigh 1991). Plants described in other studies as typical manatee forage (Husar 1977, Colmenero-Rolon 1985) were not found in the Coswine Swamps, except for *Montrichardia*. Five of the plants present in our study area are cited in another list of commonly grazed vegetation (Best 1981), but these are anecdotal reports from Brazilian hunters.

Bank feeding by the Amazonian manatee (*Trichechus inunguis* Natterer 1883) is also a commonly reported phenomenon. Forage available to manatees is conditioned by the seasonal variation in water level. In particular, during the wet season, when the water level can rise to 15 m, the várzeas are flooded and Amazonian manatees graze on shoreline vegetation (TIMM et al. 1986, ROSAS 1994). During the dry season, food is scarce and manatees feed on a wider variety of species compared to the wet season (COLARES & COLARES 2002), or fast (BEST 1983).

There have not been many reports describing the palatability of mangrove vegetation for manatees. Table 2 shows the toxic substances found in the leaves of some plants that can be consumed by manatees. The acceptable level of tannins for manatees is set at 2-3%, but manatees have been reported to feed on *Rhizophora* spp. (BEST 1981), and this was also observed during our study. Only plants that contain saponiens, flavonoids and alkaloids seem to prevent feeding by manatees.

Although we did not find any submerged aquatic vegetation in the study area, we cannot totally exclude the possibility that manatees feed on SAV. Next to the small islands of the Iles du Salut, approximately 150 km from the Coswine Swamps, the waters are slightly clearer and harbour a large population of Green turtles, *Chelonia mydas* (L. 1758), which are seagrass feeders. However, the existence of seagrass beds is not confirmed since the majority of Green turtles observed around the Iles du Salut are juveniles (X. DESBOIS & L. KELLE personal comm.) which, in contrast to adults, are more omnivorous than herbivorous and therefore less dependent on seagrass beds (LANYON et al. 1989).

We only found a few feeding traces during the study because we focused on the vegetation survey and not on evidence of grazing. For that reason, feeding traces of manatees were not systematically searched for and only occasionally encountered. As bank vegetation is presumably the only food resource for manatees in the Coswine Swamps, the possibility of finding evidence of manatee feeding on this type of vegetation should be high.

Habitat suitability and recommendations for further studies

The northeastern region, with its abundant Red Mangrove banks, seems to be a particularly favourable area for manatees. This site provides food in sufficient quantity to support even a large manatee population and is remote from human disturbance, as access is only possible by boat. During the 3 months of the field study, we encountered canoes in only one of the two big creeks and these encounters were rare. In the smaller creeks, human presence was reported only twice. Manatees can always penetrate into this northeastern part of the Coswine Swamps, as the creeks connecting the region to the sea are up to 65 m deep.

The possibility that manatees are not resident in the area, but instead are migratory or transient cannot be excluded. During the study period, the water in the Coswine Swamps was not salty and it is possible that manatees use this area for drinking or for access to freshwater, similar to patterns observed in Mexico (OLIVERA-GOMEZ & MELLINK 2005), Brazil (BOROBIA & LODI 1992) and Florida (HARTMAN 1979). However, the fact that manatee sightings are regular and occur all year-round (DE THOISY et al. 2003) suggests the presence of a resident manatee population in the Coswine Swamps.

Therefore, the main aim of further studies on the French Guianan manatees should be to assess the number of individuals living in the waters of French Guiana. For the moment, no details on manatee habitat use patterns or any population estimates are available. Manatee aerial surveys did not produce any sightings although this was likely influenced by turbid waters (B. DE THOISY personal comm.).

Collection of manatee faeces could be used for food plant identification (Best 1981, Hurst & Beck 1988). Furthermore, it would be useful to gather additional information regarding the travel routes and habitats used by manatees. Although expensive, radio-tracking may be an appropriate method.

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