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Seasonal Movements of *Podocnemis sextuberculata* (Testudines: Podocnemididae) in the Mamirauá Sustainable Development Reserve, Amazonas, Brazil

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Abstract. – We studied the linear home range and seasonal movements of *Podocnemis sextuberculata* from September 1996 to December 1998 in the Mamirauá Sustainable Development Reserve located in the middle Solimões River, near Tefé, Amazonas, Brazil. We collected data on turtle movements and home range through mark and recapture and radiotelemetry, focusing on seasonal differences between periods of high and low water levels. Based on radiotelemetry of 6 females in the Jarauá River system, linear home range varied from 16.52 to 44.5 km. Nesting migrations from the Jarauá to the beaches of the Japurá River averaged 18.04 km. Males did not move significantly between captures. For conservation purposes, it is of critical importance to protect both the canals that the turtles use to travel between the lakes and the river as well as the deep holes in the river where mature turtles congregate during the dry season.

Key Words. – Reptilia; Testudines; Podocnemididae; *Podocnemis sextuberculata*; turtle; ecology; movements; home range; Amazonas; Brazil

Seasonal migrations of the giant Amazon River turtle, *Podocnemis expansa,* have been documented to exceed 100 km (Ojasti 1967, 1971; Pádua and Alho 1982; Moreira and Vogt 1990) and more than 400 km (von Hildebrand et al. 1997). These migrations are related to the annual nesting cycle as females move to areas of suitable nesting habitat (Pádua and Alho 1982; Fachín-Terán 1992; Bataus 1998). The seasonal timing of nesting and seasonal nesting migrations depend on patterns of annual water level variation and vary in different parts of the Amazon Basin (Soini 1997). Movements of other freshwater turtle species may also be associated with habitat changes, such as water temperature, water level, or chemical pollution, to name a few. Gibbons (1986) suggested that additional studies are needed to document how different species of turtles respond to unfavorable conditions under different circumstances.

There are relatively few studies of movements of freshwater turtles, especially in rivers, but some studies have been conducted on a variety of species: *Trachemys scripta* (Moll and Legler 1971), *Apalone mutica* (Plummer and Shirer 1975), *Graptemys pseudogeographica* and *Graptemys ouachitensis* (Vogt 1980), *P. expansa* (Moreira and Vogt 1990; von Hildebrand et al. 1997), *Kinosternon leucostomum* (Morales-Verdeja and Vogt 1997), and *Phrynops rufipes* (Magnusson et al. 1997). Moll (1980) found a radio-tagged *Batagur baska* moving 80 km from where it was captured at the mouth of Malaysia's Perak River, upstream to the nesting beaches. *Carettochelys insculpta* (Georges and Rose 1993), Costa Rican *T. scripta* (Moll 1994), and *Callagur borneoensis* (Dunson and Moll 1980) are also known to move extensive distances from their foraging grounds to their nesting beaches.

Our objective was to study another Amazon freshwater turtle species, *Podocnemis sextuberculata,* and to determine 1) the linear home range, 2) seasonal movements of females using radio transmitters, and 3) movements of both males and females based on mark–recapture.

METHODS

Study Area. — The study was conducted in the Mamirauá Sustainable Development Reserve in northwestern Brazil, near the city of Tefé, Amazonas, between 03°08′S, 64°45′W and 2°36′S, 67°13′W (Fig. 1). The reserve, established in 1990, is an area of "*varzea*" (forest flooded by sediment-laden river waters) between the Japurá, Solimões, and Auti-Paraná rivers and covering 1,124,000 ha. Mamirauá was also the first Sustainable Development Reserve established in Brazil (in 1996), is the only Brazilian protected area in Amazonian *varzea* flooded forest, and has been designated a RAMSAR site in recognition of its international importance. The objective of the reserve is conservation, investigation, and management of biodiversity with the participation of the local people (SCM 1996).

Methodology. — Turtles were captured using trammel nets from September 1996 to August 1998. The nets were

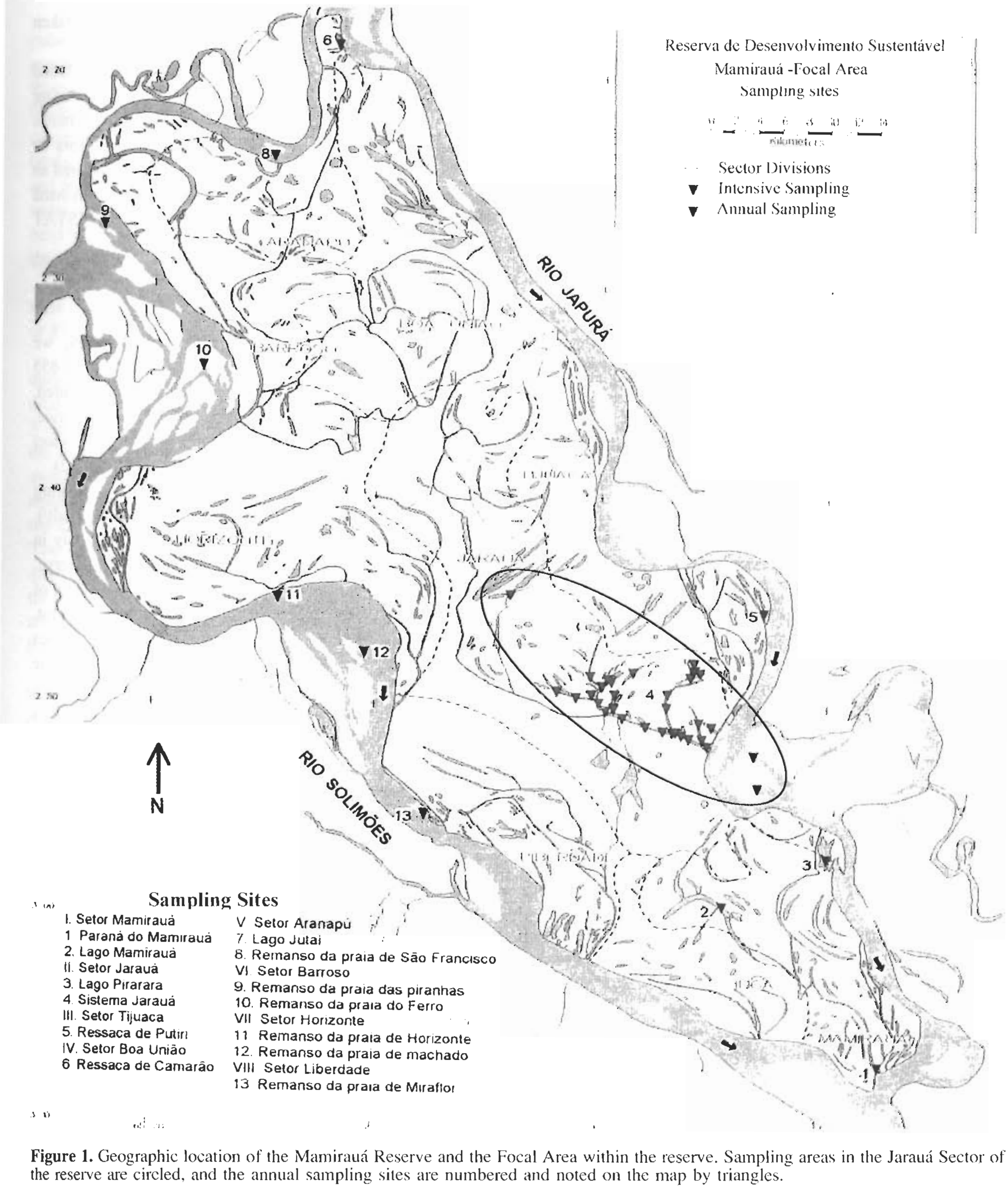

Figure 1. Geographic location of the Mamirauá Reserve and the Focal Area within the reserve. Sampling areas in the Jarauá Sector of the reserve are circled, and the annual sampling sites are numbered and noted on the map by triangles.

100–150 m long; 3.5, 4.0, and 4.5 m deep; with respective outside mesh of 60, 68, and 92 cm and inner mesh size of 11, 15, and 21 cm. Immediately on capture, the turtles were uniquely numbered on the plastron with a permanent ink marking pen and transported to a field lab the same day where they were weighed with Pesola spring scales (±1.0 g). The following straight-line measurements were taken (±1 mm) with a turtle measuring device (Cagle 1944) or digital dial caliper: maximum carapace length, maximum carapace width, maximum carapace height, maximum plastron length, maximum abdominal plate length, and maximum head width. The turtles were then induced to regurgitate their stomach contents through stomach flushing (Legler 1977).

We injected PIT tags (Avid) into the caudal musculature at the base of the tail of all turtles with distinct growth rings. All turtles were also marked with yellow individually numbered plastic Floy Cinch-up tags threaded through holes drilled in right marginals 9 and 11. In addition, to ensure long-lasting identification, each turtle was also uniquely marked in the marginal scutes with a coding system (Cagle 1939).

Capture periods ranged from 12 to 72 hours per locality. The location of capture sites was determined with a handheld GPS.

The plastic Floy tags were used mainly to obtain recapture information from local fishermen. We made announcements requesting the return of tags on the local radio station, at the general meetings in each community, and in posters placed in the communities in the reserve. Most of the work was done in the Jarauá sector of the reserve, but in addition we made a 1-month capture–recapture survey in the 200,000 ha Reserve Focal Area (Fig. 1).

In the Jarauá sector of the Reserve between October 1997 and December 1998, we used 30-MHz radio transmitters to locate turtles and estimate linear home range size and associated seasonal migrations. We attached 1 radio in October 1997 and the other 8 in 1998.

The transmitters measured 8.55 by 1.9 cm and weighed 25 g and were attached to the eighth and 10th right marginals of 9 adult female turtles by drilling two holes, 4 mm in diameter, in each scute and threading 2-mm copper wire though the holes to secure the transmitter. In addition, the transmitters were glued to the carapace with super glue (Araldite Ultraforte) and allowed to dry for 24 hours, after which a covering of duropoxy was placed over the transmitter, contouring it with the carapace, and allowed to dry for 12 hours. The turtles were then released at their capture site. Turtles were located with a Yagi antenna and Custom Telemetry receiver. Maximum range of reception of the transmitted signal was 200 m.

The turtles were located as often as possible, and the hour, date, color of the water, depth, air temperature, water surface temperature, temperature of the water at its deepest point, and GPS location were registered.

We used mark and recapture data to evaluate the movements of turtles. Movement was defined as the linear distance between the two points of capture, on the assumption that these movements are unidirectional (Lovich et al. 1992). This definition has been used with turtles inhabiting rivers (Kramer 1995).

Linear home range is defined as the distance (m) between the farthest points where a turtle was captured (Morales and Vogt 1997; Plummer 1977). Activity area during the February–June period of rising water is defined as the linear distance between the farthest points of capture during this period. Seasonal migration to the main river was defined as the distance from the last capture within the Jarauá system to the first subsequent localization in the Japurá River. We used the program CAMRIS (Ford 1993) to analyze the movement data. The distances were taken following the natural river course.

Two females with radio transmitters were excluded from the analysis because they were located only during periods of rising water. Of the 97 turtles recaptured, 5 males were excluded from the analysis because of errors in reading the GPS ($n = 4$) and 1 because it was recaptured an extremely long distance from the study area in the Amanã Reserve. Statistical analyses were made using SYSTAT (Wilkinson 1990).

RESULTS

Between September 1996 and August 1998, we captured and marked 2458 turtles (1603 males and 855 females). Of these, 2368 (96.3%) were never recaptured, 97 (3.5%) were recaptured once, and 3 (0.1%), twice. Most recaptures occurred during the period of rising water levels between December 1997 and July 1998 (Fig. 2).

Seasonal Movements (Mark–Recapture). — During the period of rising water levels (December–July), individuals of *P. sextuberculata* were found primarily in deep pools and canals along watercourses in the Reserve. During the highest water periods, the turtles moved out of these watercourses and into lakes and the flooded forest. During the period of falling water levels, adult turtles moved out of the lakes and flooded forest and into the main Japurá River. However, juveniles and some subadults stayed in the deepest pools remaining in the canals throughout the dry season. Reproductively mature turtles, as evidenced by oviductal eggs and enlarged testes, both males and females, concentrated in the deep pools near the nesting beaches, areas where there was no current and where there are numerous fallen trees and logs. We often caught several males concentrated together with a female in the trammel nets, but we never saw turtles courting or copulating.

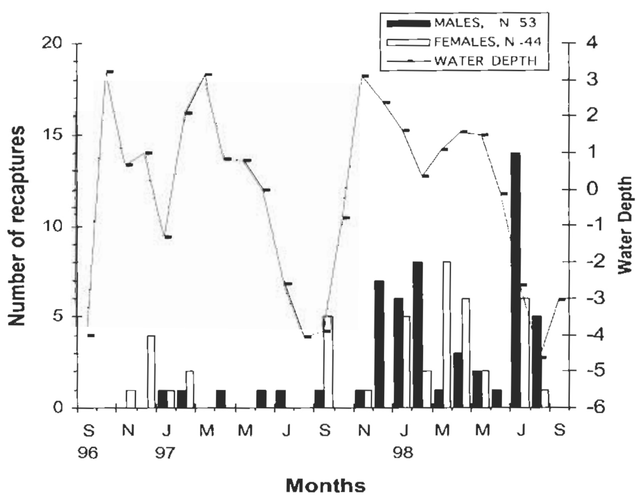

Figure 2. Temporal distribution of the number of turtles recaptured for the first time during the sampling period in the Focal Area of RDSM (bars) and water level (lines).

The period of rising water levels often begins in pulses. Heavy rainfall upstream raises the water level, resulting in the white water of the Japurá and Solimões Rivers entering the canals and backwaters mixing with the blackwater. During this period, turtles again enter the canals and backwaters to feed. During this period, the river banks are flooded, allowing the turtles to feed on the seeds and fruits of the recently inundated terrestrial plants. If the water levels fall again, the turtles leave the backwaters and head back out into the canals, entering the feeding areas for the season only when the water levels begin to rise again.

Movements (Radiotelemetry). — Eight of 9 females were located from 5–28 times (mean = 16), during a period of 87–368 days (mean = 189.1 days) (Table 1).

By using transmitters, we were able to observe that during the rising water and flooded periods, the turtles established themselves permanently in the seasonal lakes, 3 entering the central lakes where the current is less and the availability of food is higher. This concentration of available food is the result of Poaceae and other taxa of aquatic plants being retained by the trees and shrubs along the shorelines of the lakes as the water level rises or falls. Two turtles that stayed in the backwaters made short movements (50–100 m) and stayed in shallow water near the shoreline where there is less current and a concentration of Poaceae, one of the principal food types we found in the stomachs of the turtles.

During the falling water period, when the turtles are in the river, we found them in open areas where there is little current, near the shoreline where they remained for a mean of 13 ± 13.7 days, after which they moved to other areas with the same characteristics.

Data collected for females indicates that their linear home range in the Jarauá can range from 16.5 to 44.5 km, whereas the activity area in the rising water period is between 0.6 and 4.1 km (Table 1).

There was a large overlap in linear home ranges used by females in both the rising and falling water periods. Females used the same areas and habitats in both seasons. Turtles migrated from the Jarauá to the Japurá River for nesting, traveling a mean of 18.0 km (12.0–26.9 km) (Table 1).

We did not find a significant relationship between the size of the carapace and the linear home range of the females monitored with transmitters ($r^2 = 0.014$; $F_{1,4} = 0.055$; $p = 0.826$), nor did we find a relationship with the distance traveled ($r^2 = 0.048$; $F_{1,4} = 0.201$; $p = 0.677$). There was no significant relationship between the distance moved by females or the seasonal movements and the carapace length ($r^2 = 0.635$; $F_{1,4} = 6.951$; $p = 0.058$).

Linear Movements (Mark–Recapture). — The distance traveled by males from the point of original capture was not significantly correlated with carapace length ($r^2 = 0.001$; $F_{1,46} = 0.212$; $p = 0.648$), nor did we find a significant correlation between carapace length and movements of females ($r^2 = 0.135$; $F_{1,42} = 6.561$; $p = 0.014$).

Additionally, the distance traveled by males from the point of original capture was not significantly correlated to the number of days to the first recapture ($r^2 = 0.004$; $F_{1,46} = 0.182$; $p = 0.672$). However, there was a significant difference for the females ($r^2 = 0.388$; $F_{1,42} = 26.644$; $p = 0.001$) both in distance traveled and in the number of days to the first recapture (Fig. 3).

Analyzing all the recapture data, we found a sexual difference in the distance traveled between the initial capture to the first recapture ($t = -2.386$; df = 57.1; $p = 0.020$). The mean distance moved by females was greater than that for males (Table 2).

Nevertheless, when we analyzed the recapture data for turtles marked within the Jarauá River Basin, we did not find a significant difference between the sexes in the distance moved between initial capture and first recapture. ($t = -0.689$; df = 59.3; $p = 0.493$) (Table 2).

During the falling water level period, we captured two marked males in the same place where they had been caught the year before, one in the Paraná Mamirauá and the other in Lago Jutai, 367 and 368 days, respectively, after initial capture, suggesting that some turtles return to the same area annually. One female captured in 1997, in the backwater of Piranha Beach in the Solimões River, was recaptured in 1998 during the same period the following year (372 days later), downstream in the same river in the backwater of a different nesting beach at Horizonte; she moved a distance of 60.2 km.

Table 1. Description of data collected using transmitters.[a]

IND	RADIO	CL	MASS	HR	AA	SM	MON	NL	DEPTH
1	10.4	30.4	3.1		4.1		3	19	4.0–6.3
2	5.4	32.4	3.6	40.4		26.9	4	11	5.5–10
3	6.4	24.3	1.4		1.2		4	22	3.3–11
4	1.4	27.9	2.2	16.5	3.1	16.5	5	13	4.1–8.7
5	7.4	24.2	1.55	19.9		12.0	6	5	5.0–10.5
6	11.4	27.8	2.5	44.5	0.6	18.1	6	24	6.1–12.5
7	8.4	28.8	2.8	17.0	3.9	17.0	9	28	4.8–7.5
8	4.4	23.6	1.35	40.5		17.8	12	5	4.1–7.1
$\bar{X}$		27.4	2.3	29.8	2.6	18.0	6.1	16.0	
SD		3.2	0.8	13.2	1.6	4.8	3.0	8.7	

[a] IND = turtle number; CL = carapace length; HR= home range; AA = activity area in the enchente; SM = seasonal movements; MON = months with functioning radio; NL = number of localities where found; DEPTH = depth of water where turtle CL in cm; mass in Kg; HR, AA, and SM in km; depth in m; $\bar{X}$ = mean; SD = standard deviation.

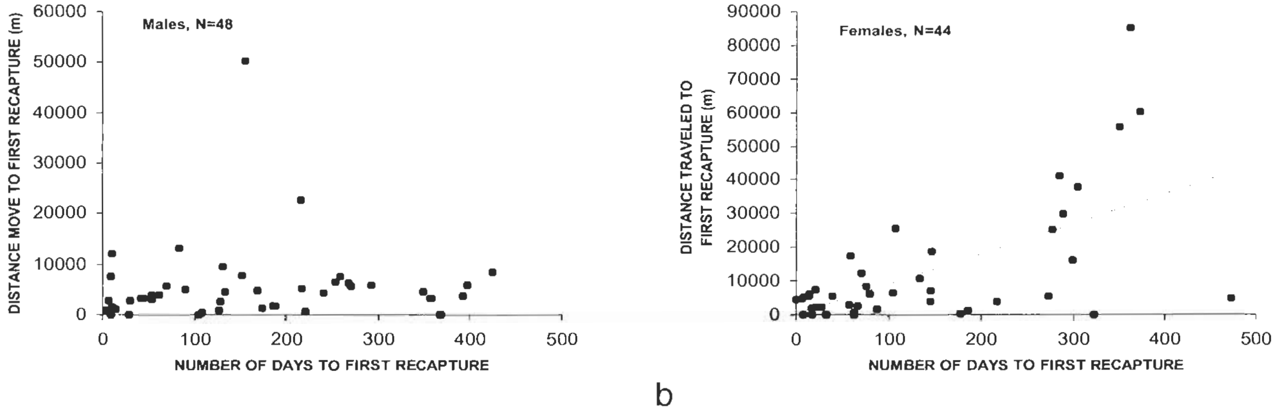

Figure 3. Relationship between number of days traveled and the distance to the first recapture of both (a) male and (b) female *Podocnemis sextuberculata*.

DISCUSSION

In the Mamirauá Reserve, the population of *P. sextuberculata* makes annual migrations, leaving the flooded forest (*varzea*), lakes, and backwaters and moving into the main river channels during the period when water levels are dropping. Turtles appear to migrate from the *varzea* into the rivers to avoid low-water conditions. Females also move from the *varzea* to reach principal nesting beaches on the Japurá and Solimões rivers. Males precede females to the deep pools near the nesting beaches to mate with females (R.C. Vogt, unpublished data). The migration from inappropriate habitats is a predictable behavior in *P. sextuberculata* that is stimulated by the annual fluctuations in the water level. *P. expansa* (Moreira and Vogt 1990) were found to leave their feeding grounds in the *varzea* forest and migrate over 65 km upstream in the Rio Trombetas to nest on high coarse sand beaches during the end of the falling water period. The females were then stimulated to leave the nesting area 2 months after nesting by the rising water levels of the river. *Podocnemis unifilis* females are bimodal in their response to lowering water levels; some females remain in the drying lakes and nest in clay soil on the margins of the lakes or canals, while others migrate to the river to nest on sand beaches. This phenomenon occurs in the Trombetas Reserve, Para, Brazil; the Guapore River, Rondonia, Brazil; and in Mamirauá (R.C. Vogt, unpublished data).

Table 2. Distances (km) moved from the first capture to the first recapture by *Podocnemis sextuberculata* in the Focal Area of the Reserve (first column) and in the Jarauá River Basin (second column).

	Males		Females	
	Focal	Jarauá	Focal	Jarauá
Mean distance (km)	5.3	4.1	12.4	4.7
Standard deviation	7.8	3.1	18.3	4.3
Range	0–5.0	0–13.1	0–85.0	0–17.4
n	48	44	44	35

Many species of turtles move great distances in response to seasonal climate and water level changes (Gibbons 1986), but responses to adverse conditions may vary between species and among populations of the same species. Cagle (1944) reported that *Chelydra serpentina* remained in a drying lake, burrowing into the mud, while *Chrysemys picta* and *T. scripta* migrated out of the lake. A similar phenomenon occurs in the Mamirauá Reserve; *P. sextuberculata* moves in response to fluctuating water levels, while most *P. unifilis* remain in the interior of the reserve and in the dry season remain buried in the mud, in canals that retain water and many aquatic plants, or in the deep holes in lakes, channels, and backwaters (Vogt, unpublished data). Bataus (1998) reported that *P. expansa* started their migration to rivers at the beginning of the falling water period and that at the same time migrations started to the collective nesting beaches. Moreira and Vogt (1990) found that female *P. expansa*, during the first 2 months after nesting, remain in the deep holes of the river near the nesting beaches and that with the initiation of the rains in December they are stimulated to move 65 km downstream to the Amazon River and off to their feeding grounds. Minimum time for this journey was 4 days. Plummer and Shirer (1975) reported that female *Apalone mutica* moved 2–6 km downstream to nest. Vogt (1980) found female *G. pseudogeographica* and *G. ouachitensis* to move up to 4 km from overwintering sites to nesting sites.

Migration of female turtles to nesting grounds is known only for a few species of Amazon turtles: *P. expansa* (Alho and Padua 1982; Moreira and Vogt 1990; Soini 1997; von Hildebrand et al. 1997; Bataus 1998), *P. unifilis* (Fachín-Terán 1992; Thorbjarnarson et al. 1993), and *P. sextuberculata* (Soini and Copula 1995).

The rapid lowering of the water level increases the velocity of the current in the *varzea* and lakes, and the aquatic vegetation (principally the Poaceae) is left on land or on the margins of the river. The turtles respond by moving to more favorable sites before the water disappears completely. Even though Poaceae remain on land during the period, *P. sextuberculata* has never been reported feeding on land.

The reduction of aquatic habitats that occurs during the dry season results in higher predation rates since turtles concentrate in the open parts of lakes where they have no refuge from predators (SCM 1996) The movement of *P. sextuberculata* to the deepest parts of the channels and their migration to the river during the low water may serve to reduce predation by piranhas (*Serrasalmus* spp.) and crocodilians; both black caiman (*Melanosuchus niger*) and spectacled caiman (*Caiman crocodilus*) are abundant in the Reserve and have been shown to be turtle predators (Fundación Puerto Rastrojo 1988). The caiman concentrate in the shallow water that remains in the channels, lakes, and backwaters. High predation of male *T. scripta* by *Alligator mississippiensis* on Capers Island, South, Carolina, USA, is responsible for the predominance of large females in the population. Since the males are smaller, they are more susceptible to alligator predation (Gibbons et al. 1979).

The distances traveled by *P. sextuberculata* vary considerably. We found a significant correlation between the distance traveled to the first recapture and the carapace length of females. The long-distance movements could be aided by the strong currents during the rising water period. Also, the search for nesting beaches during the falling water level period could influence these results. MacCulloch and Secoy (1983) did not find any relationship between the distance traveled and size in *C. picta*, attributing the movements to the strong current assisting the turtles. Gibbons (1968) found that in his study area, *C. picta* was not stimulated to move great distances since there was adequate food and nesting beaches in close proximity.

We did not find sexual differences in the distances moved by marked turtles to their first recapture in the Jarauá system. Magnusson et al. (1997) found that the linear home ranges of *P. rufipes* within a forest stream were the same for both sexes. Gibbons (1968) found supporting evidence that male *C. picta* move greater distances than females, probably to increase the probabilities of encountering mates. MacCulloch and Secoy (1983) found the same pattern in *Chrysemys picta bellii*, males moving more than females.

The dispersal of turtles occurs in the rising water level period (January–April) and the falling water level period (June–September). During the high water, the turtles have access to the flooded forest, and many habitats are connected by one continuous body of water. During this period, the *varzea* is converted into an immense continuous lake, with few areas above water. At this time the turtles move freely through the aquatic ecosystems. During the low water, the opposite occurs: access to water bodies is restricted to those that are deepest and that have permanent connections with other water bodies, such as channels and rivers. The lowering of the water level and the appearance of unfavorable habitats stimulates most of the adult turtle population to migrate to appropriate areas to survive, mate, and nest. The rest of the population, juveniles and subadults, remains in the canal or deep holes in the channel during the dry season.

The understanding of the movement patterns of *P. sextuberculata* and the identification of feeding areas and nesting beaches are of vital importance for programs of conservation and management of this species. Our data show that it is not enough to protect only the areas near the nesting habitat of some species of river turtles, since the home range and activity areas of even this small species encompass sizable areas, and they utilize different habitats during the course of the year. Only by preserving a mosaic of habitats within their range will populations of Amazonian river turtles be able to survive as humans continue to consume them and encroach on their habitats. Fortunately, throughout the Brazilian Amazon Basin, there are numerous expansive reserves offering protection for riverine turtle species in a variety of habits.

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RESUMO

Nos pesquisamos o tamanho da área de vida e movimento de iaça (*Podocnemis sextuberculata*) de setembro de 1996 a dezembro de 1998, na Reserva de Desenvolvimento Sustentável Mamirauá. A Reserva está situada no médio Solimões, perto da cidade de Tefé, Amazonas, Brazil. Os movimentos das iaçás foram estudados através dos métodos de marcação-recaptura e telemetria. Rádio-transmissores foram instalados em 9 fêmeas. O registro e a medição dos deslocamentos de seis fêmeas, indicou que a área de vida linear no Sistema Hidrológico do Jarauá varia de 16,52 a 44,50 km. O deslocamento desde o Sistema Jarauá para as áreas de nidificação no rio Japurá foi em média 18,04 km. A distância percorrida pelos machos até a primeira recaptura não foi significativamente correlacionada com o comprimento da carapaça. No entanto esta relação foi significativa para as fêmeas. A proteção dos canais que usa a iaçá para se movimentar, e os remansos nos rios, onde a população reprodutora permanece durante a vazante, são medidas importantes para a preservação desta espécie.

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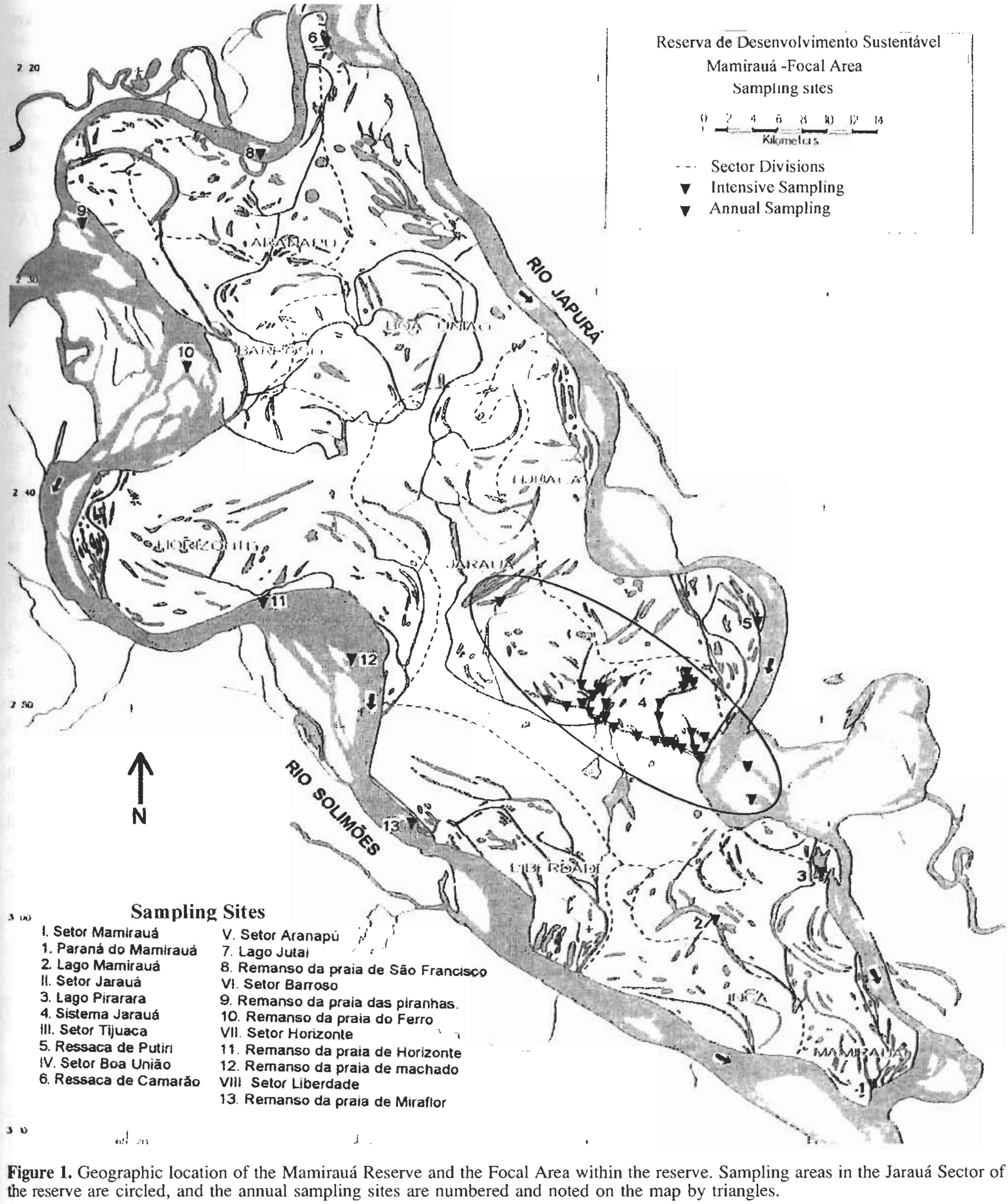

Figure 1. Geographic location of the Mamirauá Reserve and the Focal Area within the reserve. Sampling areas in the Jarauá Sector of the reserve are circled, and the annual sampling sites are numbered and noted on the map by triangles.

100–150 m long; 3.5, 4.0, and 4.5 m deep; with respective outside mesh of 60, 68, and 92 cm and inner mesh size of 11, 15, and 21 cm. Immediately on capture, the turtles were uniquely numbered on the plastron with a permanent ink marking pen and transported to a field lab the same day where they were weighed with Pesola spring scales (±1.0 g). The following straight-line measurements were taken (±1 mm) with a turtle measuring device (Cagle 1944) or digital dial caliper: maximum carapace length, maximum carapace width, maximum carapace height, maximum plastron length, maximum abdominal plate length, and maximum head width. The turtles were then induced to regurgitate their stomach contents through stomach flushing (Legler 1977).