ECOLOGICAL CORRELATES OF THE DISTRIBUTION OF TERRESTRIAL AND FRESHWATER CHELONIANS IN THE NIGER DELTA, NIGERIA: A BIODIVERSITY ASSESSMENT WITH CONSERVATION IMPLICATIONS

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RÉSUMÉ

La distribution et l'écologie des Chéloniens dulçaquicoles et terrestres ont été étudiées dans l'est du delta du Niger au Nigéria. Cinquante deux zones d'étude, distribuées le long des bassins hydrographiques des principales rivières et dans les principaux types d'environnement présents dans la région, ont été soigneusement prospectées durant plus de deux ans. Sept espèces de Chéloniens ont été trouvées ; quatre d'entre elles (*Pelomedusa subrufa olivacea, Pelusios c. castaneus, Kinixys belliana nogueyi, Kinixys erosa*) étaient pour la première fois signalées dans la région du delta du Niger. *P. castaneus, P. niger* et *K. homeana* sont apparus communs ; en revanche, *K. belliana* était extrêmement rare. En général, les espèces furent principalement notées dans les zones où dominaient la forêt marécageuse deltaïque, mais la distribution de *P. castaneus* débordait largement celle de ce type d'habitat dans la région. Un modèle statistique (basé sur la méthode de régression logistique) fut appliqué pour évaluer les effets des variables macro-environnementales sur la distribution locale des espèces. Il apparut qu'un facteur déterminant de la présence d'une ou de plusieurs de ces espèces était : (i) la présence de forêt sèche primaire pour *P. castaneus* et *P. niger* ; (ii) la présence de forêt sèche secondaire pour *K. homeana,* mais la présence d'un habitat buissonnant ou de plantations et zones cultivées n'était en aucun cas déterminante de la présence d'une des espèces étudiées ; (iii) la présence de forêt marécageuse primaire pour *P. niger* ; (iv) la présence de forêt marécageuse secondaire pour *P. subrufa, K. erosa* et *K. homeana* ; (v) la présence de mangroves pour *P. niger* et *K. homeana* ; (vi) la présence de grands cours d'eau (rivières, marigots) pour *P. subrufa.* La combinaison forêt sèche primaire/forêt marécageuse secondaire serait déterminante de la présence de cinq des sept espèces, apparaissant ainsi comme une combinaison d'habitats cruciale du point de vue de la conservation. Une analyse factorielle en composantes principales classe les sept espèces de Chéloniens et les huit paramètres du macro-environnement en cinq groupes : (1) un groupe formé par *P. subrufa* et *K. belliana* ; (2) un groupe formé par les paramètres « milieu buissonnant » et « zones cultivées/plantations » ; (3) un groupe relativement proche du (2), constitué par les paramètres « forêt sèche secondaire » et « forêt marécageuse secondaire » avec les espèces *K. erosa* et *K. homeana* ; (4) un groupe associant les paramètres « forêt sèche

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primaire », « forêt marécageuse primaire » et « grands cours d'eau permanent » aux espèces *P. castaneus, P. niger* et *Trionyx triunguis* ; (5) un groupe formé par le seul paramètre « mangrove ». Les données phénologiques suggèrent qu'une seule espèce (*P. subrufa*) serait susceptible d'estiver en saison sèche.

SUMMARY

Distribution and ecology of freshwater and terrestrial Chelonians were studied in eastern Niger Delta of Nigeria. Fifty-two study areas, sparsely distributed along the hydrographic basins of the main rivers and in the main environmental types available in the region, were carefully surveyed over more than two years. Seven Chelonian species were found; four of them (*Pelomedusa subrufa olivacea, Pelusios c. castaneus, Kinixys belliana nogueyi, Kinixys erosa*) were recorded for the first time inside the Niger Delta region. *P. castaneus, P. niger*, and *K. homeana* appeared to be common, whereas *K. belliana* was extremely rare. In general, species were recorded mainly from the areas characterized by dominant deltaic swamp forest, but the distribution of *P. castaneus* exceeded by far the distribution of this habitat in the study region. A statistical model (based on logistic regression method) was applied to evaluate the effects of the macro-environmental variables on the local distribution of the various species. It resulted that a determinant factor for the presence of the species was: (i) the presence of Primary Dry Forest for *P. castaneus* and *P. niger*; (ii) the presence of Secondary Dry Forest for *K. homeana*, but the presence of both Shrubland and Farmland/Plantation was not determinant for the presence of any species; (iii) the presence of Primary Swamp Forest for *P. niger*; (iv) the presence of Secondary Swamp Forest for *P. subrufa, K. erosa*, and *K. homeana*; (v) the presence of Mangrove Formations for *P. niger* and *K. homeana*; (vi) the presence of Permanent Big Water-Bodies (rivers, creeks) for *P. subrufa*. The combination of Primary Dry Forest and Secondary Swamp Forest would be determinant for the presence of five of seven species, thus demonstrating to be a crucial combination of habitats from the conservationistic point of view. Principal Component Factor Analysis classified the seven Chelonian species and the eight macro-environmental parameters into five groups: (1) a group formed by *P. subrufa* and *K. belliana*; (2) a group formed by the macro-environmental parameters "Shrubland" and "Farmland/Plantation"; (3) a group, relatively close to the group (2), formed by the macro-environmental parameters "Secondary Dry Forest" and "Secondary Swamp Forest", and by the species *K. erosa* and *K. homeana*; (4) a group formed by the macro-environmental parameters "Primary Dry Forest", "Primary Swamp Forest", and "Permanent big Water Body", and by the species *P. castaneus, P. niger*, and *Trionyx triunguis*; (5) a group formed by the macro-environmental parameter "Mangrove" alone. Phenology data suggested that only one of seven, if any, species could aestivate during the dry season: *P. subrufa*.

INTRODUCTION

Studies concerning biodiversity surveys of local faunas are often crucial to realize proper conservation programs (Serra-Cobo *et al.*, 1993). Some Afrotropical regions, where (i) the biodiversity is remarkably high, (ii) the scientific knowledge of the local faunas is relatively little, (iii) the human population growth is very quick, and (iv) the natural resources exploitation is dramatically increasing year-by-year due to rapid industry development, are especially critical. Nigeria is at the same time the African country with the highest human population density and the leader of the whole of Africa in terms of oil and natural gas exports, with most of this highly developed industry concentrated in the south-eastern part of the country (De Montclos, 1994), which has proven to be a fertile environment for speciation and endemism in many floral and faunal groups (Kingdon, 1990). Thus, this country seems to be particularly important from the biodiversity and conservation points of view. However, there are many animal groups of Nigeria which are very little known and that deserve careful attention by scientific authorities.

Among these poorly known animal groups, we can cite the terrestrial and freshwater Chelonians. These reptiles are little known not only in Nigeria but also in the whole of West Africa (e.g. Loveridge & Williams, 1957; Villiers, 1958; Joger, 1981; Ernst & Barbour, 1989; Iverson, 1992a, 1992b; Rodel & Grabow, 1995; Joger & Lambert, 1996; Rodel, 1997), where the few detailed available information is generally confined to terrestrial species from the semi-arid environments (e.g. see Lambert, 1993, and references therein). With regard to the Nigerian species virtually nothing is known except for a few distribution records (e.g. Romer, 1953; Joger, 1981; Iverson, 1992a). Even in the scientific reports circulating between environmentalists of the international oil companies operating in the country and in the various reports to conservation agencies no turtle data exists (cf. Powell, 1993, 1994, 1996; Singh *et al.*, 1995; etc.).

This scarcity of scientific data makes it difficult to assess the population status of Nigerian Chelonians and to establish any reliable conservation planning for them.

We have been conducting a long-term field project on the ecology and distribution of reptiles in south-eastern Nigeria (e.g. see Angelici & Luiselli, 1999). As a part of this research, we have been collecting detailed data on distribution and ecology of turtle and tortoise species.

This report includes:

(1) a synthesis of all distribution data collected in over two years of intensive field work;

(2) a description of the habitat characteristics and of the phenology of the various species;

(3) a statistical model (based on the logistic regression method) on the effects of the macro-environmental variables on the local distribution of the various species;

(4) a synthesis of the ecological and conservation implications produced by the above-mentioned effects on free-ranging populations of Chelonians, also in relation to the potential threats due to the intense landscape usage from oil-related industry activities in these fragile tropical environments.

STUDY AREA

Data given here were recorded during several field research expeditions which were done from September 1996 to early February 1999 in several localities of the eastern axis of the Niger Delta (south-eastern Nigeria, Fig. 1). The study area is situated in both the Rivers State (capital: Port Harcourt) and in the Bayelsa State (capital: Yenagoa).

The climate of this region is typical for a tropical sub-Saharan country, with well-marked dry and wet seasons and relatively modest monthly fluctuations in maximum and minimum temperatures. The dry season extends from November to April, and the wet season from May to October (with some year-to-year variations). Mean monthly maximum temperatures range between 27 and 34 °C, while minima vary between 22 and 24 °C. Annual rainfall exceeded 3 000 mm (data from the Department of Geography, Rivers State University of Science and Technology, Port Harcourt).

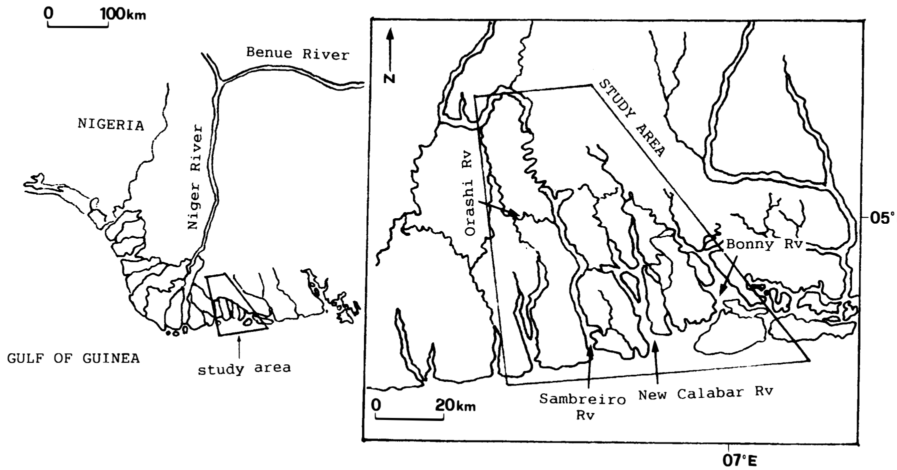

Figure 1. — Map of southern Nigeria, showing the study area (eastern Niger Delta), and rough topography of the study area, with the location of main towns and rivers.

The study areas were situated within the hydrographic basins of the rivers Bonny, New Calabar, Sambreiro, Orashi, and Taylors Creek (Fig. 1). These areas have been the objects of careful faunistic and ecological research to assess the status and the conservation priorities of selected endangered vertebrates (e.g. see Angelici *et al.*, 1998, Akani *et al.*, 1999a, 1999b).

The study region is heavily populated, with hundreds of small villages and towns interspersed within a patchy mosaic of oil palm fields, plantations (banana, plantain, pineapple, yam, coconut, sugar cane, cassava, etc.), open lands used for oil extraction platforms, forests, shrublands, and water bodies (Singh *et al.*, 1995). Port Harcourt, a city with over 500 000 people, is the main urban centre of the study region and one of the most important business centres for the oil-related industry in the whole of Africa. In general, the environment is extremely complicated, being continuously conditioned by the alternance between water and soils, but we divided the study region into three main environmental zones: (i) a deltaic swamp rainforest zone, (ii) a mainly cultivated and farmed zone, and (iii) a very wide mangrove zone (Fig. 2). The widest portions of remnant rainforest are found along the banks of the rivers (riverine forests). Rainforest patches may have dry soil (lowland dryland forest) or may be seasonally flooded and inundated swamp-forests. These swamp-forests are dominated by *Raphia vinifera* and *Raphia hookeri*, and other common plant species are *Uapaca staudtii, Sterculia oblonga, Ceiba pentandra, Pandanus* sp., and *Pterocarpus santalinoides*; typical tree species include *Terminalia superba, Piptadeniastrum africanum*, and *Lophira alata.* Mangroves (dominant species are *Avicennia marina* and *Rhizophora racemosa*) are found along the brackish water river tracts, and form enormous extensions along the coast ("coastal mangroves"). It should be noted that mangrove forests of Nigeria are the widest in all of Africa and the third-largest in the world, and that approximately 60 % of the Nigerian mangrove forest is situated in the Niger Delta (Singh *et al.*, 1995).

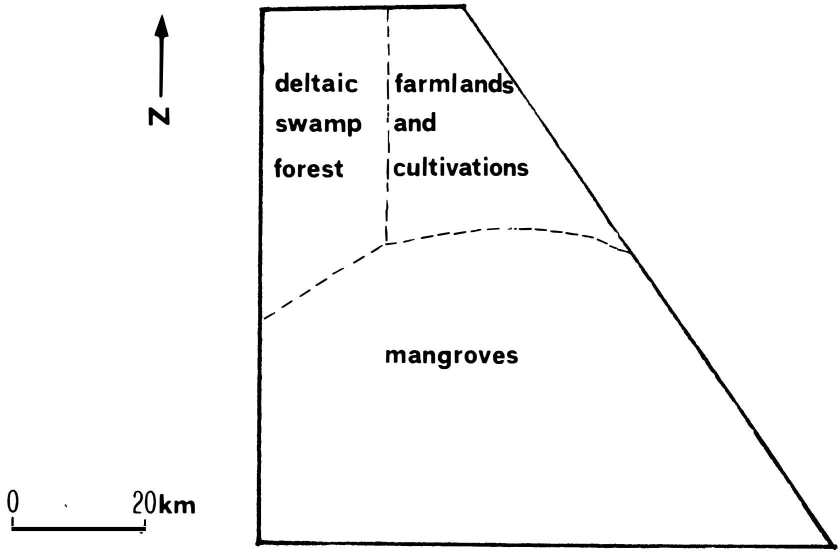

Figure 2. — Schematic division of the study region on the basis of the main environmental characteristics. Note that mangroves occupy a very large territory within the study region.

The courses of the rivers Sambreiro, and especially Orashi River and Taylors Creek, are characterized by the presence of wider rainforest patches along the banks than the courses of the rivers Bonny and New Calabar, and are characterized by a higher vegetation diversity (Cescon & Politano, 1997). Conversely, the Bonny and New Calabar Rivers are characterized by wider mangrove formations and only a few remnant rainforest patches (e.g. at Peterside, see Table I for the relative geographic coordinates). More details of the vegetation and environmental features of the entire area are reported in Cescon & Politano (1997), and more general information on the environment is found in Powell (1993), Singh *et al.* (1995), and Isoun *et al.* (1996).

METHODS

Fifty-two randomly selected study plots (each with a surface of 20 to 200 ha) were intensively surveyed for the presence of Chelonians (Cescon & Politano, 1997). The following eight macro-environmental parameters were identified within the study region: (1) primary dry forest (PDF); (2) secondary dry forest (SDF); (3) shrubland (SHL); (4) primary swamp-forest (PSF); (5) secondary swamp-forest (SSF); (6) mangrove (MGR); (7) farmland and plantation (FPL); (8) large water body (main river tract or wide lake, PWB).

We characterized our study plots according to these eight parameters. The place-names, the geographic coordinates, and the macro-environmental parameters of each study area are presented in table I. The 52 study areas are always indicated with the toponym of the closest village or town as in the map of the study

Table I

Gazetter of the place-names, geographic coordinates, and macro-environmental parameters of 52 study places situated in the eastern Niger Delta region of Nigeria. Code: 1 = presence; 0 = absence. Code for the macro-environmental parameters: primary dry forest = PDF; secondary dry forest = SDF; shrubland = SHL; primary swamp-forest = PSF; secondary swamp-forest = SSF; mangrove = MGR; farmland and plantation = FPL; large water body (main river tract or wide lake) = PWB.

No	Place-name	Lat (N)	Lon (E)	PDF	SDF	SHL	PSF	SSF	MGR	FPL	PWB
1	Kreigeni	05°17'	06°37'	0	1	1	0	0	0	1	1
2	Abarikpo	05°08'	06°37'	1	0	0	0	0	0	1	0
3	Otari	04°53'	06°41'	1	1	0	0	1	0	1	1
4	Rumuji	04°57'	06°46'	0	0	1	0	0	0	1	0
5	Orubiri	04°42'	07°01'	0	0	1	0	0	1	1	0
6	Soku	04°40'	06°40'	0	1	1	0	1	0	1	1
7	Tombia	04°46'	06°53'	0	1	1	0	1	1	1	0
8	Tombia II	04°46'	06°51'	0	0	0	0	0	1	0	0
9	Opu-Ogbogolo	04°54'	06°34'	1	1	1	0	0	0	1	1
10	Peterside	04°29'	07°10'	1	1	1	0	1	1	1	1
11	Bonny Island	04°25'	07°15'	0	1	1	0	1	1	1	1
12	Mbikiri	04°33'	07°20'	0	0	0	0	0	1	1	1
13	Okrika	04°38'	07°10'	0	0	1	0	1	1	1	1
14	Buguma	04°43'	06°50'	0	1	1	0	1	0	1	1
15	Onitu	05°05'	06°28'	0	1	1	0	1	0	1	1
16	Rumuoro	04°55'	06°52'	0	1	1	0	0	0	1	1
17	Kiribureru	04°27'	06°48'	0	0	0	0	0	1	1	1
18	Igbeta-Ewoama	04°34'	06°21'	0	0	0	0	0	1	1	1
19	Abelkiri	04°44'	06°49'	0	1	0	0	1	1	1	1
20	Degema	04°48'	06°48'	0	1	1	0	0	1	1	1
21	Ogbele	05°00'	06°50'	1	1	1	1	1	0	1	1
22	Elebele	04°51'	06°20'	0	1	1	0	1	1	1	1
23	Elem-Sangama	04°40'	06°39'	0	1	1	1	1	1	1	1
24	Iserekiri	04°44'	06°36'	0	1	1	0	1	0	1	1
25	Opikiri	04°46'	06°36'	1	1	0	0	1	0	1	1
26	Ogbemakoku	04°47'	06°35'	1	1	0	0	1	0	1	1
27	Okoba	04°52'	06°41'	1	1	0	1	1	0	1	1
28	Aseingbene	05°05'	06°19'	1	1	1	1	1	0	0	1
29	Egbada	05°18'	06°46'	0	1	1	0	0	0	1	0
30	Ibawa	05°09'	06°46'	0	0	1	0	1	0	1	0
31	Etiema	04°34'	06°22'	0	1	1	0	0	0	1	0
32	Dariama	04°38'	06°47'	0	0	1	0	0	1	1	1
33	Orugbanikiri	04°41'	06°50'	0	0	1	0	1	1	1	1
34	Ogbokuma	04°52'	06°46'	0	0	1	0	1	1	1	1
35	Ahoada	05°04'	06°38'	0	1	1	0	1	0	1	0
36	Odiokwu	05°06'	06°37'	0	1	1	0	1	0	1	1
37	Oblebe	05°13'	06°41'	0	1	1	0	1	0	1	1
38	Egita	05°15'	06°41'	0	1	1	0	1	0	1	1
39	Obagi	05°13'	06°37'	1	1	1	0	1	0	1	1
40	Bikkiri	04°46'	06°36'	0	1	1	0	0	1	1	1
41	Old Sangama	04°43'	06°39'	0	1	1	0	1	0	1	1
42	Egunughan	04°56'	06°36'	1	1	1	1	1	0	1	1
43	Akwukoeterre	04°53'	06°48'	0	0	1	0	0	1	1	1
44	Adanta	04°57'	06°53'	0	0	1	0	1	1	1	1
45	Ihie	05°17'	06°45'	0	1	1	0	1	0	1	1
46	Obonoma	04°43'	06°48'	0	1	1	0	1	1	1	1
47	Fekorukiri	04°44'	06°37'	0	1	1	0	1	0	0	1
48	Rumuehuo	04°55'	06°47'	0	1	1	0	1	0	1	1
49	Ubimini	05°16'	06°48'	0	1	1	0	1	0	1	1
50	Awarra	05°21'	06°49'	0	1	1	0	1	0	1	0
51	Itelema	04°50'	06°49'	0	0	1	0	0	1	1	1
52	Oduhoa	04°56'	06°50'	0	1	1	0	1	0	1	1

region (scale 1:250,000) presented in Cescon & Politano (1997). The hierarchical cluster of the macro-environmental parameter similarity among the study areas (cases processed: $n = 52$) is presented in figure 3.

Chelonians were searched for during surveys conducted to assess the environmental impact of gas and oil transmission systems on the local fauna (Cescon & Politano, 1997), and contextually to field research on the ecology and distribution of snakes, monitors, and Crocodilians (e.g. see Luiselli *et al.*, 1998; Akani *et al.*, 1999a; Angelici & Luiselli, 1999; Luiselli & Akani, 1999).

Field trips were conducted under every weather conditions. The various study areas, which often were very isolated and impossible to reach by car, were joined by boat or by helicopter. The field work was done regularly approximately from 0800 hrs to 1800 hrs. Because of potential security risks due to groups of criminals operating in the region, we were normally unable to conduct field trips during twilight and nocturnal hours. Anyway, probably the turtle activity is very reduced or even suspended during nocturnal time.

Terrestrial species were searched for by means of walking trails that included all the macrohabitats available in each study area. Freshwater turtles were captured by hand on land or in shallow stream pools, by dip nets, by indigenous designed traps, and by baited hoop traps. Traps were fitted with floats to prevent submergence during heavy rains (Van Loben Sels *et al.*, 1997). Many additional specimens were obtained from local hunters or from bush-meat markets of local tribes (Ojonugwa, 1986; Akani *et al.*, 1998). Chelonians (mainly the terrestrial ones) constitute a local delicacy and are considered holy animals ("dgyou-dgyou" animals) in the animistic cults of some villages (Akani *et al.*, 1998).

When turtles were captured, data on habitat, activity, and sex were recorded (cf. Dodd *et al.*, 1994). We also measured carapace and plastron lengths (CL and PL, to $\pm$ 0.2 cm) using a meter stick suspended between batons held vertically at each end of the shell (Lambert, 1993). Turtles were marked with a unique sequence of shell notches (Cagle, 1939) for future recognization and released at their point of capture. When possible, even the specimens collected from hunters or from bush-meat markets were also sexed and measured.

The taxonomy of African Chelonians is in some cases still relatively confused (e.g. some *Pelusios* species), and we followed indications of Ernst & Barbour (1989). No specimens were killed for the purposes of this study. Photographic records of the various species are stored in the collections of the authors.

STATISTICAL PROCEDURES

Data were statistically processed by means of a SPSS (version 4.5, for Windows) personal computer package, with all tests being two-tailed and with alpha set at 5 %.

The effects of the macro-environmental parameters on the presence/absence of a given chelonian species in a given study area were assessed by using a logistic regression model (forward stepwise conditional procedure) for discrete values (Hosmer & Lemeshow, 1989). In this analysis, the study areas were the cases (total $n = 52$), the presence/absence of the given chelonian species was the dependent variable, and the macro-environmental parameters were the covariates (total $n = 8$). Principal Component Analysis (PCA) was used to classify the distribution of the various species in the multivariate space in relation to the macro-

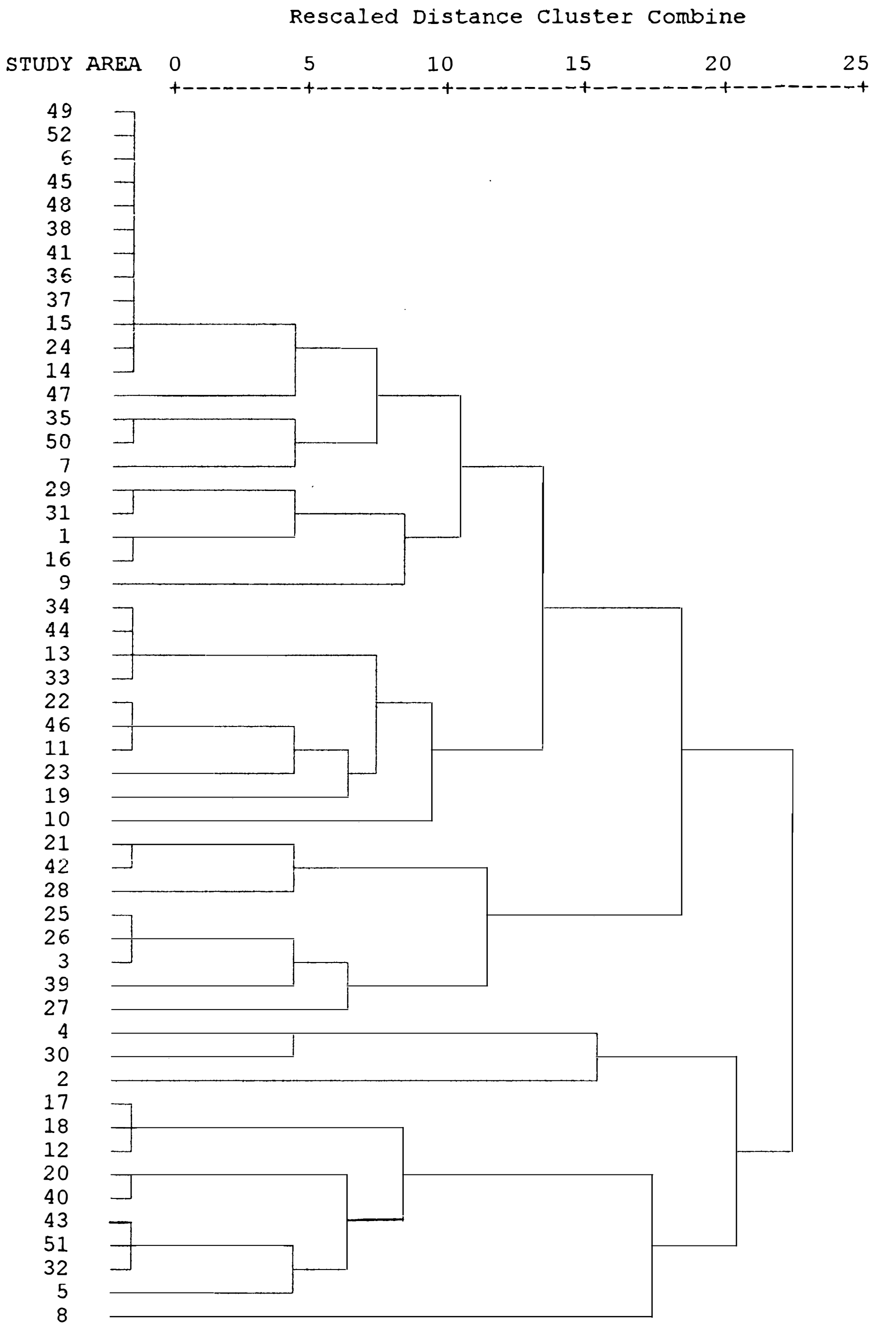

Figure 3. — Hierarchical cluster of macro-environmental parameter similarity among 52 study areas in the eastern Niger Delta region of Nigeria.

environmental parameters found in the study region. In this analysis, species and macro-environmental parameters were entered together as independent variables ($n = 15$), and study areas were the processed cases ($n = 52$).

RESULTS AND DISCUSSION

List of the species and general considerations

We found three terrestrial turtle species and four aquatic species. The observed species were (vernacular names following Iverson, 1992):

Pelomedusidae

*** *Pelomedusa subrufa olivacea* (Schweigger, 1812) - Helmeted turtle;
*** *Pelusios castaneus castaneus* (Schweigger, 1812) - West African mud turtle;
*** *Pelusios niger* (Duméril and Bibron, 1835) - West African black turtle;

Testudinidae

*** *Kinixys belliana nogueyi* (Lataste, 1886) - Bell's hinge-back tortoise;
*** *Kinixys erosa* (Schweigger, 1812) - Serrated hinge-back tortoise;
*** *Kinixys homeana* (Bell, 1827) - Home's hinge-back tortoise;

Trionychidae

*** *Trionyx triunguis* (Forsskal, 1775) - African softshell turtle.

No species is new for Nigeria (Iverson, 1992a). However, *P. subrufa, P. castaneus, K. belliana,* and *K. erosa* have not been recorded before in the Niger Delta region (see maps in Iverson, 1992a). Moreover, some of these species (e.g. *P. castaneus* and *K. erosa*) were previously recorded from a very few sites in Nigeria (Iverson, 1992a).

According to Iverson's (1992a) distribution maps, *P. subrufa* was previously known from several Nigerian localities, but the two places closest to the eastern Niger Delta region were Lagos State (approximately 480 km NW of Port Harcourt) and Benue State (approximately 450 km NE of Port Harcourt). In terms of environmental characteristics, the former area is likely to be quite similar to Port Harcourt area (moist lowland forest patches and wide cultivations), but the latter area is no doubt more open and arid (Guinea savanna, see Singh *et al.*, 1995). *P. castaneus* was previously recorded in Nigeria only from two localities in the Cross River State, situated about 250-280 km NE of Port Harcourt. These localities, however, were situated within the region of the continuous forest as well as the Niger Delta region itself (Gartshore, 1985; Singh *et al.*, 1995). *K. belliana nogueyi* was previously recorded from several Nigerian places, including a single locality along the Niger River course situated approximately 250 km N of Port

Harcourt, and characterized by a very different environment (shrublands and bushy derived savanna). *K. erosa* was previously recorded from only two sites in Nigeria: near Musin (Lagos State) and Makurdi. Both localities were far from the eastern Niger Delta region (respectively, 460 km W of Port Harcourt, and 370 km NE of Port Harcourt), and, at least the latter locality is characterized by a very different vegetation type (Guinea savanna, see Singh *et al.*, 1995). *K. homeana, P. niger*, and *T. triunguis* were previously collected from the Niger Delta region (e.g. see Iverson, 1992a), and their continued presence was confirmed by our research.

Other chelonian species, potentially present in the study region, could have perhaps "escaped" our attention. *Pelusios adansonii* (Schweigger, 1812) is known from several Nigerian localities, including the surroundings of Obuasi, Famiso, Ibadan (Oyo State), and several places situated in the northern part of the country (e.g. Lake Tchad region, see Iverson, 1992a). Moreover, this species has been captured in the surroundings of Idah, in an area situated along the Niger river course, approximately 220 km north of Port Harcourt. This latter record is quite interesting, as the general environment of the Idah area is relatively similar to that of Port Harcourt area, despite being much less covered by forests (savanna-forest mosaic vegetation type) and more dry. The other Nigerian localities where *P. adansonii* was captured were apparently less similar to the eastern Niger Delta region. *Pelusios gabonensis* (Duméril, 1856) has never been recorded for Nigeria (Iverson, 1992a). However, given the general distribution of the species (present from Liberia to Ghana, and again from central Cameroon to Congo, see Iverson, 1992a), it is likely that it occurs in Nigeria, including the southernmost regions and the Niger Delta. The African spurred tortoise *Geochelone sulcata* (Miller, 1779), the largest of the world's continental tortoise species, is known only from the dry open fields of northern Nigeria, and thus it is surely absent from the wet regions of southern Nigeria (Loveridge & Williams, 1957; Ernst & Barbour, 1989; Iverson, 1992a; Lambert, 1993). The flapshell turtles *Cyclanorbis elegans* (Gray, 1869) and *Cyclanorbis senegalensis* (Duméril and Bibron, 1835), which are known to inhabit the drainage of Niger River north of the study region (Iverson, 1992a) and are thus potentially present even in the Niger Delta, were not found during the present research. Future research will be necessary to establish whether relictual populations of any of these latter species are present in the Niger Delta area.

The number of Testudinidae species we recorded in the Niger Delta ($n = 3$) is exactly the same as that reported by Iverson (1992b) as species richness expected for the region. Conversely, the single Trionychidae species is lower than that expectable ($n = 2$-3, see Iverson, 1992b). The same is true for the three Pelomedusidae species, where Iverson (1992b) predicted five species.

Distribution

The distribution of the various chelonian species within the 52 sites is summarized in table II. *P. castaneus* and *K. homeana* were identified in most localities, whereas *K. belliana* was the rarest (Fig. 4).

The preliminary distribution maps (10×10 km grid) of the various chelonian species in the eastern Niger Delta region are presented in figure 5. It should be noted that: *P. subrufa* and *K. belliana* were observed only along the Sambreiro River basin; *P. castaneus* and *P. niger* were observed in every surveyed river basin (Taylors Creek, Bonny, New Calabar, Sambreiro, and Orashi); *K. homeana* was

TABLE II

Distribution of the various chelonian species within 52 study places situated in the eastern Niger Delta region of Nigeria. For numbers associated with each locality, see table I.

Species	Locality with ascertained presence
P. subrufa olivacea	3-4-9-20-21-29-30-31
P. castaneus	3-4-9-10-11-12-25-26-27-28-29-32 33-34-35-36-37-38-39-40-41-42-43-44
P. niger	10-26-27-28-29-35-36-38-39-41-42-43
K. belliana nogueyi	3-4-5-9-45
K. erosa	22-23-26-27-35-46-47
K. homeana	5-14-16-22-23-24-25-26-27-28-29-35-36-37-38-39-48-49-50
T. triunguis	4-26-28-41-42-51-52

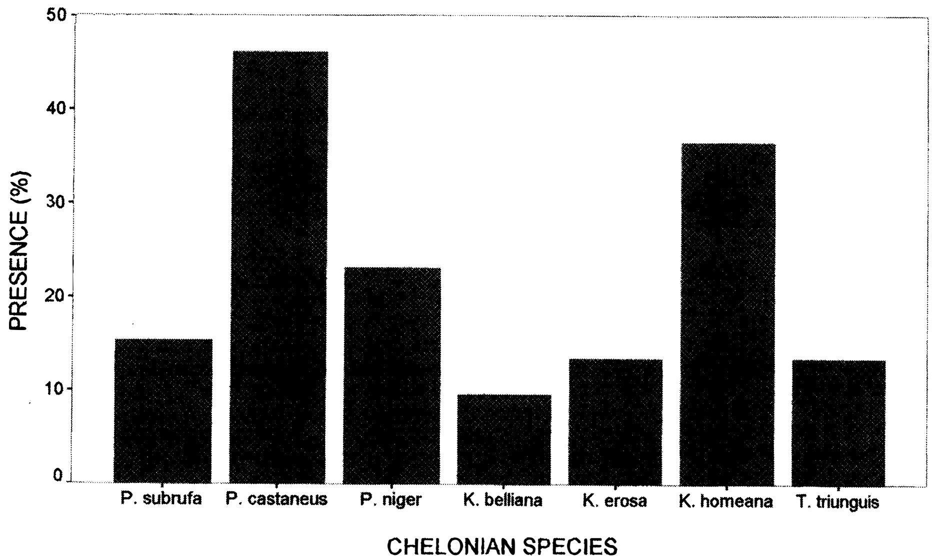

Figure 4. — Frequency of occurrence of the various chelonian species in the eastern Niger Delta region of Nigeria, based on the numbers of "positive" localities (i.e. localities where the presence of a given species was ascertained).

observed in every surveyed river basin but Bonny River; *K. erosa* was observed only along the Sambreiro and Orashi river basins; and *T. triunguis* was observed only along the Orashi and New Calabar River basins. However, interviews with reliable fishermen suggest that this latter species could be much more widespread, and Trionychidae turtles are perfectly described by fishermen from Taylors Creek, Sambreiro and Bonny Rivers as well. Concerning these fishermen, it should be

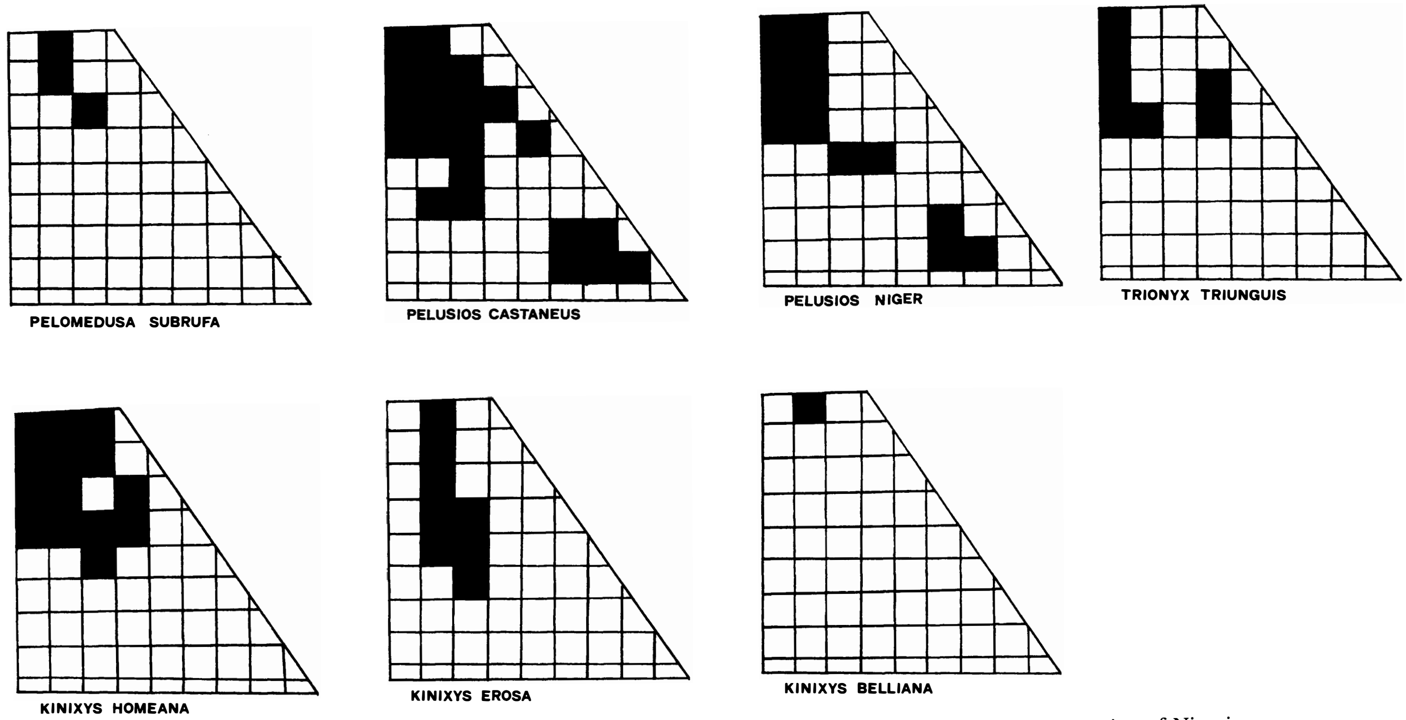

Figure 5. — Distribution maps of the various turtles and tortoises in the eastern Niger Delta region of Nigeria.

noted that they were unable to discriminate between *Trionyx* and *Cyclanorbis* species, so it is possible that even species of *Cyclanorbis* could eventually be recorded in the surveyed region of Nigeria.

A dendrogram clustering the seven chelonian species in terms of affinities of "positive" and "negative" localities (i.e. localities where the presence or the absence of a given species was ascertained) is presented in figure 6. Based on this dendrogram, it is evident that *P. niger* and *K. homeana* are clustered together, whereas another close cluster is formed by *P. subrufa* and *K. belliana,* including (at a lower degree) also *K. erosa* and *T. triunguis*). *P. castaneus* was separate from every other species.

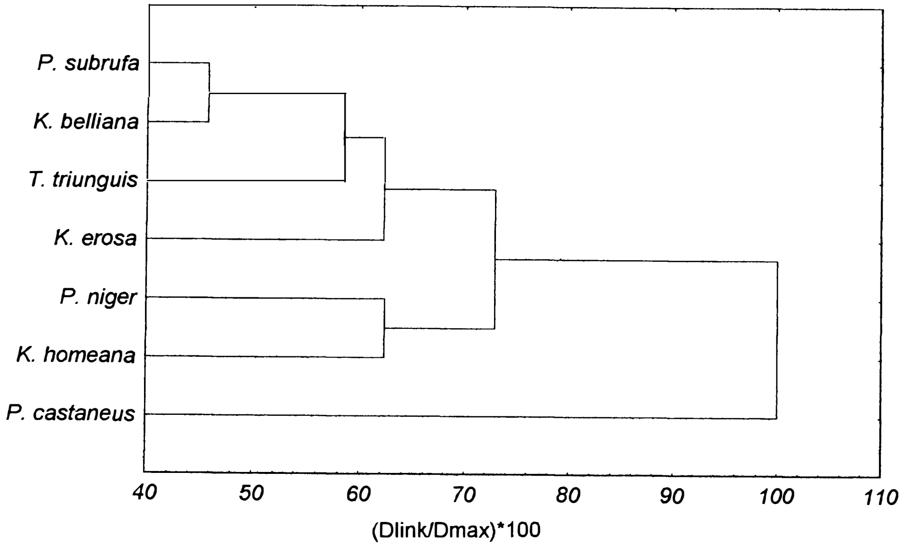

Figure 6. — UPGMA dendrogram (standardized to 100 %) showing the similarity among species in terms of distribution of "positive" and "negative" localities (i.e. localities where, respectively, the presence and the absence of a given species was ascertained).

Habitats

A preliminary indication of the habitats frequented by the various chelonian species can be derived from a comparison of figure 2 with the distribution maps of the various species (Fig. 5). Most species were recorded mainly from the map grids characterized by dominant deltaic swamp forest, and only the distribution of *P. castaneus* extended much beyond this habitat. On the contrary, *P. niger, K. erosa, K. homeana,* and *T. triunguis* had distribution ranges widely overlapping with the distribution of the swamp rainforest in the study region. With regard to the map grids currently characterized by large farmlands with small remnant forest patches (see Fig. 2), it should be noted that they represent a recent forest-derived environmental type due to human activity. Thus, it is not surprising that some typically forest taxa (e.g. *K. homeana*) are still widely distributed in this recently formed environmental type (see Fig. 5). *P. castaneus* was frequently found in rivers, creeks, streams, small lakes, marshes, and in the smaller temporary ponds which dessicate during the dry season (e.g. in the surroundings of Ahoada). For instance, this species was abundant in the small swamps of Peterside and Bonny Island (lower course of Bonny River), as well as along the Orashi River course (e.g., in the surroundings of Elem-Sangama), the Taylors Creek course, and the Sambreiro River course (e.g. in the vicinities of Otari). Moreover, *P. castaneus* was commonly observed both in water bodies surrounded by rainforest patches (e.g. in several sites situated along the upper Orashi River course) and in water bodies within open fields, shrublands, and derived savanna lands. The fact that this species was observed in such a wide range of different habitats is not surprising, as *P. castaneus* is well-known to be an habitat generalist throughout most of its geographic range (Ernst & Barbour, 1989). With regard to southeastern Nigeria, it was frequently found by us even in the territories of Eket (Akwa-Ibom State, 04° 50' N; 07° 59' E), Calabar (Cross River State, 04° 48' N; 08° 21' E), and Itu (Cross River State, 05° 14' N; 07° 59' E). *P. niger* inhabited similar habitats, but, compared with the previous species, appeared to be more linked to permanent water bodies such as creeks, rivers, small lakes, and permanent marshes. It was found in water bodies surrounded by both heavily forested patches and derived savanna or scrublands. According to Ernst & Barbour (1989), this species prefers savannas, but our records indicate a wider habitat preference. In some sites (e.g. along the Orashi, Sambreiro, and Bonny Rivers) this species cohabited with *P. castaneus*. *P. subrufa* was found in muddy ponds, situated both inside derived savanna fields (e.g. in Omogo, upper Sambreiro River course) and inside rainforest patches (e.g. in Egbada, upper Sambreiro River course). It was found mainly in temporary water bodies, this sighting being in agreement with earlier published literature (Ernst and Barbour, 1989). *T. triunguis* was recorded less frequently than the two *Pelusios* species, and appeared more specialized in terms of habitat frequented, always being found in large, slow-moving river tracts, with heavily forested banks (e.g. upper Orashi and Sambreiro River courses). In Itelema (New Calabar River course) it inhabited the river course characterized by brackish water and mangroves along the banks. The fact that this large softshell turtle can enter brackish and even salt waters has been noted previously (Loveridge & Williams, 1957; Ernst & Barbour, 1989). *K. belliana* was rarely found in the field, and it may be the least common chelonian species of the eastern Niger Delta region. This tortoise was observed in the open forest, including clearings and bushy edges, which is surprising, because it it known as a savanna species just entering coastal plain and dune forests (Pritchard, 1979; Branch, 1988; Ernst & Barbour, 1989). In Madagascar, *K. belliana belliana* is known to inhabit highly forested areas, where possibly it has been introduced by man (Kuchling, 1986). *K. homeana* and *K. erosa* were found in heavily forested patches, including wet and swamp forest sites (see also Naulleau, 1988). These two species were observed practically in the same type of habitats, and were also found sympatric in some areas (e.g. in the forests surrounding Ahoada). It is of special interest that they were observed not only in wide forested areas (e.g. along the Orashi River course), but also in the small fragments of forest which are interspersed among the enormously wide mangrove formations growing along the lower courses of the rivers New Calabar and Sambreiro. These terrestrial chelonians were observed in the forests of Buguma, Sangama, Minama, Obonoma-Abelkiri, and Abonnema. Monitoring these isolated populations could be very useful for defining accurate conservation plannings for these species. Given the low forested surface available in these isolated spots (on average less than 10 km^2), the remaining *Kinixys* populations are likely to be constituted by a few reproductive adults, currently submitted to serious risks of extinction by hunting activity of local human tribes (Akani *et al.*, pers. obs.). In any case the coexistence of these three closely related tortoises is important from the conservationist and the ecological points of view.

EFFECTS OF THE MACRO-ENVIRONMENTAL PARAMETERS ON THE PRESENCE/ ABSENCE OF THE VARIOUS CHELONIAN SPECIES

The similarities among species in terms of positive/negative localities are presented by UPGMA tree diagram in figure 6. The presence of five out of seven species was significantly correlated with the presence of at least one macro-environmental parameter, whereas for two species it was impossible to find any parameter which significantly affected the presence/absence of the given species in a given place.

The presence of *P. subrufa* was significantly correlated with the presence of PWB ($r = 0.290$, $P = 0.016$) and SSF ($r = 0.201$, $P = 0.050$), and tended to be correlated with the presence of MGR ($r = 0.154$, $P = 0.081$; for the other macro-environmental parameters P values ranging from 0.218 to 0.794). The presence of *P. castaneus* correlated significantly only with PDF ($r = 0.268$, $P = 0.007$; for the other parameters P values ranging from 0.254 to 0.962). The presence of *P. niger* correlated significantly with PDF ($r = 0.321$, $P = 0.005$), MGR ($r = 0.289$, $P = 0.009$), and with PSF ($r = 0.200$, $P = 0.039$), and tended to correlate with SDF ($r = 0.146$, $P = 0.070$; for the other parameters P values from 0.177 to 0.797). The presence/absence of *K. belliana* was not significantly correlated with any parameter (P values from 0.171 to 0.963). The presence of *K. erosa* correlated significantly only with SSF ($r = 0.217$, $P = 0.047$), and tended to correlate with both PSF ($r = 0.181$, $P = 0.067$) and SDF ($r = 0.177$, $P = 0.070$; for the other parameters P values from 0.299 to 0.886). The presence of *K. homeana* correlated significantly only with SDF ($r = 0.299$, $P = 0.0044$), MGR ($r = 0.284$, $P = 0.006$), and with SSF ($r = 0.166$, $P = 0.048$; for the other parameters P values ranging from 0.251 to 0.905). The presence/absence of *T. triunguis* was not significantly correlated with any parameter (P values ranging from 0.130 to 0.986).

Generally, the presence of PDF was a determinant factor for the presence of two chelonian species (*P. castaneus* and *P. niger*), SDF for the presence of a single species (*K. homeana*), SHL and FPL were not determinant for the presence of any species, PSF was determinant for the presence of a single species (*P. niger*), SSF was determinant for the presence of three species (*P. subrufa, K. erosa*, and *K. homeana*), MGR was determinant for the presence of two species (*P. niger* and *K. homeana*), and PWB was determinant for the presence of only *P. subrufa.* It is interesting to note that a combination of PDF and SSF would be determinant for the presence of five of seven species, thus demonstrating to be a crucial combination of habitats from the conservationist point of view.

The results of PCA classified the processed variables (i.e. the seven chelonian species and the eight macro-environmental parameters) into five main groups (Fig. 7): (1) a group formed by only *P. subrufa* and *K. belliana*; (2) a group formed by the macro-environmental parameters SHL and FPL; (3) a group, relatively

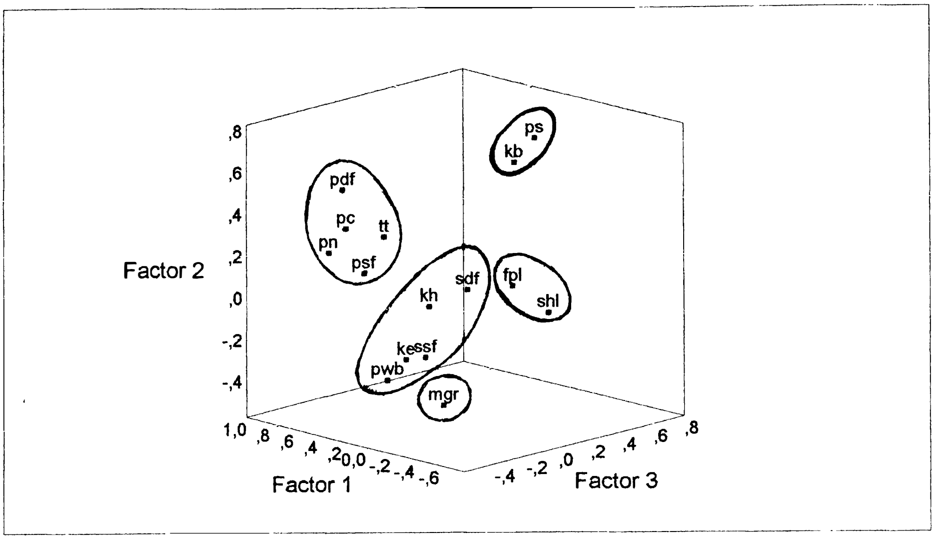

Figure 7. — Plot of the results of a Principal Component Analysis performed on 15 variables (7 chelonian species and 8 macro-environmental parameters) and 52 cases (the 52 study areas). For more details, see text. Codes for the macro-environmental parameters are the same as in table I. Symbols for species: kb = *Kinixys belliana*; kh = *Kinixys homeana*; ke = *Kinixys erosa*; tt = *Trionyx triunguis*; pc = *Pelusios castaneus*; pn = *Pelusios niger*; ps = *Pelomedusa subrufa.*

close to the group (2), formed by the macro-environmental parameters SDF, and SSF, and by the species *K. erosa* and *K. homeana*; (4) a group formed by the macro-environmental parameters PDF, PSF, and PWB, and by the species *P. castaneus, P. niger,* and *T. triunguis*; (5) a group formed by the macro-environmental parameter MGR alone.

PHENOLOGY

Several Afrotropical reptiles are characterized by very pronounced seasonality in activity patterns. Thus, it is interesting to check whether pronounced seasonality is found also in the Niger Delta chelonians.

All the few specimens of *P. subrufa* observed in the field (n = 10) were found in July, August, and September, i.e. during the wet season. Surveys conducted during the dry season (February, March, and April) in the same areas did not produce any *Pelomedusa* specimen. Thus, although our sample is too small to give firm conclusions, we think that this species aestivates during the dry season months. Ernst & Barbour (1992) reported that this species buries itself in the mud bottoms when the temporary pools dry up, resting there till the next rainy season. Both *Pelusios* species were frequently observed in the field during both the wet and the dry season. Decreased activity during the dry season is possible, but we are still collecting field data and more pertinent conclusions will be presented in a forthcoming paper. In any case, the fact that *Pelusios* activity is not suspended during the dry season is consistent with the fact that these turtles tend to inhabit permanent water bodies. However, it should be noted that, according to Ernst & Barbour (1992), *P. castaneus* specimens are forced to aestivate buried either in the sand on shore or in the bottom in the places where their natural habitat is dry during the dry season. Our data on *K. belliana* are so few that we cannot address any reliable indication. This species is said to aestivate obligately during the dry months, usually in mud bottoms of drying waterholes (Ernst & Barbour, 1992). *K. erosa* and *K. homeana* were observed during both the wet and dry seasons without any evident difference in the frequency of observation (Luiselli *et al.*, unpubl. data). Field observations of active specimens of these species during the dry season have been presented by Blackwell (Ernst & Barbour, 1992), and Nigerian specimens of *K. erosa* may mate during the late phase of the dry season (April). *T. triunguis* was rarely observed in the field, but in most cases during the dry season. Thus, also considering that this species is a typical inhabitant of permanent water bodies, we can exclude that it shows any "diapause" during the dry months of the year.

CONCLUSIONS

With regard to species distribution, this study has been relevant because it demonstrates the occurrence in the eastern Niger Delta of some chelonian species which had never been recorded from this territory. Considering that some of these species proved to be widespread and locally very abundant (and thus have surprisingly "escaped" the attention of previous researchers), we are led to think that much more research on chelonian distribution is deserved in central and western Africa, and especially in Nigeria, where the local chelonian distribution seems to be poorly known.

The Niger Delta area proved to be remarkable in terms of species richness, given the firm records of presence of seven nearly sympatric chelonian species. This high chelonian diversity would be expected if we consider that (i) the Niger Delta region is one of the wettest of the African continent, and (ii) annual rainfall proved to be a highly significant correlate of chelonian species richness at the global scale (Iverson, 1991). Concerning this latter issue, it should be however noted that some bias in Iverson's (1991) analyses could have possibly arisen from the too large scale used for the distribution and climatic data, thus affecting the eventual conclusions. With regard to the Niger drainage, for instance, Iverson (1991, p. 81) reported the occurrence of 11 species, of which 8 were aquatic. These numbers were clearly generated including all the species potentially present along the whole river drainage. However, these numbers ran against climatic data from a single spot (Enugu) which is not representative at all of the many climatic types available along the drainage, from the semi-arid zones of Burkina-Faso and north Nigeria to the wet rainforest zones of the Delta in southern Nigeria. Thus, it seems reasonable to hypothesize that the whole statistical analysis would have partially changed if Prof. Iverson would have tried to correlate the species richness with climatic data coming from another locality of the Niger drainage, situated e.g. in Burkina Faso or in the Port Harcourt region. Of course, we are led to think that the same bias could be true also for several other large river drainages in the world (e.g. Nile, Congo, Volta, etc.), thus seriously affecting the results of the global correlations.

Another remarkable result of our surveys is the discovery of a zone of near sympatry between three *Kinixys* species. Indeed, this overlapping distribution of these three tortoises is surprising. On the one hand, it was already well known that the distribution of the two forest species (*K. erosa* and *K. homeana*) widely overlap in central-western Africa (Ernst & Barbour, 1989; Iverson, 1992a), and thus our data on these two species are just confirmatory. On the other hand, it was quite unpredictable that the distribution ranges of *K. belliana*, a mainly savanna tortoise, and these two forest species overlap in the eastern Niger Delta. Available distribution accounts (e.g. Iverson, 1992a) show in fact that the distribution ranges of *K. belliana* and *K. erosa* are in general mutually exclusive, the former species being practically lacking from Cameroon, Equatorial Guinea, Gabon, Congo, and Zaire, where the latter species is widespread (Ernst & Barbour, 1989; Iverson, 1992a). However, the nearly contiguous presence of *K. belliana* and *K. erosa* was observed in savanna-forest mosaic landscapes of northern Zaire (Lanza & Vanni, 1976). In this regard, it is interesting to note that the eastern Niger Delta region should be a zone of contact between savanna and forest reptile faunas: for instance, (1) the snakes *Dispholidus typus* and *Naja nigricollis,* two typical savanna inhabitants, are quite common in this region, entering also remnant forest and thick forest places (Akani *et al.*, 1999b); (2) *P. subrufa*, a typical savanna turtle, is also present in the study region; and (3) even the forest and the savanna forms of the Nile monitor lizard (i.e. *Varanus niloticus niloticus* and *Varanus niloticus ornatus*) could possibly have a sympatry zone in the Niger Delta region (Boheme & Ziegler, 1997; but see also Angelici & Luiselli, 1999). Because of all these reasons, it is obvious that the Niger Delta region is extremely important under the biogeographic point of view, thus requesting the highest attention of scientists interested in both biodiversity assessment and conservation (Oates *et al.*, 1992; Singh *et al.*, 1995; Tooze, 1995).

What about interspecific competition among Niger Delta chelonian species? Our data are of course too preliminary to state anything on this issue, but some considerations could be addressed. In general herpetological studies of competition, wide overlaps between coexisting species in terms of (i) food niche, (ii) spatial (macrohabitat) niche, and (iii) temporal (daily activity) niche have been interpreted as indices of strong actual competition (e.g. see Pianka, 1973; 1986). However, whether the temporal dimension could be a serious index of niche analysis has been strongly questioned (e.g. see Jaksic, 1982), and thus it seems operatively less questionable to limit our reasoning to only trophic and spatial dimensions. On the basis of our PCA results, it is clear that wide overlap along the spatial dimension occurs between: (i) *P. subrufa* and *K. belliana*, (ii) *K. erosa* and *K. homeana*, (iii) *P. castaneus* and *P. niger.* With regard to case (i), interspecific competition is likely to be absent, given the obviously different microhabitats frequented by the two taxa (the former being a marsh semiaquatic species, the latter a terrestrial species). On the other hand, the coexistence of the two *Kinixys* species (case ii) should be an interesting matter of research for the future, as it is possibly regulated by some mechanisms of interspecific competition (Barbault, 1981). Both *K. erosa* and *K. homeana* are classified into the same area of the multivariate space, and feed also on similar things (mainly earthworms, ground arthropods, plants, seed, and fruits; see Ernst & Barbour, 1989; Luiselli *et al.*, unpubl. data). With regard to case (iii), it is likely that the coexistence of the two *Pelusios* species is really conditioned by competition, given their similar habitat preferences, similar food habits (mainly invertebrates, plants, algae, etc.), and similar body sizes. Another indirect evidence of competition could be the fact that, in the spots where these two species are found together, one is alternatively much more (or much less) common than the other (Akani *et al.*, pers. obs., 1997-98). However, much more research is deserved to properly evaluate these evidences.

Furthermore, the application of the logistical regression model to our data has permitted to demonstrate that a careful management of dry forest and swamp forest patches will be crucial for the reliable conservation of the whole chelonian diversity of the region, since these macro-environments strongly correlated with the presence/absence of most species. This evidence should be an important criterion for the environmental works of competent authorities and international industry companies operating in the region (e.g. in the field of oil production) (see also Akani *et al.*, 1999b).

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