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Effects of habitat alteration caused by petrochemical activities and oil spills on the habitat use and interspecific relationships among four species of Afrotropical freshwater turtles

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Abstract. The large-scale effects of habitat alteration produced by oil-industry related pollution on the habitat use of four species of freshwater turtles (*Pelusios castaneus*, *Pelusios niger*, *Pelomedusa subrufa*, *Trionyx triunguis*) were studied in the River Niger Delta, southern Nigeria (West Africa) between 1996 and 2004. The numbers of turtle specimens observed during our study declined drastically in polluted sites, despite a nearly identical field effort. The number of specimens of all turtle species declined considerably at all habitat types, but complete disappearance in polluted areas was found only with regard to one habitat type for *Trionyx triunguis* and two habitat types for *Pelomedusa subrufa*. The mean values of species dominance and diversity indexes were not statistically significant between pristine and altered areas. Based on the interspecific similarity in proportional frequencies of turtle specimens found in each habitat type, a multivariate set of analyses (UPGMA) showed that the turtles were arranged in three 'ecological' clusters: a group formed by *Pelomedusa subrufa* at both polluted and unpolluted areas and *Trionyx triunguis* at polluted areas; (ii) a group formed by *Pelusios castaneus* in polluted areas and *Pelusios niger* in polluted areas; (iii) a group formed by *Pelusios castaneus* in unpolluted areas and *Pelusios niger* in unpolluted areas; however, this latter cluster was not very close, as the linkage distance was close to 80% of Euclidean distance. Habitat use similarity among turtles in both polluted and unpolluted study areas was evaluated by the use of two types of overlap formulas (Pianka and Czechanowski) and the use of Monte Carlo randomisations in order to control for the eventual role of chance in the actual data matrix. These data indicated that, for a pair of species (*Pelusios niger* vs. *Pelusios castaneus*), there was a statistically significant increase in the similarity of habitat use in the polluted areas vs. the unpolluted areas, and that this pattern was not dependent on the chance. Considering that these two species are ecologically and morphologically similar, we conclude that the most likely consequence at the community level is an increase in the intensity of interspecific competition for space between *Pelusios niger* and *Pelusios castaneus* in the polluted areas. Although the direction of the intensification of this competition process could not be easily predicted, it is likely that the species which is least adapted to life in main rivers and creeks may be disadvantaged over the other competitor. The general implications for habitat preservation are also discussed.

Introduction

There is consensus among scientists in considering habitat loss and fragmentation as one of the major threatening factor for freshwater turtles at the global scale (for instance, for a study case see Buhlmann 1995; and for a review see Mitchell and Klemens 2000). Many turtle species have established populations in small wetlands (less than 0.4 ha surface) which are normally not protected by law. By using computer simulations to predict the effects of the loss of small wetlands in the northeastern United States, Gibbs (1993) predicted widespread extinctions of turtle populations to be likely if habitat preservation was limited to large wetlands. Burke et al. (2000) agreed with this view and suggested that freshwater turtle conservation should be based also on the preservation of very small wetlands. Unfortunately, the number of species of freshwater turtles that have been carefully studied with regards to the links between their ecology, habitat characteristics and conservation, are still too few to draw firm conclusions on their management at the global scale (Burke et al. 2000). In addition, the great majority of these studies are based on species from temperate Europe and North America with very little known about tropical species, particularly those from the African continent. It is therefore essential that studies on the 'ecological distribution' of the freshwater turtles in relation to habitat loss, fragmentation, pollution, and human activities are needed if we want to preserve the turtle fauna of tropical Africa.

One particular and noteworthy aspect of habitat loss for turtles is the contamination of their natural habitats by oil and its derivatives in the oil-producing areas of the globe. Petrochemical activity produces pollution that is extremely hazardous to wildlife because of its persistence in the environment, its bioaccumulation in the food chain and its toxicity (Fu et al. 2003). In addition, pollutants may be carried long distances by air, rivers and ocean currents to contaminate regions remote from the source, and hence may represent a substantial negative factor for turtle biodiversity, especially in the tropical hotspots (e.g., see Mitchell and Klemens 2000, and references therein). For instance, negative effects of oil spills on marine turtles have been accurately depicted, among others, by Lutcavage et al. (1997). Apart from direct mortality caused by natural habitat contamination, the effects of oil spills and of the petrochemical industry development may of course produce also destruction of forest and modification of river characteristics (e.g., the destruction of bank plants and aquatic vegetation, and the alteration of river courses to facilitate the placement of pipelines, which results in habitat loss and fragmentation), and the creation of access roads into forest and mangrove sites, which encourages people to utilize these new areas to start cultivation-plots, markets and settlements. All these processes may contribute to habitat fragmentation (e.g., Plummer 1976; Moll 1980; Christiansen 1981; Wibbels et al. 1991; Burke et al. 2000; Moll and Moll 2000; etc).

Apart from the direct field studies on the conservation of single endangered turtle species or populations, turtle conservationists also need urgently the publication of research on particular study systems which may allow for extrapolations and generalizations to other study areas around the globe. Only after these generalizations have been done, will we be in a good position to implement reliable conservation strategies for the preservation of turtle biodiversity that can work at a large scale (e.g., Moll and Moll 2000). In this regard, the River Niger Delta region in southern Nigeria (West Africa) seems to be a particularly promising study region for turtle conservationists because: (i) it is one of the worldwide largest wetlands being characterized by a complicated mosaic of rivers, creeks, streams, marshes, ponds, and swamps, of over 20,000 km^2 surface; (ii) it houses a remarkable diversity of chelonian species (Luiselli et al. 2000), (iii) it is currently overpopulated by millions of people (De Montclos 1994); and (iv) its general wetland ecosystem has been profoundly altered in the last 40 years by the development of the industrial installations and pipelines for the extraction, production, and transport of oil and natural gas, Nigeria being currently the first oil-producer in sub-Saharan Africa (De Montclos 1994). In addition, the pipelines for the transport of oil and its derivatives have been repeatedly broken (intentionally and unintentionally) during the last years, with thousands of cases of oil spills and resulting contamination of the natural environment (for a synthesis of a few of these major cases, see Table 1).

Because of all the above-mentioned arguments, a long term study on the ecology of freshwater turtles in both altered and unaltered sites has been carried out since the middle of the '90s by us and our co-workers. We studied the effects of oil industry contamination on a turtle community, and more precisely on its habitats (Luiselli and Akani 2003), diet habits (Luiselli et al. 2004), and home range patterns and oviposition strategies (Luiselli et al. 2005). These studies showed that the oil spillage considerably reduced the species' diversity of that turtle community (with 50% of the species being lost) and also caused a decline in the population abundance of those species which were able to survive the catastrophic pollution event. Turtles at the polluted area also showed different homing patterns from conspecifics at a control unpolluted area

Table 1. Major oil spillage events in the coastal zone of the Niger delta region, that likely affected turtle habitats and ecology.

Location of spill	Date	Barrels of oil lost	
Gocon's Escravos spill	1978	300,000	Chevron
Forcados Terminal tank failure	1978	500,000	SPDC
Apoi 20 blow-out	1980	–	Texaco
Funiwa 5 blow-out	1980	400,000	Texaco
Abudu Pipeline Spill	1982	18,818	SPDC
Jesse fire incidence (pipeline vandalization)	1998	40,000	NNPC
Idoho off shore platform	1998	40,000	MPNU
Yorla 10 blow-out	2001	35,000	SPDC

Symbols: SPDC = Shell Petroleum Development Company; NNPC = Nigerian National Petroleum Company; MPNU = Mobil Petroleum Nigeria Unlimited.

(Luiselli et al. 2005) and, at least in one species (*Pelusios niger*), there was a considerable change in habitat use, as it shifted from an intensive use of swamps into the rainforest before spillage to an almost complete abandonment of this habitat type after the spillage event (Luiselli and Akani 2003).

The few studies summarized above were carried out at a single study area which was contaminated by a oil spillage about 10 years earlier, but it is not known whether the results presented therein can be generalized to the level of the whole study region, i.e., of a different and much larger spatial scale. In practice, it is still unknown whether the freshwater and river turtle communities of the Niger Delta region really experience important changes in community structure and specific richness as a response to the thousands of oil spills, some of which of huge proportions, which have occurred in this region during the last decades (Carbone 2003). In particular, our aims in this paper are to answer to the following questions:

(1)Considering that in southern Nigeria there are extended areas that have been polluted by oil spills in the last 20 years (Carbone 2003), has the ecological distribution and habitat use of turtles changed at a regional scale in response to pollution of their natural habitat?

(2)If yes, what are the most likely ecological consequences at the community level?

(3)Based on the data acquired, what are the main habitats to be preserved?

Our aims are to address broad indications of the community changes of turtles in areas polluted vs. unpolluted, in the hope to give some noteworthy considerations of conservation interest both for the local agencies and the international audience of conservationists. However, it should be considered that, given the broad scope of this article, the huge number of independent oil spills, the different quantity of oil spilled at each site, the different community composition of turtles at the various sites (community composition which was unknown before the oil spillage events in the great majority of the areas), and the spatial–temporal interactions of the various oil spills, may all be confounding factors for our analysis. Hence, although we search in this paper for constant and general patterns and although we are confident that this general approach may produce important data for the years to come, however we recognize the shortcomings of an analysis which could not take into full account the spatial–temporal incidence of the various cases of oil spills on the community ecology of turtles.

Materials and methods

Study areas

The field study was carried out in several areas of the River Niger Delta, southern Nigeria (West Africa). The list of study areas, in relation to their general habitat characteristics, conservation status, and the eventual occurrence of recent oil spills, is given in Table 2. The study areas were selected as representative of all the natural habitats available to turtles in the Niger Delta region (Luiselli et al. 2000), including freshwater and brackish water bodies, temporary and permanent water bodies, rivers, as well as creeks, ponds, marshes, and swamps (Table 2).

Protocol

The field study was conducted between September 1996 and April 2004. Data were gathered contextually to other studies on reptiles in the study region (e.g., see Akani et al. 1999), and a total of 313 field days (and 2843 man/h) were spent purposely for carrying out the present study. A nearly identical field effort was performed in all the surveyed habitats, both in unpolluted and polluted areas. However, hilly streams in polluted areas were not surveyed simply because there were no cases of oil-linked pollution in this type of habitat.

The following habitat types were surveyed: RMA = rivers (main axes); RSA = rivers (secondary axes); MCR = mosaic of creeks; HST = hilly streams; MSP = mosaic of small ponds; SWP = swamps and marshes; LIP = lakes and isolated big ponds.

RMA included all the main axes of the ten rivers surveyed (see Table 2 for the toponyms); RSA included the secondary axes of the same rivers (i.e., small tributaries, etc.); the general habitat of both RMA and RSA was generally similar, but the depth of water and the width of the river was usually much higher in RMA than in RSA. MCR included the mosaic of small creeks, often with muddy bed and low water-depth, that is typical of wide sectors of the River Niger Delta. HST included the small streams with stony bed and scarce aquatic vegetation, which are found in the forest zone of the extreme south-eastern Nigeria (in Cross River State). MSP included the mosaic of small ponds (0.1–0.9 ha surface; most of them of 0.3–0.4 ha surface) which are seasonally (during the rainy season) or permanently inundated, and that widely occur in the deltaic swampy rainforest. SWP included the wide coastal swamps and marshes that occur in some sectors of southern Nigeria (e.g., around Lekki), and LIP included only lakes and ponds of a size larger than 1 ha surface.

Each surveyed area (Table 2) was assigned to the category 'in good health conditions' or 'in altered conditions' depending on the apparent general ecological conditions at the time of surveying (1996–2004). We considered different aspects to give our health assessment: (i) extent of the forest coverage along the surveyed streams, creeks, marshes and ponds; (ii) density of stems greater than 30 cm diameter at breast height (dbm) in 15 random plots throughout each study area; (iii) density of stems greater than 30 cm diameter at breast height (dbm) in 15 random plots throughout each study area; (iv) number of specimens observed and species diversity of frogs, snakes, lizards, and rodents at each study area during the survey period (see Akani et al. 1999,

Table 2. Rivers (and surrounding freshwater and lenthic habitats) of Niger Delta surveyed during the present study, and their habitat condition.

Rivers and locations	Habitat and micro-habitat	Pristine/in good health	Oil polluted 10–15 yrs ago	State
(1) Bonny River				
Bonny Town	Marine/sandy beaches		Yes	Rivers
Peterside	Brackish/Mangrove/ Fresh water swamp		No	Rivers
Alakiri	Brackish/Mangrove		Yes	Rivers
Orubiri	Brackish/muddy beaches		Yes	Rivers
Elem Kalabari	Brackish/sandy beaches		No	Rivers
Okrika Jetty	Brackish/sandy beaches		Yes	Rivers
Port-Harcourt Harbour	Brackish/sandy beaches		Yes	Rivers
Bakana (upstream)	Brackish/sandy beaches		No	Rivers
Kidney Island	Brackish/sandy beaches		No	Rivers
Isaka	Brackish/muddy beaches		No	Rivers
(2) New Calabar River				
Tombia	Brackish/freshwater creek	Yes	No	Rivers
Bukuma (= Buguma)	Brackish/freshwater creek/muddy beaches	Yes	No	Rivers
Iwofe	Brackish/freshwater creek/muddy beaches		Yes	Rivers
Chola	Freshwater stream/swamps		Yes	Rivers
Aluu	Freshwater stream/swamps		No	Rivers
Rumuji	Freshwater stream/swamps		No	Rivers
Elele Alimini	Freshwater stream/swamps		No	Rivers
(3) Sombreiro River				
Ahoada	Freshwater stream/swamps	Yes	No	Rivers
Rumuekpe	Freshwater stream/swamps		Yes	Rivers
Ndele	Freshwater stream/swamps		Yes	Rivers
Degema and Ogonokum	Brackish/Mangrove	Yes	No	Rivers
Okomo (black water)	Brackish/Mangrove		Yes	Rivers
(4) Orashi River				
Oguta	Freshwater stream/swamps	Yes	No	Rivers
Ndoni	Freshwater stream/swamps	Yes	No	Rivers
Mmahu	Freshwater stream/swamps	Yes	No	Rivers
Obrikom	Freshwater stream/swamps	Yes	No	Rivers
Omoku	Freshwater stream/swamps	Yes	No	Rivers
Obagi	Freshwater stream/swamps	Yes	No	Rivers
Mbiama (Oshika)	Freshwater stream/swamps	Yes	No	Rivers
(5) Taylor Creek				
Zarama	Freshwater/turbid in rainy season	Yes	No	Bayelsa
(6) Nun River	Freshwater/sandy beaches/ turbid in rainy season		No	Bayelsa
Kaiana	Freshwater stream/swamps		No	Bayelsa
Diebu	Freshwater stream/swamps		Yes	Bayelsa
Peremabiri	Brackish/Mangrove		No	Bayelsa
(7) Forcados River				
Abari	Freshwater stream/swamps	Yes	No	Delta
Patani	Freshwater stream/swamps	Yes	No	Delta

Table 2. Continued.

Rivers and locations	Habitat and micro-habitat	Pristine/in good health	Oil polluted 10–15 yrs ago	State
Burutu (tidal)	Brackish/Mangrove		No	Delta
Forcados Town	Brackish/Mangrove (very poor condition)		No	Delta
Ijaw Burutu	Brackish/Mangrove (luxuriant condition)	Yes	No	Delta
(8) Ramos River				
Nomadi	Freshwater stream/swamps	Yes	No	Delta
Ogeriagbene	Freshwater stream/swamps	Yes	No	Delta
Orugbene	Freshwater stream/swamps	Yes	No	Delta
Ayagbene	*Raphia* swamps of large size	Yes	No	Delta
(9) Etiope River				
Abraka	Freshwater river with transparent water	Yes	No	Delta
Mosogan	Freshwater river with transparent water	Yes	No	Delta
Jesse	Freshwater river with transparent water	Yes	No	Delta
(10) Brass River				
Nembe	Brackish/Mangrove/muddy beaches		Yes	Bayelsa
Etiama	Brackish/Mangrove/muddy beaches		Yes	Bayelsa
Oloibiri	Brackish/Mangrove/muddy beaches		Yes	Bayelsa
Ogbia	Brackish/Mangrove/muddy beaches		Yes	Bayelsa

2004; Angelici and Luiselli 2005 for the methods of trapping and data collection used); (v) assessment of the richness of fish fauna by interviews with 5 independent fishermen at each study area; (vi) assessment of the richness of wildlife by interviews with 5 independent hunters at each study area. We gave a indicative score ranging from 0 to 4 (0, extremely altered; 4, very well conserved) for each of these six parameters, and then calculated the mean score for each study area. When the mean score was < 1.5, the study area was assigned to the 'altered' category; when it was > 2.5 it was assigned to the 'good health' category; when the score fell in-between the above-mentioned values, the study area was considered 'unclassified', and hence excluded from the analyses. Although the logic of the areas classification is quite empirical, nonetheless it seemed certainly reliable for the scopes of this article, and in any case by far the best procedure to be applied in a logistically difficult and ecologically little-known study region as the Niger Delta region.

A combination of different collecting techniques were employed to getting the highest number of specimens as possible. Several standard turtle-collecting methods were used at each study area, including baited hoop traps, dipnetting, and trawling (see also Gibbons et al. 2001, for a similar procedure). To avoid unbalanced effort in the various areas, an identical trap design was used, that is: at each study area we placed 200 hoop traps (baited with fish and pieces of crabs), situated at an average distance of 30 m each from another. Traps were left for 7 days at each study area, and inspected regularly. Each study area was also trawled (Gibbons et al. 2001), and visited throughout on foot or by canoes along non-linear transects, and turtles encountered were captured by hand and by nets. Surveys lasted 7 days at each study area. Although we did all the possible efforts to avoid unbalanced sampling efficiency among sites, nonetheless we could not exclude that some biases due to different intrinsic sampling efficiency at each site may have arisen during the execution of this research project. However, if some biases due to among-sites different sampling efficiency have occurred, these should have been probably relatively minor, and in any case impossible to detect correctly and experimentally.

Once the turtles were captured, they were measured (plastron length), sexed, identified to species, and permanently individually marked by unique sequences of notches filed into the marginal scutes. No specimens were intentionally killed during the course of this study.

We focused our study on just four species of turtles because these were the only species that were captured by us frequently enough for data analysis. Species which were locally very rare (e.g., *Pelusios gabonensis*) hence were omitted from the data analysis.

Statistics

Quantitative biodiversity analyses were made according to the following indexes: Species Diversity was calculated using Margalef's Diversity Index (Magurran 1988):

$$D_{\mathrm{mg}} = (S - 1) \ln N$$

where S is the total number of species, and N is the total number of individuals.

Species Dominance was assessed using the Berger–Parker index (Magurran 1988):

$$d = N_{\max}/N$$

where $N_{\max}$ is the total number of individuals of the most abundant species. An increase in the value of the reciprocal form of the index ($1/d$) indicates an increase in diversity and reduction in dominance (Magurran 1988).

For calculating the similarity in habitat use of the various turtle species between the two types of areas (altered or in good health), we calculated the overlap indices of Pianka (1973) and Czechanowski (Feinsinger et al. 1981) for the habitat type frequency use of the four turtle species.

Pianka's formula for species j and k, with resource utilizations p_{1i} and p_{2i}, is:

$$O_{j,k} = O_{2,1} = \Sigma p_{2i} \times p_{1i} / \sqrt{\Sigma(p_{2i}^2 \times p_{1i}^2)}$$

In this formula the values range from 0 (no overlap) to 1 (total overlap).

Czechanowski's formula for species 1 and 2, with resource utilizations p_{1i} and p_{2i}, is:

$$O_{1,2} = O_{2,1} = 1.0 - 0.5 \times \Sigma \; | p_{1i} - p_{2i} |$$

Graphically, this index corresponds to the intersection of the utilization histograms of the two species, and also ranges from 0 (no overlap) to 1 (total overlap) (Gotelli and Entsminger 2000).

We calculated these indices using the program 'EcoSym 700' (Gotelli and Entsminger 2000). We performed a cross-tabulation on those frequencies to determine where differences in habitat types used existed for each species between the two types of study areas (polluted vs unpolluted). By means of the 'EcoSym' package, we performed Monte Carlo simulations (1000 iterations) to create 'pseudo-communities' (Pianka 1986) and statistically compared the derived patterns with those in the actual data matrix. We used the RA3 model in 'EcoSym' to evaluate the similarity in habitat use (= overlap); this model randomises particular resource states used by each species while retaining niche breadth. This model has been shown to have robust statistical properties for detecting non-random niche overlap patterns (or, as in our study case, similarity in resource use between types of study areas of a same species; Winemiller and Pianka 1990). As we did not have a static measure of habitat type availability at the study area, therefore we used the default setting of equiprobable resource states available in 'Ecosym'. The assumption of equiprobability of resource states means in our study case that the various habitat type states (= resource states) are equally usable (= abundant) by all species.

Statistical analyses were done by 'Statistica version 6.0' for Windows PC package, and Monte Carlo simulations were done by 'Ecosym 700' PC package. All tests were two-tailed, with alpha set at 5%. To avoid statistical problems due to non-indipendence of the data (Mathur and Silver 1980), data on habitat use was recorded only once from individual turtles, i.e., the recaptured turtles were never used again for data recording and analyses. For uniformity, data relative to the first time a given specimen was encountered were recorded.

Results

The numbers of turtle specimens observed during our study declined from 1160 (1149 if we exclude hilly stream habitats) in unpolluted sites to 454 in polluted sites, despite a nearly identical field effort. The total numbers of turtle individuals found along unpolluted and polluted water bodies of Niger Delta during the study project, in relation to habitat type, are given in Table 3. Although the number of specimens of all turtle species declined considerably at all habitat types, nonetheless complete disappearance in polluted areas was found only with regard to *Trionyx triunguis* in LIP, and *Pelomedusa subrufa* in LIP and SWP. In all these cases, however, the number of specimens was extremely low also in unpolluted areas (Table 3).

The mean value of D_{mg} was slightly higher in pristine than in altered areas, but the difference was very close to statistical significance (one-way ANOVA,

Table 3. Numbers of turtle individuals found along unpolluted and polluted water bodies of Niger Delta during the study project, in relation to habitat type.

Species	RMA	RSA	MCR	HST	MSP	SWP	LIP	Total
Unpolluted Areas								
Trionyx triunguis	28	36	7	0	0	0	2	73
Pelusios niger	39	104	138	7	162	47	77	567
Pelusios castaneus	21	53	91	4	131	131	72	499
Pelomedusa subrufa	0	0	0	0	8	1	1	10
Total	88	193	236	11	301	179	152	
Polluted Areas								
Trionyx triunguis	7	6	1	Not surveyed	0	0	0	14
Pelusios niger	31	48	71	Not surveyed	43	16	28	237
Pelusios castaneus	14	33	51	Not surveyed	40	36	26	200
Pelomedusa subrufa	0	0	0	Not surveyed	3	0	0	3
Total	52	87	123	Not surveyed	86	52	54	

Totals in the last right column are calculated without taking into account turtle numbers found in hilly streams. Symbols: RMA = rivers (main axes); RSA = rivers (secondary axes); MCR = mosaic of creeks; HST = hilly streams; MSP = mosaic of small ponds; SWP = swamps and marshes; LIP = lakes and isolated big ponds.

$p = 0.058$), whereas the mean value of *d* did not vary significantly (one-way ANOVA, $p = 0.163$) between pristine and altered areas (Figure 1). The slightly higher values of D_{mg} in altered areas depended on the lesser numbers of turtles observed at those sites, despite the number of species observed ($n = 3$) remained constant (Table 4).

The proportional frequencies of turtle specimens found in each habitat type, in both unpolluted and polluted areas, are given in Table 5. A UPGMA dendrogram on these habitat data clustered the turtles into three ecological groups based on their general habitat affinity (Figure 2):

(i) a group formed by *Pelomedusa subrufa* at both polluted and unpolluted areas and *Trionyx triunguis* at polluted areas;

(ii) a group formed by *Pelusios castaneus* in polluted areas and *Pelusios niger* in polluted areas;

(iii) a group formed by *Pelusios castaneus* in unpolluted areas and *Pelusios niger* in unpolluted areas; however, this latter cluster was not very close, as the linkage distance was close to 80% of Euclidean distance (Figure 2).

Monte Carlo simulations of overlap data indicated that, apart from a very few cases (always involving *Pelomedusa subrufa* in the pairwise comparisons), the data matrix on turtle habitat use similarity were not derived by chance (Table 6). Hence, the observed overlaps were in most cases reliable indicators of habitat use similarity among species, and among different types of study areas (altered or in good health). These data (see Table 6) showed that there was a statistically significant ($p < 0.05$) increase in the habitat use similarity between *Pelusios niger* and *Pelusios castaneus* in the polluted study areas vs. the unpolluted study areas, and that this increase was not determined by chance.

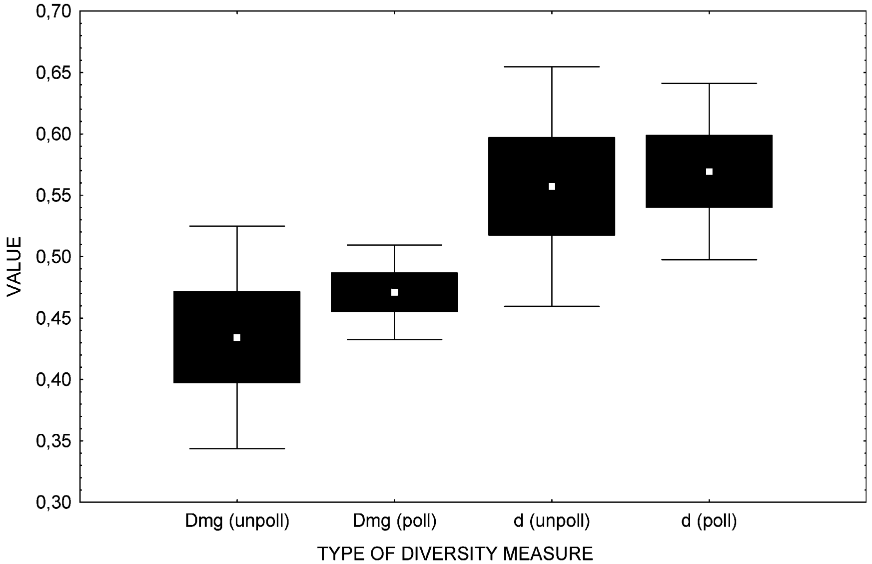

Figure 1. Box- and-whisker plot showing means and dispersion measures (SD and SE) of the values of D_{mg} and d in unpolluted and polluted areas. For more details, see the text.

Discussion

General considerations

Before discussing the main results obtained during this study, it is necessary to shortly remind the primary shortcoming of our methodology, i.e. that, despite all our efforts, it was impossible to remove the eventually confounding patterns generated by the long period of time of our surveys between oiled and un-oiled sites.

Table 4. Values of formulas for species diversity (D_{mg}) and species dominance (d) of the various habitat types along unpolluted and polluted water bodies of Niger Delta.

Habitat type	D_{mg} (Unpolluted areas)	D_{mg} (Polluted areas)	d (Unpolluted areas)	d (Polluted areas)
RMA	0.447	0.506	0.443	0.596
RSA	0.380	0.448	0.539	0.551
MCR	0.366	0.416	0.585	0.577
HST	0.417	–	0.636	–
MSP	0.350	0.449	0.538	0.500
SWP	0.385	0.506	0.732	0.692
LIP	0.597	0.501	0.506	0.500

Values are calculated on the basis of the numbers of turtle individuals found during the study project, in the various habitat types. Symbols: RMA = rivers (main axes); RSA = rivers (secondary axes); MCR = mosaic of creeks; HST = hilly streams; MSP = mosaic of small ponds; SWP = swamps and marshes; LIP = lakes and isolated big ponds.

Table 5. Proportion of turtle specimens found in each habitat type, both in unpolluted and in polluted areas.

	T. triunguis (unpoll)	*T. triunguis* (poll)	*P.niger* (unpoll)	*P.niger* (poll)	*P.castaneus* (unpoll)	*P.castaneus* (poll)	*P.subrufa* (unpoll)	*P.subrufa* (poll)
RMA	38.3	50	6.9	13.1	4.2	7	0	0
RSA	49.3	42.8	18.3	20.2	10.6	16.5	0	0
MCR	9.6	7.2	24.3	29.9	18.2	25.5	0	0
MSP	0	0	28.6	18.1	26.2	20	80	100
SWP	0	0	8.3	6.8	26.2	18	10	0
LIP	2.7	0	13.6	11.8	14.4	13	10	0

Sample sizes are given in Table 3. Symbols: RMA = rivers (main axes); RSA = rivers (secondary axes); MCR = mosaic of creeks; MSP = mosaic of small ponds; SWP = swamps and marshes; LIP = lakes and isolated big ponds.

In general, we found a considerable reduction in the absolute numbers of turtles found in altered areas in comparison with those found in pristine areas. Considering that the field effort was nearly identical in both types of study areas, it can be concluded that direct and indirect effects of oil-pollution had strongly affected the abundance of turtles in the Niger Delta, thus reinforcing evidence showed by Luiselli and Akani (2003) from a single study area in the same geographic region. Indeed, studies focused on a single area by Luiselli and Akani (2003) showed a local extinction of *Trionyx triunguis* and *Pelomedusa subrufa*, which appeared more sensitive than the other species possibly

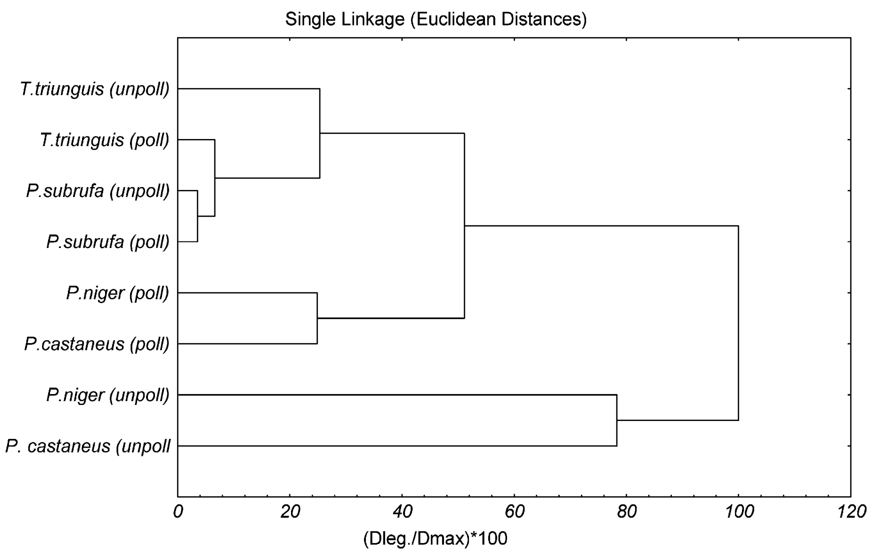

Figure 2. UPGMA dendrogram on the percent affinities between turtle species in relation to the physical characteristics of the various water bodies at unpolluted and polluted study areas in the River Niger Delta, southern Nigeria.

Table 6. Values of overlap formulas calculated between pairs of species, both in polluted sites and in unpolluted sites.

	TT (U)	PN (U)	PC (U)	PS (U)	TT (P)	PN (P)	PC (P)	PS (P)
TT (U)	****	0.503	0.314	**0.005**	0.978	0.644	0.499	0
PN (U)	0.375	****	0.894	0.681	0.435	0.953	0.957	0.632
PC (U)	0.271	0.811	****	0.681	0.265	0.812	0.949	**0.580**
PS (U)	0.028	0.469	0.462	****	**0**	0.451	0.544	**0.985**
TT (P)	0.883	0.324	0.220	0	****	0.587	0.433	0
PN (P)	0.457	0.863	0.698	0.349	0.405	****	0.948	0.406
PC (P)	0.358	0.890	0.841	0.400	0.306	0.857	****	0.463
PS (P)	0	0.286	0.262	0.800	**0**	0.181	0.200	****

Values obtained by Pianka's formula are above the diagonal, and those obtained by Czechanowski formula are below the diagonal. In boldface are presented those values that, after Monte Carlo simulations (1000 randomisations, see the text for more details), proved to depend just on chance, and not on statistically reliable data. Symbols: P = polluted areas; U = unpolluted areas; TT = *Trionyx triunguis*, PN = *Pelusios niger*, PC = *Pelusios castaneus*, PS = *Pelomedusa subrufa.*

because of their specific ecological/life-history characteristics (large size and mainly carnivorous habits in the former species, suboptimal specialization to rainforest habitats and hence very low population density also in the pristine habitats in the latter species). Does this extinction pattern occur also at the large scale of the geographic region studied? Broadly speaking, it seems yes, as we observed complete disappearance of *Trionyx triunguis* in polluted LIP habitat, and *Pelomedusa subrufa* in polluted LIP and SWP. On the other hand, in all habitat types, the other two species declined but never went extinct (however, given the low numbers of individuals observed, the real viability of these populations in the long time is still to be established). Concerning both *Trionyx triunguis* and *Pelomedusa subrufa*, it should be reminded that, however, the number of specimens was extremely low also in unpolluted areas (Table 3), thus suggesting that LIP (for both species) and SWP (for *Pelomedusa subrufa*) are in any case sub-optimal habitats for these turtles in the Niger Delta region.

Because of the lack of extinction in the various habitats, the values of D_{mg} were not significantly different (although close to statistical significance) between pristine and polluted habitats, whereas the values of d indicated a trend for dominance indexes to be higher in polluted sites, as an effect of the strongest preponderance of the adaptable *Pelusios* species.

Did the ecological distribution of turtles change at a global scale as a response to wide pollutions of their natural habitat?

According to our tree-clustering model, it resulted that the various turtle species responded differently to the changed environmental conditions due to the alteration of their natural habitat. More precisely, *Pelomedusa subrufa* exhibited a similar habitat preferences at both polluted and unpolluted areas (although it must be reminded that the sample size for this species was low and hence the statistical power of our analysis was not strong enough to be sure) and *Trionyx triunguis* did the same, whereas the two species of *Pelusios* clearly modified their habitat preferences, with a much stronger similarity in habitat preferences of *P. niger* and *P. castaneus* in polluted areas than in unpolluted areas. We suppose that the lack of habitat shifts in both *Pelomedusa subrufa* and *Trionyx triunguis* may reflect a scarce adaptability of these species to the massive habitat alteration, hence a reduced ability to survive to the new altered habitats. For both species, this trend may be valid only for the lowland wet forest habitat, as both are well known to be relatively adaptable and very widespread in less wet regions (e.g., Ernst and Barbour 1989). The same was clearly not true for the two *Pelusios* species, that, indeed, survived much better than the other two species in oil-polluted habitats.

What are the most likely ecological consequences at the community level?

Our study documented that *Pelusios castaneus* and *Pelusios niger*, which are potential competitors because of comparable body sizes (but the former species is larger than the latter), general ecological traits, and similar dietary habits (Luiselli and Akani 2003; Luiselli et al. 2000, 2004, 2005), had a significantly higher similarity in habitat use in polluted than in pristine areas. The most likely consequence at the community level is an increase in the intensity of interspecific competition for space between these species (Schoener 1974, 1982, 1983). Indeed, in most of the ecologically- and morphologically-similar sympatric reptiles the spatial niche is the main niche axis to be partitioned (Pianka 1973, 1986; Toft 1985).

Although in this case study the direction of the intensification of the competition process between these two *Pelusios* species could not be easily predicted, it is likely that the species which is least adapted to life in main rivers and creeks may be disadvantaged over the other species, given that (i) space can become a limited resource, and (ii) small marshes, swamps, and ponds tend to be too much polluted for the turtle survival. In the long-term, it is therefore possible that the species most adapted to large, permanent water bodies, would become increasingly more common than the other, perhaps forcing the other competitor to unsuited niches. A similar phenomenon, although caused by entirely different reasons (i.e., deforestation of terrestrial habitats), was observed in Nigerian cobras, with a generalist savannah species (*Naja nigricollis*) which challenges a specialist forest species (*Naja melanoleuca*) in its niche, and increasingly forces the forest specialist to live into spatially reduced niches which are unsuited to the invader species (Luiselli and Angelici 2000; Luiselli 2001; Luiselli et al. 2002).

What are the main habitats to be preserved?

Gibbs' (1993) computer simulations predicted widespread extinctions of turtle populations if habitat preservation will be limited to large wetlands, because many turtle species have established populations in small wetlands (less than 0.4 ha surface) which are normally not protected by laws. Although Gibbs' view was later reinforced by other studies (e.g., see Burke et al. 2000), his prediction has never been tested with species from the Afrotropics. Thus, our study may be valuable also because it allowed us to collect data that can be important for testing Gibbs' prediction. In general, our study revealed a relative low variance between habitat types in species richness (generally ranging from 2 to 3 species, with only LIP housing four species), D_{mg} as well as d. In addition, even in pristine sites, two species appeared more or less abundant, whereas two species were either absent or apparently rare. Indeed, also in LIP habitat, two of the four species present (i.e., *Pelomedusa subrufa* and *Trionyx triunguis*) were very scarce in our samples. These considerations led us to think that, at the geographic scale of the River Niger Delta in southern Nigeria, it is impossible to rank the various habitats in terms of their importance for turtle conservation, because the mosaic of the various habitats available had an evident relevance for turtle conservation, in that all the habitats housed a nearly identical variety of turtle species, with comparatively similar values of D_{mg} and d. Considering that *Pelomedusa subrufa* and *Trionyx triunguis* appeared clearly the most endangered species in this area (because of their reduced distribution, see Luiselli et al. 2000, and the strong effect of oil-industry related pollution and habitat alteration on them, see this study), we suggest that the main habitats to be protected should be those that currently house the largest populations of these species, i.e. MSP for *Pelomedusa subrufa*, and RMA and RSA for *Trionyx triunguis*.

Overall, our study is another example documenting the importance of preserving patchy mosaics of different types of freshwater–marshy habitats for effectively protecting the turtle biodiversity in tropical areas. It will be of great interest for the future to document the responses of other communities of freshwater and river turtles, more species-rich than those studied in this paper, to oil pollution and consequent habitat loss, in order to have a more reliable framework where to understand the expected patterns of decline of these chelonians under this type of ecological cataclysms. In this regard, the turtle communities of tropical Asia seem to be particularly interesting, since they are much more rich in species than those occurring in tropical Africa (e.g., Van Dijk et al. 2000).

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References

Akani G.C., Barieenee I.F., Capizzi D. and Luiselli L. 1999. Snake communities of moist forest and derived savanna sites of Nigeria: Biodiversity patterns and conservation priorities. Biodivers. Conserv. 8: 629–642.

Akani G.C., Politano E. and Luiselli L. 2004. Amphibians recorded in forest swamp areas of the River Niger Delta (southeastern Nigeria), and the effects of habitat alteration from oil industry development on species richness and diversity. Appl. Herpetol. 2: 1–22.

Angelici F.M. and Luiselli L. 2005. Patterns of specific diversity and population size in small mammals from arboreal and ground-dwelling guilds of a forest area in southern Nigeria. J. Zool. (London) 265: 9–16.

Buhlmann K.A. 1995. Habitat use, terrestrial movements, and conservation of the turtle *Deirochelys reticularia* in Virginia. J. Herpetol. 29: 173–181.

Burke V.J., Lovich J.F. and Gibbons J.W. 2000. Conservation of freshwater turtles. In: Klemens M.W. (eds), Turtle Conservation. Smithsonian Institution Press, Washington, D.C., pp. 156–179.

Carbone M. 2003. Morte di un delta. Airone 260: 52–60.

Christiansen J.L. 1981. Population trends among Iowa's amphibians and reptiles. Proceedings of the Iowa Academy of Science 88: 24–27.

De Montclos J.M. 1994. Le Nigèria. Kurthala, Paris.

Ernst C.H. and Barbour R.W. 1989. Turtles of the World. Smithsonian Institution Press, Washington, D.C.

Feinsinger P., Spears E.E. and Poole R.W. 1981. A simple measure of niche overlap. Ecology 62: 27–32.

Fu J., Mai B., Sheng G., Zhang G., Wang X., Peng P., Xiao X., Ran R., Cheng F., Peng X., Wang Z. and Tang U.W. 2003. Persistent organic pollutants in environment of the Pear River Delta, China: an overview. Chemosphere 52: 1411–1422.

Gibbs J.P. 1993. Importance of small wetlands for the persistence of local populations of wetland associated animals. Wetlands 13: 25–31.

Gibbons J.W., Lovich J.E., Tucker A.D., Fitzsimmons N.N. and Greene J.L. 2001. Demographic and ecological factors affecting conservation and management of the Diamondback terrapin (*Malaclemys terrapin*) in South Carolina. Chelonian Conserv. Biol. 4: 64–76.

Gotelli N.J. and Entsminger G.L. 2000. EcoSym: Null Model Software for Ecology. Aquired Intelligence Inc., New York.

Luiselli L. 2001. The ghost of a recent invasion in the reduced feeding rates of spitting cobras during the dry season in a rainforest region of tropical Africa? Acta Oecol. 22: 311–314.

Luiselli L. and Akani G.C. 2003. An indirect assessment of the effects of oil pollution on the diversity and functioning of turtle communities in the Niger Delta, Nigeria. Animal Biodivers. Conserv. 26: 55–63.

Luiselli L. and Angelici F.M. 2000. Ecological relationships in two Afrotropical cobra species (*Naja melanoleuca* and *Naja nigricollis*). Can. J. Zool. 78: 191–198.

Luiselli L., Angelici F.M. and Akani G.C. 2002. Comparative feeding strategies and dietary plasticity of the sympatric cobras *Naja melanoleuca* and *Naja nigricollis*, in three diverging Afrotropical habitats. Can. J. Zool. 80: 55–63.

Luiselli L., Politano E. and Angelici F.M. 2000. Ecological correlates of the distribution of terrestrial and freshwater chelonians in the Niger Delta, Nigeria: a biodiversity assessment with conservation implications. Revue d' Ecologie (Terre et Vie) 55: 3–23.

Luiselli L., Akani G.C., Politano E., Odegbune E. and Bello O. 2004. Dietary shifts of sympatric freshwater turtles in pristine and oil-polluted habitats of the Niger Delta, Southern Nigeria. Herpetol. J. 14: 57–64.

Luiselli L., Akani G.C., Bello O.A., Angelici F.M., Ude L. and Politano E. 2005. Home range area may vary considerably in relation to habitat contamination in two African terrapins (*Pelusios castaneus* and *Pelusios niger*) from pristine and oil polluted habitats. Amphibia–Reptilia 26: in press.

Lutcavage M.E., Plotkin P., Witheringdon B. and Lutz P.L. 1997. Human impacts on sea turtle survival. In: Lutz P.L. and Musick J.A. (eds), The Biology of Sea Turtles. CRC Press, Boca Raton, pp. 387–409.

Magurran A.E. 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton.

Mathur D. and Silver C.A. 1980. Statistical problems in studies of temperature preferences of fishes. Can. J. Fish. Aquat. Sci. 37: 733–737.

Mitchell J.C. and Klemens M.W. 2000. Primary and secondary effects of habitat alteration. In: Klemens M.W. (eds), Turtle Conservation. Smithsonian Institution Press, Washington, D.C., pp. 5–32.

Moll D. 1980. Dirty river turtles. Nat. Hist. 5: 42–49.

Moll E.O. and Moll D. 2000. Conservation of river turtles. In: Klemens M.W. (eds), Turtle Conservation. Smithsonian Institution Press, Washington, D.C., pp. 126–155.

Pianka E.R. 1973. Lizard species diversity. Ecology 48: 333–359.

Pianka E.R. 1986. The Ecology and Natural History of Desert Lizards. Princeton University Press, Princeton.

Plummer M.V. 1976. Some aspects of nesting success in the turtle, *Trionyx muticus*. Herpetologica 32: 353–359.

Schoener T.W. 1974. Resource partitioning in ecological communities. Science 185: 27–39.

Schoener T.W. 1982. The controversy over interspecific competition. Am. Sci. 70: 586–595.

Schoener T.W. 1983. Field experiments on interspecific competition. Am. Nat. 122: 240–285.

Toft C.A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985: 1–21.

Van Dijk P.P., Stuart B.L. and Rhodin A.G.J. 2000. Asian turtle trade. Chelonian Res. Monogr. 2: 1–164.

Wibbels T., Killebrew F.C. and Crews D. 1991. Sex determination in Cagle's map turtle: implications for evolution, development, and conservation. Can. J. Zool. 69: 2693–2696.

Winemiller K.O. and Pianka E.R. 1990. Organization in natural assemblages of desert lizards and tropical fishes. Ecol. Monogr. 60: 27–55.