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DIETARY SHIFTS OF SYMPATRIC FRESHWATER TURTLES IN PRISTINE AND OIL-POLLUTED HABITATS OF THE NIGER DELTA, SOUTHERN NIGERIA

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The diet of sympatric freshwater turtles was studied at two study areas in the Niger Delta (southern Nigeria), to test whether oil pollution affects the ecological relationships between free-ranging turtles. Two study areas, one unpolluted and one polluted by an oil spill, were used for our comparisons. Both areas had similar environmental conditions, i.e. a main river tract with banks covered by dense gallery forest, seasonal swamps in riverine forest, and almost permanent marshes with rich aquatic vegetation. Four species of turtle (*Trionyx triunguis, Pelusios castaneus, Pelusios niger,* and *Pelomedusa subrufa*), were captured in the unpolluted area, whereas only two species (*Pelusios castaneus* and *Pelusios niger*) were captured in the polluted area. At the unpolluted area, the taxonomic composition of the diets of *Pelusios castaneus* and *Pelusios niger* was similar, whereas the diets of *Pelomedusa subrufa* and *Trionyx triunguis* were very different from the other two species and one another. In the polluted area, the taxonomic composition of the diet of *Pelusios castaneus* was significantly different from that of conspecifics in the unpolluted area, and consisted mainly of plant matter, annelids (earthworms and leeches), and gastropods. The taxonomic composition of the diet of *Pelusios niger* was also significantly different from that of conspecifics at the unpolluted area, and consisted mainly of annelids and gastropods, and secondarily of plant matter. Amphibian prey (eggs, tadpoles, and adults), which were one of the main food types for all turtles in the unpolluted area, practically disappeared from the diet of turtles at the polluted area. It was evident from this study that the two species that survived the oil spill event shifted considerably in their dietary preferences. In particular, in both species there was an obvious trend towards a reduction in the breadth of the trophic niche, with many fewer food categories eaten at the polluted area compared to the unpolluted area. It is suggested that such reduction in trophic niche breadth may depend directly on the reduced availability of most food sources (particularly amphibians, fish, and environmentally-sensitive invertebrates) in the polluted area, despite over 10 years having elapsed since the spill, and restoration operations at the site. It is likely that the above-mentioned reduction in trophic niche breadth also depended on the shifts in habitat use by the surviving turtles, which tended to concentrate into single habitat types in the polluted area, compared to the unpolluted area where they were more habitat generalists.

Key words: Chelonia, community ecology, feeding ecology, pollution, resource partitioning

INTRODUCTION

The territory of the Niger Delta (southern Nigeria) is one of the largest wetland areas of West Africa and the main production area of sub-Saharan Africa for oil and its derivatives (De Montclos, 1994; Carbone, 2002). This territory risks serious environmental collapse as a result of both natural habitat loss (due to deforestation for industrial reasons, and overpopulation, with several million people inhabiting an area previously almost unpopulated) and pollution. One of the main reasons of environmental pollution is the frequent occurrence of oil spills from pipelines crossing forests, swamps, and mangroves (Carbone, 2002). Several oil spills, which may have catastrophic effects on the local flora and fauna (Odu *et al.*, 1989; NDES, 1998), have been caused mainly by malicious attacks by groups of youths who retaliate against the government and damage oil companies economically by breaking pipelines.

Freshwater turtles are omnivorous (Ernst & Barbour, 1989; Luiselli, 1998; Akani *et al.*, 2001), and their communities are often characterized by rather complex interspecific relationships (Lagler, 1943; Legler, 1976; Vogt, 1981; Toft, 1985; Jackson, 1988; Moll, 1990; Stone *et al.*, 1993; Kennett & Tory, 1996; Pritchard, 2001), and thus they are important organisms for the dynamics of freshwater ecosystems (Legler, 1976; Vogt & Guzman, 1988; Luiselli *et al.*, 2000; Akani *et al.*, 2001). Because of (1) their position in food chains (Williams & Christiansen, 1981; Vogt & Guzman, 1988; Akani *et al.*, 2001), and (2) their regional abundance and considerable specific diversity (Luiselli *et al.*, 2000), freshwater turtles are among the ideal targets for studies on the effects of oil pollution on the freshwater

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ecosystems of the Niger Delta. Thus they have been used as study cases for environmental impact assessments by oil companies and other organizations operating in the study region (e.g., Politano, 1998; Luiselli & Politano, 1999; Luiselli & Akani, 2002).

By studying the turtle communities of two rainforest water bodies (one affected by an oil spill and one in good environmental condition), Luiselli & Akani (2003) previously showed that there were both direct and indirect effects of oil pollution on the complexity and habitat use of Nigerian freshwater communities of turtles. The main direct effect was a considerable reduction in turtle species diversity, with half of the species being lost after oil spillage (from four species, *Trionyx triunguis, Pelusios castaneus, Pelusios niger* and *Pelomedusa subrufa,* found in the unpolluted area, to just two in the polluted area, *P. castaneus* and *P. niger*), and with a very strong decline in the numbers of turtle specimens also for those species which were able to survive the pollution event. There was also a shift in habitat use after the oil spill by both species of *Pelusios,* and this shift may have strong effects on the long-term persistence of the species (independent of the direct pollution effects of the oil spill) because it considerably reduced habitat niche separation between these species, which are potential competitors. Therefore, it was stressed (Luiselli & Akani, 2003) that eco-ethological modifications in populations of animals subjected to oil pollution events must be studied in order to properly understand the long-term effects of these catastrophic phenomena.

By analysing the same communities of turtles, in this paper we try to determine (1) whether there is a significant shift in the species' dietary habits at the polluted area compared to the unpolluted area; and (2) if this is the case, whether these shifts may have altered significantly the respective niche positions of the turtle species.

STUDY AREAS AND METHODS

Two study areas (one unpolluted and one polluted by an oil spill) were used for our comparisons. Both areas contained similar habitats (i.e. a main river tract with banks covered by dense gallery forest, with seasonal swamps into the riverine forest and almost permanent marshes with rich aquatic vegetation). Among the plant species found in both areas were *Pterocarpus* sp., *Raphia* sp., *Triumphetta eriophlebia, Mitragyna stipulosa, Triplichiton scleroxylon, Khaya* sp., *Terminalia superba,* and *Mitragyna ciliata.* The linear distance between the two areas was approximately 20 km. Both areas were of approximately the same surface area (1 km of main river tract with its forested banks). The unpolluted study area was situated along a tributary of the Sambreiro River (Rivers State), approximately 7 km north-east of Degema town (Kula, Degema Local Government Area). The polluted study area was situated in the neighbouring area of the Sakie Stream and Baki Creek (Bayelsa State), where a well-known oil spill had occurred. On 27 January 1988 a spill of crude oil (estimated at about 1026 barrels) was detected along the Nun River delivery line of the Shell Petroleum Development Company. This was the result of a burst pipeline caused by an internal tear. The oil flowed down an area of seasonally flooded gallery swamp forest (Sakie Stream) into the Baki Creek, which links up with the Nun River to form Igbibiri Creek during the rainy season (Odu *et al.,* 1989). Four different species of freshwater turtle (*Trionyx triunguis, Pelusios niger, Pelusios castaneus* and *Pelomedusa subrufa*) were found in this river before the spill (Odu *et al.,* 1989; Akani, unpublished data), and only two (*Pelusios niger, Pelusios castaneus*) have survived until now (Luiselli & Akani, 2003). The spill was devastating, resulting in crude oil pollution upstream to a distance of 1 km (for total hydrocarbon content of waters at the study area, see Luiselli & Akani, 2003).

Data were gathered mainly during the years 2000-2002, but some additional observations were made in both study areas between 1996 and 1999. In total, these two study areas were surveyed for 20 field days at each locality, both in dry and wet seasons. Each field day lasted at least 12 hrs. Thus, in total there were 80 field days (40 in the dry and 40 in the wet seasons). The search for free-ranging turtles along non-linear transects was conducted along various microhabitats known to be frequented by these species (see Luiselli *et al.,* 2000). Several standard turtle-collecting techniques were used, including dip-netting and trawling (see also Gibbons *et al.,* 2001, for a similar procedure), and many additional specimens were brought by local villagers employed for this research project.

Once the turtles were captured, they were measured (midline plastron length), sexed, identified to species, and permanently individually marked by unique sequences of notches filed into the marginal scutes. The dietary study is based on both stomach analysis of a few dead specimens (offered in bush-meat markets) and faecal analysis of living specimens. No specimen was killed or injured by the researchers. Masses of filamentous algal mats were commonly found in stomachs (in over 65% of stomachs of all species in both study sites), but we assumed this material was ingested secondarily. However, it is uncertain whether mats of algae are only incidentally ingested. Many turtles forage directly on algae, and any large quantities of algae in faeces or stomach contents would possibly suggest deliberate consumption of this resource. In any case, as there were no significant differences in terms of frequency of algae consumption between species (in all cases, χ^2 test, at least $P>0.3$) and within species from different study areas (χ^2 test, at least $P>0.2$), to include or exclude these data from calculations appears rather irrelevant. The same was true for sand, gravel, and presumably parasitic nematodes. Faeces were collected from freshly captured free-ranging specimens.

TABLE 1. Summary of the diet data collected from turtles at the unpolluted study area in south-eastern Nigeria. Numbers represent the number of turtles that consumed each prey type. Percentages indicate the proportion of turtle specimens containing a given prey type. The total numbers of specimens examined were 14 (*Trionyx triunguis*), 217 (*Pelusios castaneus*), 113 (*Pelusios niger*), and 9 (*Pelomedusa subrufa*). Only identified items are considered for this table.

Prey type	Number of turtles containing each prey item			
	Trionyx triunguis	*Pelusios castaneus*	*Pelusios niger*	*Pelomedusa subrufa*
PLANTS				
Fruits	0	11 (5.1%)	8 (7.1%)	2 (22.2%)
Seeds	0	8 (3.7%)	4 (3.5%)	2 (22.2%)
Aquatic plants	0	16 (7.4%)	9 (7.9%)	3 (33.3%)
INVERTEBRATES				
Annelida	0	8 (3.7%)	12 (10.6%)	2 (22.2%)
Gastropoda	1 (7.1%)	11 (5.1%)	4 (3.5%)	0
Bivalvia	0	2 (0.9%)	0	0
Arachnida	0	6 (2.8%)	3 (2.6%)	0
Insecta	0	13 (6.0%)	1 (0.9%)	0
Odonata (larvae)	0	6	1	0
Coleoptera (larvae)	0	1	0	0
Nepa sp.	0	2	0	0
Hemiptera unidentified	0	1	0	0
Ephemeroptera	0	1	0	0
Larvae (unidentified)	0	2	0	0
Crustacea	1 (7.1%)	41 (18.9%)	27 (23.9%)	3 (33.3%)
VERTEBRATES				
Fish	11 (78.5%)	114 (52.5%)	79 (69.9%)	6 (66.7%)
Anurans (adults)	5 (35.7%)	8 (3.7%)	14 (12.4%)	0
Anuran eggs	0	20 (9.2%)	17 (15.0%)	2 (22.2%)
Anuran tadpoles	10 (71.4%)	49 (22.6%)	33 (29.2%)	4 (44.4%)
Indeterminate	2 (14.3%)	1 (0.4%)	1 (0.9%)	0

To avoid statistical problems due to pseudoreplication of observations (Mathur & Silver, 1980; Hurlbert, 1984), diet data were recorded only once from individual turtles, i.e. the recaptured turtles were not used again for data recording and analyses. For uniformity, data relative to the first time a given specimen was encountered were recorded. To avoid biases in data resulting from dissection of stomachs and analysis of faecal pellets, we did not analyse the total number of food items, but simply recorded the presence of the various items in each individual turtle. This procedure was necessary because it is difficult to count exactly the total number of items of a given food type found in the faeces of the turtles, whereas the same operation is much easier when dissecting turtle stomachs.

All data were statistically analysed using STATISTICA (version 5.0, for Windows) PC+ package (Statsoft Inc., 1996), with all tests being two-tailed and alpha set at 5%. To partially remove the sample size problem in between-site comparisons (for instance, 217 *P. castaneus* were found at the unpolluted site compared to only 21 at the polluted site; likewise 113 versus 39 *P. niger*; see below), χ^2 tests were conducted category by category: i.e. to compare fruit in unpolluted and polluted sites. When df=1, Yates' correction was applied to the χ^2 test. However, due to the difficulty of identifying the ingested plant material, we assumed that a single type of plant was eaten by a single individual, although it may well be possible that the same individual may have ingested several plant categories.

RESULTS

DIET OF TURTLES IN THE UNPOLLUTED AREA

A total of 510 turtles (*Trionyx triunguis, n*=23; *Pelusios castaneus, n*=314; *Pelusios niger, n*=160; and *Pelomedusa subrufa, n*=13) was captured in the unpolluted area (Luiselli & Akani, 2003). Identifiable food items were obtained from stomachs and/or faecal pellets of 14 *Trionyx triunguis*, 217 *Pelusios castaneus*, 113 *Pelusios niger* and 9 *Pelomedusa subrufa* (Table 1). Contingency table analysis revealed that males and females did not differ significantly in terms of taxonomic diet composition in either *Pelusios* species (at least $P>0.27$), whereas the same analysis was not performed on the other two species due to small sample sizes.

Based on the proportion of animals containing a given prey type, the data show that: (1) the diet of *Trionyx triunguis* consisted mainly of aquatic vertebrates, i.e. tadpoles and fish (each of them found in > 70% of individuals) and ranid frogs (> 35% of individuals); (2) the diet of *Pelusios castaneus* was very diverse, with small fish being the most common food source (found in > 50% of individuals); (3) the diet of *Pelusios niger* was also very diverse, but the main prey were clearly small fish (found in about 70% of individuals) followed by tadpoles (found in about 30% of individu-

TABLE 2. Summary of the diet data collected from turtles at the polluted study area in south-eastern Nigeria. Numbers represent the number of turtles that consumed each prey type. Percentages indicate the proportion of turtle specimens containing a given prey type. The total numbers of specimens examined were 21 (*Pelusios castaneus*) and 39 (*Pelusios niger*). Only identified items are considered for this table.

Prey type	Numbers of turtles containing each prey item	
	Pelusios castaneus	*Pelusios niger*
PLANTS		
Fruits	4 (19%)	3 (7.7%)
Seeds	16 (76.2%)	12 (30.8%)
Aquatic plants	14 (66.7%)	13 (33.3%)
INVERTEBRATES		
Annelida	9 (42.9%)	24 (61.5%)
Gastropoda	12 (57.1%)	27 (69.2%)
VERTEBRATES		
Anuran tadpoles	2 (9.5%)	4 (10.2%)
Anurans (adults)	1 (4.8%)	4 (10.2%)
Fish	3 (14.3%)	5 (12.8%)

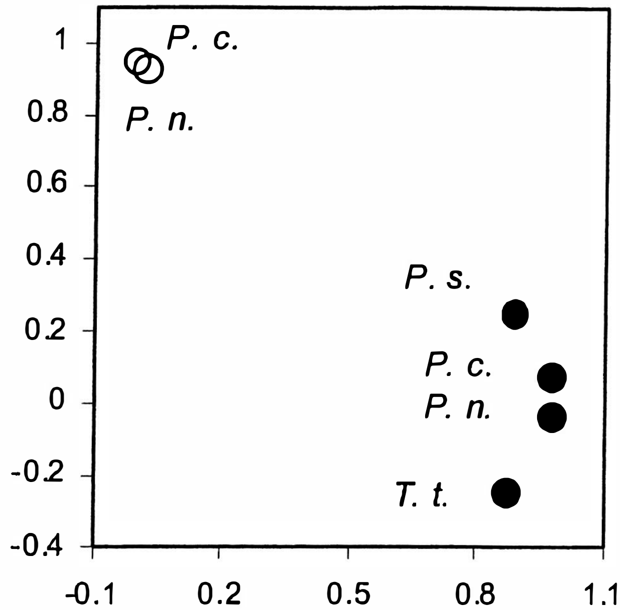

FIG. 1. Factorial plan of a Principal Component Analysis (PCA) on the diet similarities across turtle species (VARIMAX standardized rotated model), based on the proportion of specimens containing each food type. Solid circles indicate the unpolluted area, hollow circles the polluted area. Abbreviations: *P.c., Pelusios castaneus*; *P.n., P. niger*; *T.t., Trionyx triunguis*; *P.s., Pelomedusa subrufa*.

als); (4) the diet of *Pelomedusa subrufa* consisted also of many small fish (found in over 65% of specimens), but plant matter accounted for a higher percentage of food than in the other three species; (5) amongst invertebrates, crustaceans were commonly eaten by all species.

DIET OF TURTLES IN THE POLLUTED AREA AND COMPARISONS BETWEEN SITES

A total of 88 turtles (*Pelusios castaneus, n*=31; *Pelusios niger, n*=57) was captured in the polluted area (Luiselli & Akani, 2003). The presence of the other two turtle species (*Trionyx triunguis* and *Pelomedusa subrufa*) was documented prior to the oil spill (Odu *et al*., 1989; Luiselli & Akani, 2002), but today they appear to be completely extirpated (Luiselli & Akani, 2002, 2003). Identifiable food items were obtained from stomachs and/or faecal pellets of 21 *Pelusios castaneus* and 39 *Pelusios niger* (Table 2). Contingency table analysis revealed that males and females did not differ significantly in terms of diet composition in either species of *Pelusios* (P>0.46 for both).

Based on the proportions of turtles containing a given prey type, the data show that: (1) the taxonomic composition of the diet of *Pelusios castaneus* was very different from that of conspecifics at the unpolluted area, and consisted mainly of plant matter (seeds and aquatic plants, each of them found in > 65% of the individuals), and of annelids (earthworms and leeches) and gastropods (found in 42-57% of individuals). Moreover, there were significant differences between the sites in terms of frequency of occurrence in faeces of fruits (χ^2=30.16, df=1, P<0.0001), seeds (χ^2=450.92, df=1, P<0.0001), aquatic plants (χ^2=100.02, df=1, P<0.0001), annelids (χ^2=164.80, df=1, P<0.0001), gastropods (χ^2=184.28, df=1, P<0.0001), anuran tadpoles (χ^2=40.69, df=1, P<0.0001) and fish (χ^2=227.68, df=1, P<0.0001); (2) the taxonomic composition of the diet of *Pelusios niger* was also very different from that of conspecifics in the unpolluted area, and consisted mainly of annelids and gastropods (found in 61-69% of the individuals) and secondary plant matter (found in > 30% of the individuals). Moreover, there were significant differences between sites in terms of frequency of occurrence in faeces of seeds (χ^2=110.12, df=1, P<0.0001), aquatic plants (χ^2=53.71, df=1, P<0.0001), annellids (χ^2=143.03, df=1, P<0.0001), gastropods (χ^2=551.83, df=1, P<0.0001), anuran tadpoles (χ^2=44.80, df=1, P<0.0001), and fish (χ^2=306.13, df=1, P<0.0001); (3) amphibian prey (eggs, tadpoles, and adults), which was one of the main food types for all turtles in the unpolluted area, practically disappeared from the diet of turtles in the polluted area, and the same was true for fish, insects and crustaceans.

The ordination of the various turtle species in a PCA factorial plan (with a standardized VARIMAX rotated model) is presented in Fig. 1. In this PCA factorial plan (det. corr. matrix = -3.499; eigenvalues = 3.482 with 58.04% of total variance explained, and 1.906 with 31.8% of total variance explained), based on the similarities between species in terms of food types which were eaten, it appeared that: both *Pelusios niger* and *P. castaneus* in the polluted area were differentiated from

TABLE 3. Summary of the diet data collected from turtles at the unpolluted study area in south-eastern Nigeria, according to season (dry season: October to April; wet season: May to September). Numbers represent the number of turtles that consumed each prey type. Percentages indicate the proportion of turtle specimens containing a given prey type The total numbers of specimens examined were 7 (dry season) and 7 (wet season) for *Trionyx triunguis*, 105 and 112 for *Pelusios castaneus*, and 60 and 53 for *Pelusios niger*. Data for *Pelomedusa subrufa* are not presented in this table because only one specimen with identifiable food was collected in the dry season. Only identified items are considered for this table.

Prey type	*Trionyx triunguis* Dry	*Trionyx triunguis* Wet	*Pelusios castaneus* Dry	*Pelusios castaneus* Wet	*Pelusios niger* Dry	*Pelusios niger* Wet
PLANTS						
Fruits	0	0	6 (5.7%)	5 (4.5%)	8 (13.3%)	0
Seeds	0	0	5 (4.8%)	3 (2.7%)	1 (1.7%)	3 (5.7%)
Aquatic plants	0	0	6 (5.7%)	10 (8.9%)	5 (8.3%)	4 (7.6%)
INVERTEBRATES						
Annelida	0	0	3 (2.8%)	5 (4.5%)	7 (11.7%)	5 (9.4%)
Gastropoda	0	1 (14.3%)	3 (2.8%)	8 (7.1%)	1 (1.7%)	3 (5.7%)
Bivalvia	0	0	2 (1.9%)	0	0	0
Arachnida	0	0	6 (5.7%)	0	3 (5%)	0
Insecta	0	0	5 (4.8%)	8 (7.1%)	0	1 (1.9%)
Odonata (larvae)	0	0	3	3	0	1
Coleoptera (larvae)	0	0	1	0	0	0
Nepa sp.	0	0	0	2	0	0
Hemiptera unid.	0	0	1	0	0	0
Ephemeroptera	0	0	0	1	0	0
Larvae (unidentified)	0	0	0	2	0	0
Crustacea	0	1 (14.2%)	18 (17.1%)	23 (20.5%)	17 (28.3%)	10 (18.9%)
VERTEBRATES						
Fish	6 (85.7%)	5 (71.4%)	51 (48.6%)	63 (56.2)	38 (63.3%)	41 (77.3%)
Anurans (adults)	2 (28.6%)	3 (42.8%)	2 (1.9%)	6 (5.3%)	9 (15%)	5 (9.4%)
Anuran eggs	0	0	2 (1.9%)	18 (16.1%)	3 (5%)	14 (26.4%)
Anuran tadpoles	4 (57.1%)	6 (85.7%)	23 (21.9%)	26 (23.2%)	11 (18.3%)	22 (41.5%)
Indeterminate	2 (28.6%)	0	1 (0.9%)	0	1 (1.7%)	0

TABLE 4. Summary of the diet data collected from turtles at the polluted study area in south-eastern Nigeria, divided by season (dry season: October to April; wet season: May to September). Numbers represent the number of turtles that consumed each prey type. Percentages indicate the proportion of turtle specimens containing a given prey type. The total numbers of specimens examined were 10 (dry season) and 11 (wet season) for *Pelusios castaneus* and 17 and 22 for *Pelusios niger*. Only identified items are considered for this table.

Prey type	*Pelusios castaneus* Dry	*Pelusios castaneus* Wet	*Pelusios niger* Dry	*Pelusios niger* Wet
PLANTS				
Fruits	2 (20%)	2 (18.2%)	1 (5.9%)	2 (9.1%)
Seeds	9 (90%)	7 (63.6%)	7 (41.2%)	5 (22.7%)
Aquatic plants	6 (60%)	8 (72.7%)	6 (35.3%)	7 (31.8%)
INVERTEBRATES				
Annelida	8 (80%)	1 (9.1%)	15 (88.2%)	9 (40.9%)
Gastropoda	2 (20%)	10 (90.9%)	12 (70.6%)	19 (86.4%)
VERTEBRATES				
Anuran tadpoles	0	2 (18.2%)	0	4 (18.2%)
Anurans (adults)	0	1 (9.1%)	0	4 (18.2%)
Fish	1 (10%)	2 (18.2%)	2 (11.8%)	3 (13.6%)

all the other turtle species (including conspecifics) in the unpolluted area. In this analysis, the four turtle species in the unpolluted area correlated significantly with Factor 1 (high positive scores correlated with fish, amphibians of all ages, and crustaceans), whereas the two *Pelusios* species in the polluted area were arranged in completely separate positions and correlated with Factor 2 (high positive scores correlated with annelids and gastropods).

SEASONAL DIETARY CHANGES IN THE TWO STUDY AREAS

Seasonal variations in turtle diets at both the study areas is presented in Table 3 (unpolluted area) and Table 4 (polluted area). Seasonal variation in the diet of *Pelomedusa subrufa* at the unpolluted area was not studied because only one specimen with identifiable food was collected in the dry season. After pooling sexes of all species because of their non-significant differences in prey composition (see above), diet composition was apparently similar between seasons in *Trionyx triunguis*, but the sample size was not large enough to allow any robust statistical test. On the other hand, diet composition was varied seasonally in both *Pelusios castaneus* and *Pelusios niger*. For *Pelusios castaneus,* there were significant differences between seasons in the frequency of consumption of gastropods (χ^2=10.21, df=1, P<0.0014) – which were consumed more in the wet season, and amphibian eggs (χ^2=131.52, df=1, P<0.0001) – which were also consumed more in the wet season. For *Pelusios niger,* the significant differences between seasons were found in the frequency of consumption of fruits (χ^2=7.05, df=1, P=0.0078) and crustaceans (χ^2=4.49, df=1, P=0.034) – which were consumed more in the dry season, and amphibian eggs (χ^2=59.02, df=1, P<0.0001)and tadpoles (χ^2=23.36, df=1, P<0.0001) – which were consumed more in the wet season.

Diet composition was also very different between seasons in both *Pelusios castaneus* and *Pelusios niger* in the polluted study area. For *Pelusios castaneus,* the significant differences were found in the frequency of consumption of annelids (χ^2=62.15, df=1, P<0.0001) – which were consumed more in the dry season, and gastropods (χ^2=37.53, df=1, P<0.0001) – which were consumed more in the wet season. For *Pelusios niger,* the significant differences were found only in the frequency of consumption of annelids (χ^2=14.89, df=1, P=0.0001) – which were consumed more in the dry season, although gastropods, amphibian adults and tadpoles were consumed more in the wet season but not at a statistically significant level. The interseasonal differences in the frequency of consumption of annelids in either species were mainly due to the preponderance of leeches in the water of the polluted area during the dry season. These animals were often observed while sucking the blood of the turtles, and so it may be hypothesized that *Pelusios* turtles, which live in small groups, may easily forage on these annelids by ingesting leeches sucking blood from themselves or their conspecifics.

DISCUSSION

Before any discussion of the present data, the theoretical limitations of our study procedure must be noted. As we did not compare the feeding habits of the turtles in the same study plot before and after the oil spill, we could not directly test whether the environmental pollution had any direct effect on the dietary changes of the species, but we can indirectly test this hypothesis by assuming that the feeding habits of the various species were the same in the two study areas, given the close geographic position (just 20 km linear distance) and the similar habitat characteristics.

There is very little literature available on the feeding ecology of the four turtle species studied here (e.g. Ernst & Barbour, 1989), and the only detailed data relate to Nigerian populations of *Pelusios castaneus* (Luiselli, 1998) and *Trionyx triunguis* (Akani *et al.*, 2001). At least with regard to diets of these two species, our data from the unpolluted study area are consistent with those available in the literature, and indicate that *Trionyx triunguis* is more carnivorous than the three sympatric pelomedusids (Ernst & Barbour, 1989; Luiselli, 1998; Akani *et al.*, 2001).

The examination of the data available on diet similarity (this study) and habitat use (see Luiselli *et al.*, 2000; Luiselli & Akani, 2002) of the three pelomedusids suggests that *Pelusios niger* and *Pelusios castaneus* are potentially strong competitors, although they exhibit clear-cut differences in microhabitats - one species is linked to seasonal and ephemeral water bodies and the other to permanent water bodies - whereas *Pelomedusa subrufa* is distinctly ecologically different from the other two species (Luiselli *et al.*, 2000). Unfortunately, no such diet and ecological comparison can be done with regard to the turtles from the polluted area, because, to the best of our knowledge, there is no similar study available in the literature.

Our data on the evident shifts in diet composition of the two species of the genus *Pelusios* are likely attributable to the effects of oil pollution, which has probably changed the food resource availability for turtles considerably. This would have produced the observed dietary shifts, chiefly towards an increase in the consumption of vegetation, annelids, and gastropods, and a reduction in the consumption of the vertebrate prey, by the two *Pelusios* species. In addition, a logical interpretation of our multivariate analysis is that these oil-induced changes in food resource availability may have forced the two surviving turtle species to exploit nearly the same trophic resources, which are possibly the only remaining abundant resources in the polluted environment. As a consequence, these two potential competitors, which were situated in more distant positions of the multivariate space in the unpolluted area, were very close to one another in the polluted area. In particular, in both species there was an obvious trend towards a reduction in the breadth of the trophic niche, with many fewer food categories eaten at the polluted area compared to the unpolluted area. Such a reduction in the trophic niche breadth may depend directly on the reduced availability of most food sources (particularly amphibians, fish, and environmentally-fragile invertebrates) in the polluted area, despite over 10 yrs having elapsed since the spill, with restoration operations taking place in the interim. Insects and Crustacea are absent food categories at the polluted site, where fish and tadpole consumption was also considerably reduced, suggesting a drastic impoverishment of aquatic life. Though clearly apparent in the PCA analysis, this pattern needs further investigation because - due to the fact that our samples are small - we can confidently say what these species eat, but we are not sure of the significance of the absence of some food categories in the faeces.

It is likely that the reduction in trophic niche breadth depended also on the shifts in habitat use by the surviving turtles, which tended to concentrate into single habitat types in the polluted area, whereas they were more habitat generalists in the unpolluted area (Luiselli & Akani, 2002, 2003). However, different species may ingest the same general prey category with the same frequency while differing considerably in the species (or genera or orders) that they feed on. Thus, it is possible that the interspecific dietary relationships are more complex than those described in this study.

It is also obvious from the present study that the ecological effects of oil spills are catastrophic for the wildlife of tropical water bodies, not only immediately after the event, but also many years after the event, due to a complex sequence of ecological modifications in the environment, and to new types of ecological relationships emerging between species. Further studies must be conducted to investigate in detail these long-term ecological effects.

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