A comparative analysis of the diets of *Pelusios* turtles across Africa

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Abstract: *Pelusios* is an Afrotropical endemic genus of freshwater turtles that have adapted to a variety of habitats, with savannas and forests being their two main habitat types. Although considered generally carnivorous, these turtles have rarely been subjected to detailed field surveys for determining their quantitative diet. In this paper, by using both literature and original data, we analyse the diet of several *Pelusios* populations: three *P. adansonii* populations from South Sudan, one *P. nanus* from Zambia, seven *P. castaneus* from Nigeria, Benin and Togo, and four *P. niger* from Nigeria. All species were omnivorous but with a clear preponderance of the prey items being of animal origin (amphibians, fish, arthropods and anellids). Saturation curves revealed that the diet composition of all the surveyed populations was adequately assessed, and the diversity profiles indicated that all the populations were relatively similar in terms of overall dietary diversity. All species appeared substantially generalist in terms of their diet composition, although the effects of season (wet versus dry) were not adequately assessed by our study.

Keywords: Chelonians; Pelomedusidae; Foraging ecology
Introduction

*Pelusios* is an Afrotropical endemic genus of freshwater turtles that have adapted to a variety of habitats, with savannahs and forests being their two main habitat types. Although considered generally carnivorous, these turtles have rarely been subjected to detailed field surveys for determining their quantitative diet. In this paper, by using both literature and original data, we analyse the diet of several *Pelusios* populations: three *P. adansonii* populations from South Sudan, one *P. nanus* from Zambia, seven *P. castaneus* from Nigeria, Benin and Togo, and four *P. niger* from Nigeria.

Dorsal and ventral view of *Pelusios niger* from the Niger Delta (southern Nigeria). This species is linked to forest and forest-derived areas, and inhabits permanent waterbodies.
Methodology

Literature data included three populations of *P. castaneus* and two populations of *P. niger* studied in the Niger Delta, Nigeria (Luiselli, 1998; Luiselli et al., 2004). Original data came from additional four populations of *P. castaneus*, two of *P. niger*, and one of *P. nanus*. Overall, original field studies were conducted between 1996 and 2020, in some savanna sites as well as in rainforest sites, in both perennial waterbodies (rivers, streams, lakes) and in temporary ponds.

Study areas

Map of Africa showing the location of the sites where the diet of *Pelusios* spp. was studied. Land use categories are also shown in the maps. Localities for both literature and original data are pooled in this map.
Diet composition of each population was described as the percentage of stomachs containing a given food item and not on the basis of the total number of items of each food category in stomachs. This was necessary because it is often impossible to count the number of items from feces analysis. We evaluated whether our sampling effort captured the true food items richness and diversity within each study population by building a rarefaction curve for food type discoveries at each site.
The study species

Pelusios niger

Pelusios nanus

Pelusios castaneus

Pelusios adansonii
Results and Discussion

Overall, diet data on 1260 *Pelusios* individuals were collected: 668 were *P. castaneus*, 310 were *P. niger*, 213 were *P. adansonii*, and 69 were *P. nanus*. 705 turtle individuals were captured in Nigeria, 56 in Benin, 217 in Togo, 213 in South Sudan and 69 in Zambia. The synopsis of the diet composition by species and by country/study area is given in Table 1.

| Nigeria Benin Togo Nigeria Nigeria Nigeria Nigeria South Sudan South Sudan South Sudan Zambia | forest for-derived forest for-derived savannah castaneus castaneus castaneus castaneus for-derived for-derived for-derived adansonii adansonii adansonii savannah savannah savannah nanus |
|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| N   | 217 | 21 | 65 | 92 | 56 | 135 | 82 | 113 | 39 | 77 | 81 | 133 | 41 | 39 | 69 |
| Fruits | 5.1 | 19 | 5 | 7 | 0 | 2.22 | 0 | 7.1 | 7.7 | 0 | 0 | 0 | 2.44 | 5.13 | 0 |
| seeds | 3.7 | 76.2 | 10.3 | 15.9 | 5.37 | 15.56 | 13.4 | 3.3 | 30.8 | 5.2 | 0 | 0 | 7.32 | 10.26 | 7.25 |
| Aquatic plants | 7.4 | 66.7 | 52.8 | 38.5 | 55.3 | 25.19 | 20.7 | 7.9 | 33.3 | 27.3 | 16.0 | 30.8 | 43.9 | 38.5 | 8.7 |
| Algae | 0 | 0 | 1.4 | 6.6 | 0 | 2.96 | 0.0 | 0.0 | 0.0 | 3.9 | 13.6 | 0 | 0.00 | 0.00 | 0.00 |
| Annelida | 3.7 | 42.9 | 8.3 | 4.9 | 12.5 | 12.59 | 19.5 | 10.6 | 61.5 | 6.5 | 7.4 | 12.8 | 19.5 | 46.2 | 17.4 |
| Gastropoda | 5.1 | 57.1 | 29.2 | 36.1 | 0 | 4.44 | 15.9 | 3.5 | 69.2 | 6.5 | 25.9 | 1.5 | 19.5 | 10.3 | 4.3 |
| Bivalvia | 0.9 | 0 | 0 | 0 | 0 | 0.00 | 0.0 | 0.0 | 0.0 | 1.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Arachnida | 2.8 | 0 | 0 | 0 | 0 | 0.74 | 0.0 | 2.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Insecta | 6 | 0 | 12.5 | 10.6 | 12.5 | 31.85 | 43.9 | 0.9 | 0.0 | 27.3 | 30.9 | 30.8 | 51.2 | 43.6 | 68.1 |
| Crustacea | 18.9 | 0 | 11.1 | 9 | 10.71 | 8.89 | 2.4 | 23.9 | 0 | 42.9 | 13.6 | 4.5 | 14.6 | 53.8 | 2.9 |
| Fish | 52.5 | 14.3 | 45.8 | 7.4 | 25 | 30.37 | 14.6 | 69.9 | 12.8 | 80.5 | 58.0 | 15.8 | 31.7 | 20.5 | 0.0 |
| Anura adults | 3.7 | 4.8 | 5.6 | 18 | 5.37 | 24.44 | 25.6 | 12.4 | 10.2 | 20.8 | 23.5 | 7.5 | 14.6 | 15.4 | 0.0 |
| Anura eggs | 9.2 | 0 | 0 | 0 | 0 | 4.44 | 8.5 | 15 | 0 | 0.0 | 7.4 | 0.0 | 2.4 | 0.0 | 4.3 |
| Anura tadpole | 22.6 | 9.5 | 0 | 0 | 0 | 0.00 | 6.1 | 29.2 | 10.2 | 0.0 | 0.0 | 0.0 | 0.0 | 10.3 | 10.1 |
| Reptiles | 0 | 0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 3.9 | 1.2 | 0.0 | 0.0 | 2.6 | 0.0 |
| birds | 0 | 0 | 0 | 0 | 0 | 0.0 | 0.0 | 0.0 | 9.1 | 6.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| small mammals | 0 | 0 | 0 | 0 | 0 | 0.0 | 8.8 | 9.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Indeterminate | 0.4 | 0 | 0 | 0 | 0 | 5.36 | 2.96 | 3.7 | 0.9 | 0 | 3.9 | 6.2 | 3.0 | 12.2 | 10.3 |

Table 1. Synopsis of the diet composition of turtles
Saturation curves revealed that the diet composition of all the surveyed populations was adequately assessed (Graphic 1), and the diversity profiles indicated that all the populations were relatively similar in terms of overall dietary diversity (Graphic 2).

*Pelusios niger* fed on larger sized prey types (including terrestrial vertebrates) than the other species, but this was an effect of its much larger body size. On the other hand, *P. nanus* (the smallest species in the group) fed mainly upon invertebrates, and was the only species that had no fish remains in stomachs or faeces.
More in detail, terrestrial vertebrates were found in three out of four *P. niger* populations, and in up to 9.9% of the examined individuals within each population, whereas they were never observed in other *Pelusios* species apart from one population of *P. adansonii* (2.6% of the examined individuals). Fish remains, that as reported in the previous slide were never seen in *P. nanus*, were found in all the other 14 *Pelusios* populations, with frequencies of occurrence ranging from 7.4% (in a *P. castaneus* population from a forest-derived area) to 80.5% (in a *P. niger* population from a rainforest area in Nigeria).
If we consider, as a metric of dietary preference by *Pelusios* spp., the % frequency of occurrence of a given prey type across populations (calculated based on the number of populations in which at least one individual ate a certain type of food compared to the total number of populations examined (n = 15)), aquatic plants, Gastropoda, fish and frogs represented the main food categories for these turtles (Graphic 3).

The various turtle populations did not show any clear species-specific pattern, but most *P. castaneus* populations clustered together, and two of out of three *P. adansonii* populations clustered together with *P. castaneus*, in a UPGMA tree-diagram with Euclidean distances (Graphic 4). A UPGMA tree-diagram with Euclidean distances also showed that forest and forest-derived populations clustered together in terms of taxonomic diet composition, whereas savannah populations formed another well defined group (Graphic 5).
Effects of vegetation cover and turtle body size

Our GLM results (Table 2) showed a negative effect of vegetation cover on Anura adults consumption by turtles, while showed that the frequencies of Anura tadpoles, fish, reptiles and birds on Pelusios diets increased with the increase of vegetation cover. The GLM model also showed positive effects of individual body size on algae, Bivalvia, reptiles, birds and small mammals consumption by turtles, while underlined that the predation on Arachnida decreased with the increased of turtles body size (Table 3).

|                          | Estimate | St. Error | Wald     | p         |
|--------------------------|----------|-----------|----------|-----------|
| Anura tadpoles           | 0.035197 | 0.009961  | 12.48426 | 0.000410  |
| Anura adults             | -0.13081 | 0.019494  | 45.02788 | 0.000000  |
| Fish                     | 0.009662 | 0.002308  | 17.52001 | 0.000028  |
| Reptiles                 | 0.274646 | 0.056558  | 23.58069 | 0.000001  |
| Birds                    | 0.210985 | 0.025179  | 70.21284 | 0.000000  |

Table 2. Output of the GLM model on the relationship between vegetation cover and diet in four species of Pelusios from tropical Africa. Only significant variables are presented in this table.

|                          | Estimate | St. Error | Wald     | p         |
|--------------------------|----------|-----------|----------|-----------|
| Algae                    | 0.112020 | 0.009507  | 138.8375 | 0.000000  |
| Bivalvia                 | 1.514130 | 0.231157  | 42.90536 | 0.000000  |
| Arachnida                | -0.060554| 0.015102  | 16.0784  | 0.000061  |
| Reptiles                 | 0.389812 | 0.000062  | 38937600 | 0.000000  |
| Birds                    | 0.098272 | 0.032757  | 9.00000  | 0.002700  |
| Small mammals            | 0.084896 | 0.028299  | 9.00000  | 0.002700  |

Table 3. Output of the GLM model on the relationship between turtle body size and diet in four species of Pelusios from tropical Africa. Only significant variables are presented in this table.
Conclusions

Overall, our study revealed that all species were substantially generalist in terms of their diet composition, although the effects of season (wet versus dry) were not adequately assessed by our study. In addition, we showed that all species were omnivorous but with a clear preponderance of the prey items being of animal origin (amphibians, fish, arthropods and anellids). The relative head size and shape probably influenced the ingestion performance of the various species: indeed, when considering only the prey items that were found almost intact in the flushed stomachs, the species with the most massive head (P. niger) at a given body size was particularly able to ingest very large prey items compared to other species. The ecological consequences (minimization of interspecific competition strength) of these differences in ingestion performance should be further analyzed by ad-hoc studies.
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