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A Comparative Analysis of the Diets of *Pelusios* Turtles across Africa †

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† Presented at the 1st International Electronic Conference on Biological Diversity, Ecology, and Evolution, 15–31 March 2021.

Abstract: *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. 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. General Linear Models (GLM) 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. 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

Citation: Lastname, F.; Lastname, F.; Lastname, F. Title. *Proceedings* **2021**, 65, x. https://doi.org/10.3390/xxxxx

Received: date
Accepted: date
Published: date

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1. 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 [1]. Although considered generally carnivorous [1], these turtles have rarely been subjected to detailed field surveys for determining their quantitative diet [2,3]. In this paper, by using both literature and original data, we present a preliminary analysis of the diet of several *Pelusios* populations belonging to four distinct species (Figure 1): 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. Our aims with this paper is also to provide a database that can be used for further, deeper analysis of the feeding habits of *Pelusios* populations across Africa.

2. Materials and methods

Literature data included three populations of *P. castaneus* and two populations of *P. niger* studied in the Niger Delta, Nigeria [2,3]. Original data came from additional four populations of *P. castaneus*, two of *P. niger*, and one of *P. nanus*. The geographic position of the various study areas are presented in Figure 2. 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 (Figure 3). Concerning free-ranging turtles, the methodology used for obtaining the food items were carefully described in [2] and in [3]. All captured turtles were sexed by examining their plastron and caudal shape, measured for curved carapace length, curved carapace width, plastron length and plastron width, 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), stomach-flushing (as described in [4]) and fecal pellet analysis of living specimens (specimens were singly kept into plastic boxes until defecation occurred). Specimens captured into baited traps [5] were not included in the analyses; so we included in this study only those turtles that did not eat "artificially attractive" food during our studies. No specimen was killed or injured by the researchers.

We included algae in our diet data analyses, although these may have been ingested secondarily by turtles, at least on some instances. Feces were separately placed into alcohol for later dissection and examination under binocular microscope.

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, using the software PAST 4.0.

Generalized Linear Models (GLM, see [6]) were used to test the relationship between body size and vegetation cover on the diet of four species of turtles. In the models three different vegetation classes (savannah, derived forest and forest) and three body size classed as dependent variables and the frequencies of different prey species as predictors were used. In the models, computing by all effects procedure, the identity link function and a normal distribution of error were used [7].

All parametric tests were used only after having verified the normality and homoscedasticity of the used variables by Kolmogorov-Smirnov test. Even/uneven sex-ratio and intersexual differences in frequency of consumption of food items were assessed by observed versus expected χ^2 test, with P-value generated after 9999 Monte Carlo permutations. In the text, means are indicated ± 1 Standard Deviation (S.D.).

3. Results and discussion

3.1. Diet composition by species

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.

Saturation curves revealed that the diet composition of all the surveyed populations was adequately assessed (Figure 4), and the diversity profiles indicated that all the populations were relatively similar in terms of overall dietary diversity (Figure 5).

Pooling data from the various species, it resulted that the main bulk of the *Pelusios* spp. diet consisted of invertebrates (present in 75.2% of the examined specimens, n = 1260), followed by plant materials (found in 46.1% of the turtles) and by small vertebrates (22.8%) (Table 1). However, there were remarkable differences between species: *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. Indeed, 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) (Table 1). 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 feces (Table 1). Fish remains 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) (Table 1).

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)), it resulted that aquatic plants, Gastropoda, fish and frogs represented the main food categories for these turtles (Figure 6).

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 (Figure 7). 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 (Figure 8).

3.2. 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).

4. 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 inter-specific competition strength) of these differences in ingestion performance should be further analyzed by ad-hoc studies.

Figures, Tables and Schemes

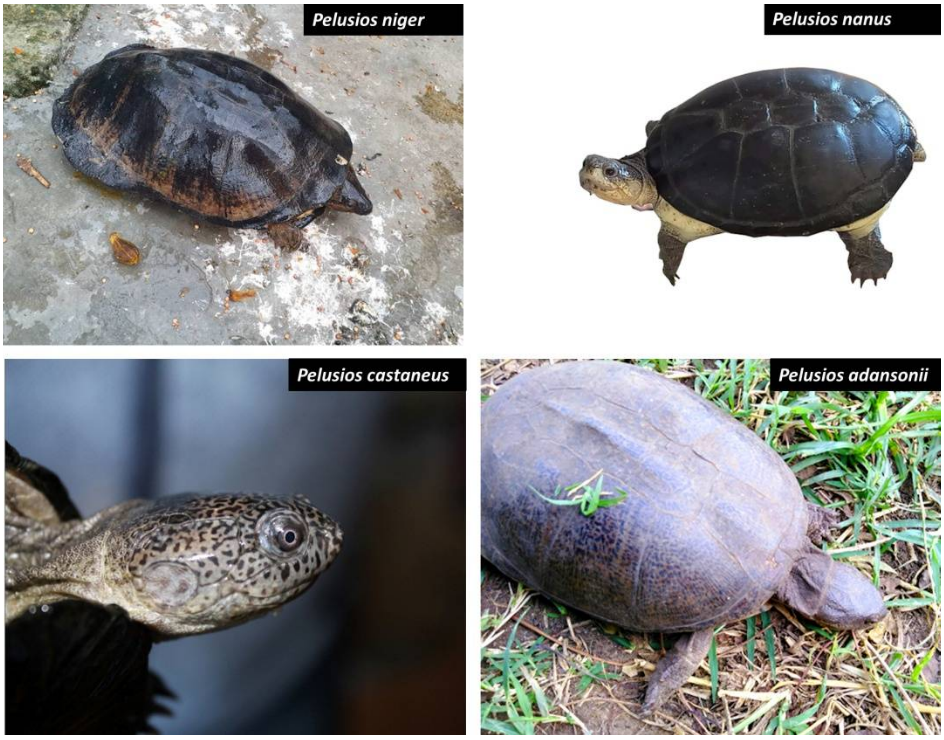

Figure 1. The four study species.

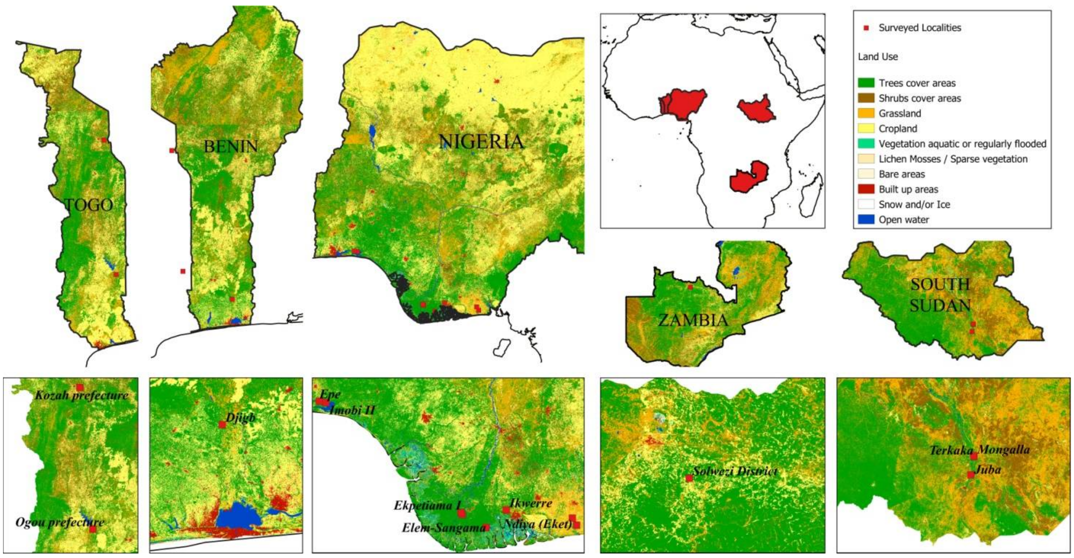

Figure 2. Map of Africa showing the location of the sites where the diet of *Pelusios* spp. was studied. Land use categories are also shown in the maps. Localities for both literature and original data are pooled in this map.

Figure 3. Typical habitats of *Pelusios* spp. in tropical Africa.

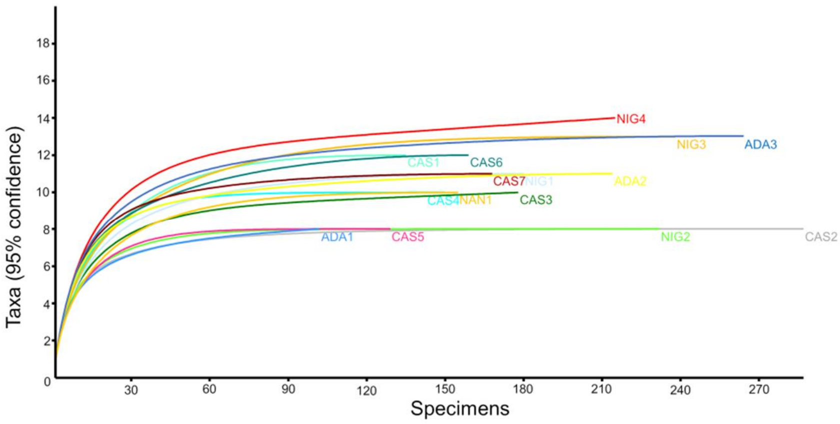

Figure 4. Saturation curves for the diet of the various populations of *Pelusios* spp. analyzed in this paper. NIG = *P. niger*; CAS = *P. castaneus*; ADA = *P. adansonii*; NAN = *P. nanus*. The numbers represent distinct populations within each species. All NIG came from Nigeria; CAS 1-4 from Nigeria, CAS5 from Benin, CAS 6-7 from Togo; ADA 1-3 from South Sudan; and NAN1 from Zambia.

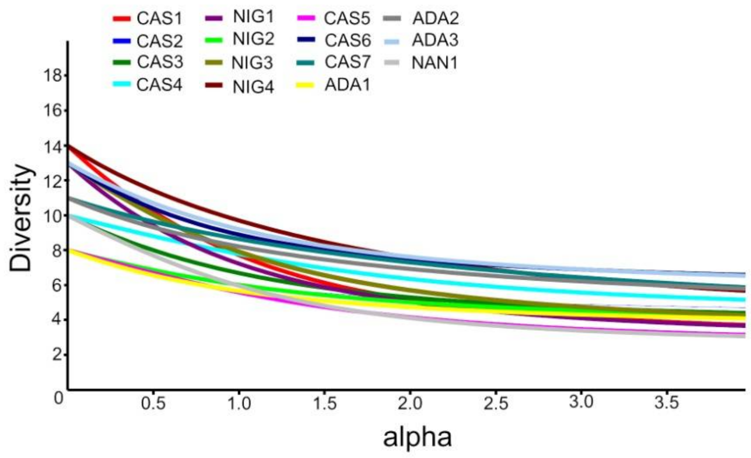

Figure 5. Diversity profiles for the diet of the various populations of *Pelusios* spp. analyzed in this paper. NIG = *P. niger*; CAS = *P. castaneus*; ADA = *P. adansonii*; NAN = *P. nanus*. The numbers represent distinct populations within each species. All NIG came from Nigeria; CAS 1-4 from Nigeria, CAS5 from Benin, CAS 6-7 from Togo; ADA 1-3 from South Sudan; and NAN1 from Zambia.

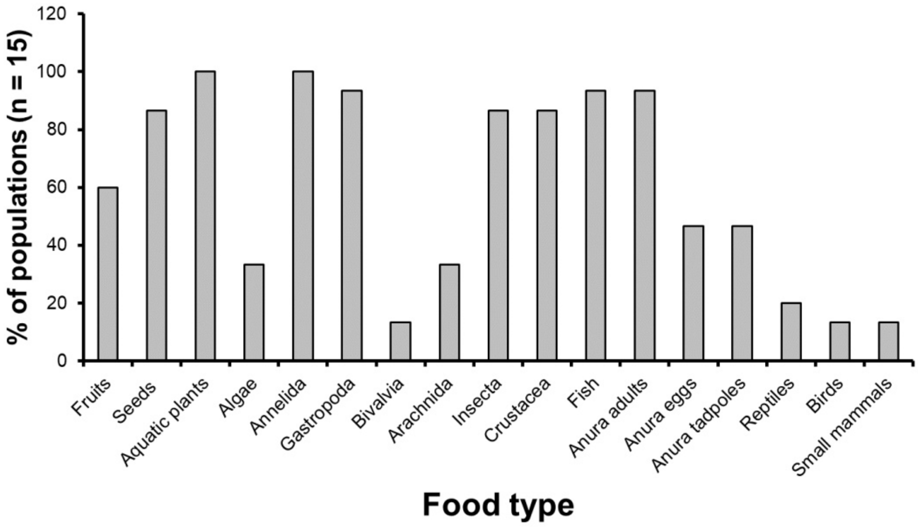

Figure 6. Percentage of *Pelusios* spp. populations that included a given food type in the diet. In this graphic, the percentages are calculated based on the number of populations in which at least one individual in a given population ate a certain type of food compared to the total number of populations examined (n = 15).

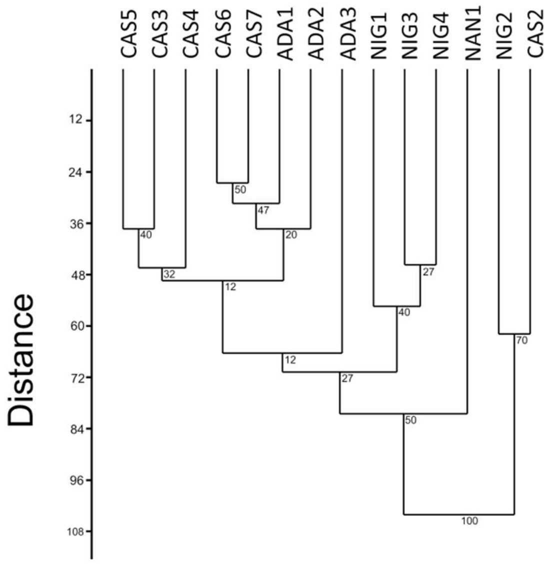

Figure 7. UPGMA, with Euclidean distances and 40 bootstraps as branching measurement, showing the dissimilarities among the various *Pelusios* populations as for their taxonomic composition of the diet is concerned. NIG = *P. niger*; CAS = *P. castaneus*; ADA = *P. adansonii*; NAN = *P. nanus*. The numbers represent distinct populations within each species. All NIG came from Nigeria; CAS 1-4 from Nigeria, CAS5 from Benin, CAS 6-7 from Togo; ADA 1-3 from South Sudan; and NAN1 from Zambia.

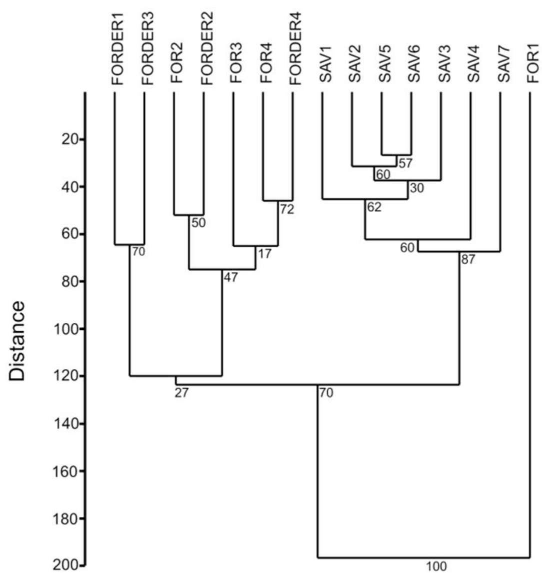

Figure 8. UPGMA, with Euclidean distances and 40 bootstraps as branching measurement, showing the dissimilarities among the main habitats of the various study areas where *Pelusios* FOR = forest; FORDER = forest-derived; SAV = savannah. FOR 1-4 and FORDER 1-4 were from Nigeria; SAV1 from Benin, SAV 2-3 from Togo, SAV 4-6 from South Sudan and SAV 7 from Zambia.

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Table 1. Diet composition (% of stomachs containing a given food item) of *Pelusios* species across countries. N = number of individuals examined; for-derived = forest-derived savannah/plantation mosaic.

	Nigeria	Nigeria	Nigeria	Nigeria	Benin	Togo	Togo	Nigeria	Nigeria	Nigeria	Nigeria	South Sudan	South Sudan	South Sudan	Zambia
	forest	for-derived	forest	for-derived	savannah	savannah	savannah	forest	for-derived	forest	for-derived	savannah	savannah	forest	savannah
	castaneus	*castaneus*	*castaneus*	*castaneus*	*castaneus*	*castaneus*	*castaneus*	*niger*	*niger*	*niger*	*niger*	*adansonii*	*adansonii*	*adansonii*	*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	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
Arachnida	2.8	0	0	0	0	0.74	0.0	2.6	0	0.0	0.0	0.0	0.0	2.6	30.4
Insecta	6	0	12.5	10.6	12.5	31.85	43.9	0.9	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 tadpoles	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	3.9	1.2	0.0	0.0	2.6	0.0
birds	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	0.0	0	0	7.8	9.9	0.0	0.0	0.0	0.0
Indeterminate	0.4	0	0	0	5.36	2.96	3.7	0.9	0	3.9	6.2	3.0	12.2	10.3	5.8

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
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 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.

	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

Supplementary Materials: None.

Author Contributions: For research articles with several authors, a short paragraph specifying their individual contributions must be provided. The following statements should be used "Conceptualization, L.L.; methodology, L.L.; formal analysis, L.L., M.D.V.; investigation, all authors; resources, L.L.; data curation, F.P., D.D.; writing—original draft preparation, L.L.; writing—review and editing, all authors; supervision, L.L., G.C.A., E.A.E.; funding acquisition, L.L., F.P.; All authors have read and agreed to the published version of the manuscript.

Funding: Chelonian Research Foundation, Mohamed Bin Zayed Species Conservation Fund, Conservation International and Turtle Conservation Fund (to L.L. and F.P.)

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data are presented in the paper; additional data are available from authors on request.

Acknowledgments: We thank Prof J. E. Fa, Dr G. H. Segniagbeto, Dr E, M. Hema, and Dr S. Gonedele Bi, for helpful collaboration during the various research phases of this study.

Conflicts of Interest: The authors declare no conflict of interest.

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