

## TROPHIC NICHES OF FOUR SYMPATRIC RAINFOREST ANURANS FROM SOUTHERN NIGERIA: DOES RESOURCE PARTITIONING PLAY A ROLE IN STRUCTURING THE COMMUNITY ?

Edem A. ENIANG<sup>1,2</sup>, Richard KING<sup>2</sup>, Jerry LEA<sup>3</sup>, Dario CAPIZZI<sup>4</sup> & Luca LUISELLI<sup>4</sup>

### RÉSUMÉ

Le partage des ressources est un mécanisme qui peut réduire l'intensité de la compétition interspécifique dans un cortège d'espèces syntopiques, morphologiquement et éco-éthologiquement semblables. La documentation du partage des ressources, entre quatre espèces d'Anoures sympatriques, a été recherchée par l'examen du régime alimentaire (par dissection stomacale) de spécimens obtenus auprès de fournisseurs de viande de brousse dans le sud-est du Nigéria. Pour l'ensemble des quatre espèces, nous avons trouvé au total 32 différents types de proies. *Ptychadena oxyrhynchus* en a consommé 28, contre 17 pour *P. aequiplicata*, 15 pour *Bufo maculatus* et 10 seulement pour *Hoplobatrachus occipitalis*. Pour les courbes cumulatives de diversité des trois premières espèces un plateau a été atteint, montrant que la composition des régimes pouvait être considérée comme correctement établie. Les proies communes, consommées par les quatre espèces d'Anoures, étaient des Formicoidea, des Coléoptères adultes, des Aranéides, des Isopodes, des Oligochètes et des Pulmonés. Les proies communes, consommées par trois des quatre amphibiens, étaient des Dermaptères, des Hémiptères, des Odonates adultes et des Orthoptères. Les largeurs de tête variaient significativement entre les espèces d'Anoures ; toutefois, les deux espèces de *Ptychadena* ne montraient pas de différence significative entre elles sur ce point. Pour trois espèces, la largeur de tête était significativement corrélée au volume de proies dans l'estomac. Le partage des ressources (en termes de types de proies) a été trouvé particulièrement net entre deux espèces de *Ptychadena* étroitement apparentées. La divergence entre *Ptychadena oxyrhynchus* et *P. aequiplicata* apparut telle que des analyses multivariées ont placé chacune d'elles, du point de vue alimentaire, plus près de *Hoplobatrachus occipitalis* ou de *Bufo maculatus* que de son congénère. Une divergence si forte semblerait jouer un rôle majeur dans le maintien de la structure de ce peuplement mixte d'Anoures.

---

<sup>1</sup> Biodiversity Preservation Group, 93 Ndidem Usang Iso Road, P.O. Box 990, Calabar (Cross River State), Nigeria

<sup>2</sup> Department of Forestry and Wildlife, University of Uyo, Uyo (Akwa-Ibom State), Nigeria. E-mail: edemeniang@yahoo.com

<sup>3</sup> Department of Zoology, Delta State University, PMB 1, Abraka (Delta State), Nigeria. E-mail: jerryleainabraka@yahoo.co.uk

<sup>4</sup> Centre of Environmental Studies "Demetra", and F.I.Z.V., via Olona 7, I-00198 Rome, Italy. E-mail: lucamclu@tin.it

## SUMMARY

Resource partitioning is a mechanism that can reduce the intensity of inter-specific competition between morphologically and eco-ethologically similar, syntopic species. Evidence for resource partitioning, between four syntopic anuran species, was investigated by examining the diet (through stomach dissection) of frogs bought from bush meat traders in south-eastern Nigeria. Considering the four species together, a total of 32 different prey types were found. *Ptychadena oxyrhynchus* consumed 28 of them, while *P. aequiplicata* consumed 17, *Bufo maculatus* 15 and *Hoplobatrachus occipitalis* only 10. For the first three species, the cumulative-diversity curves indicated that a plateau phase was reached, i.e. that the prey composition could be considered reliably assessed. Common prey items, which were consumed by all four anuran species, were: Formicoidea, Coleoptera adults, Araneidae, Isopoda, Oligochaeta, and Pulmonata. Common prey items, which were consumed by three of the four amphibians, were: Dermaptera, Hemiptera, Odonata adults, and Orthoptera. Head width varied significantly between species, but there was no statistical difference between the two *Ptychadena* species. Head width was significantly correlated with prey volume in the stomach in each of three species. Resource partitioning (in terms of prey types) was found to be particularly strong between two closely related species of *Ptychadena*. The divergence between *Ptychadena oxyrhynchus* and *P. aequiplicata* was such that multivariate analyses placed each one of them closer in feeding ecology to either *Hoplobatrachus occipitalis* or *Bufo maculatus*, than to their congener. Such strong divergence is hypothesized to play a major role in maintaining the structure of this mixed anuran community.

## INTRODUCTION

Studies on the community structure of tropical frog assemblages have traditionally attracted much attention from scientists, and indeed there are plenty of data available for both Neotropical and Asia-tropical species at either the adult or larval stage (e.g., see Heyer, 1973, 1974, 1976; Heyer & Bellin, 1973; Toft, 1976; Jones, 1982; Neckel-Oliveira *et al.*, 2000, etc). On the other hand, mechanisms underlying the maintenance of community structure of Afrotropical anuran assemblages have received far less attention. The only detailed studies concern wet-savannah communities from the Ivory Coast (Barbault, 1972, 1974a, b, 1976) which, due to the quality of the data collected over many years, have formed the bench-mark for amphibian research in tropical areas. Other Afrotropical amphibian community studies have been conducted in Kenya (Bowker & Bowker, 1979), and general surveys are available for some West African savanna anurans (Rödel, 1999) and for amphibians from the Mount Nimba area of Guinea, Ivory Coast and Liberia (see Lamotte, 1998, and references therein). Data on anuran community ecology in the lowland rainforest areas of West Africa are especially limited, and generally only take the form of preliminary lists of species. Southern Nigeria has been particularly neglected and, apart from a few taxonomic studies (e.g., Schiötz, 1963) and some simple species lists (Romer, 1953; Reid *et al.*, 1990), nothing is known on the ecology and structure of the amphibian communities there; whereas data are available for the reptiles of the region (e.g., Luiselli *et al.*, 1998, 1999; Akani *et al.*, 1999).

In this paper, we present a detailed study on the diet composition of four sympatric frog species at a marsh area of south-eastern Nigeria, situated inside the continuous Guinea-Congo rainforest zone. Our aims are to reveal any patterns of resource partitioning, which could play a major role in maintaining the structure of this community, particularly because of the presence of two syntopic, closely related, morphologically and behaviourally similar species of *Ptychadena* that are

potentially in strong competition with each other. Indeed, in a study system like our own, one might expect resource partitioning because it is a mechanism that reduces the intensity of inter-specific competition and it should occur whenever several morphologically and eco-ethologically similar species are syntopic, except, perhaps, when resources are abundant (e.g., see Barbault, 1981; Pianka, 1986, and references therein).

## MATERIAL AND METHODS

### THE SPECIES

Four species of anurans were found at the study area: three were Ranidae, i.e. *Ptychadena oxyrhynchus* (Smith, 1849), *Ptychadena aequiplicata* (Werner, 1898), *Hoplobatrachus* (= *Dicroglossus*) *occipitalis* (Günther, 1858), and one was Bufonidae, i.e. *Bufo maculatus* (Hallowell, 1954). *Ptychadena oxyrhynchus* is widespread in tropical Africa and is common in south-eastern Nigeria and Cameroon. This species occupies a diverse range of habitats, including forests (Sanderson, 1936; Guibé & Lamotte, 1998), farmbush (Amiet, 1986), savannas (Schiotz, 1963, 1964; Amiet, 1986) and forest clearings (Schiotz, 1964; Lawson, 1993). Although it is a highly aquatic frog, its tremendous jumping ability has enabled it to extend its range beyond the forest sites to the grassy borders of the forest and even to the wide wet savannas (Lamotte, 1998). *Ptychadena aequiplicata*, on the other hand, is more commonly associated with forested areas (Lamotte, 1998); it has been recorded in the Nigeria-Cameroon region, most notably in closed canopy forests (Schiotz, 1964; Perret, 1966; Lawson, 1993) but also in cultivated areas (Sanderson, 1936). *Hoplobatrachus occipitalis* is a large, highly aquatic ranid frog, with a wide distribution across west Africa, occurring in wet savannas (Lamotte, 1998; Rödel, 1999), forests, cultivated areas and around human settlements (Sanderson, 1936); it has also been reported in the very dense forests of south-eastern Nigeria (e.g., in Elem-Sangama, eastern Niger Delta, and in Okwangwo, Cross River National Park; Akani & Luiselli, unpublished data). The single bufonid species, *Bufo maculatus*, is strictly terrestrial, and is found in forests (Perret, 1966), farmbush, derived savannas (Amiet, 1986) and around villages and roads (Lawson, 1993); it is certainly the most common anuran in the south-eastern Nigeria region (Akani *et al.*, unpublished data).

### STUDY AREA

The field study was carried out during the wet season of the year 2001, at a swampy area situated halfway between the towns of Uyo and Ikot-Ekpene (Akwa-Ibom State), in south-eastern Nigeria. The study area was a permanent marsh, at the border between a secondary forest patch and extensive farmland.

## METHODS

All frogs examined in this study were bought from local fishermen when offered for sale in bush-meat markets. They were thus already dead at the time of examination and our study did not require any useless killing or injuring of any individuals. Based on (i) interviews with local sellers, and (ii) personal monitoring of the fishing and hunting activities of local people, we concluded that all the frog specimens used for this study came from a single microhabitat where they were fully sympatric, i.e. the marsh and its vegetated borderline. Each frog was identified to species level, sexed, and dissected. After dissection, the specimens were placed in alcohol and stored as part of a collection at the Biodiversity Preservation Group (Calabar, Nigeria). Head (inter-tympanum) width (mm) of each specimen was measured as a straight line between the middle points of each tympanic membrane. Snout-vent-length was significantly correlated with width in all species (in all cases, at least  $r > 0.97$ ,  $P < 0.00001$ ). Thus we used only head width as operative measure to correlate prey size with predator size. Frog stomachs were individually fixed in alcohol and given a reference number to link them to the specimens, from which they came. Stomachs were then taken to the laboratory, dissected, and the prey items were spread out into Petri dishes and examined using a dissecting microscope. Food items were identified to the lowest taxon possible and their lengths and widths were measured when feasible, using an optical micrometer. Later, individual food volumes were estimated with the formula for a prolate spheroid (Vitt & Morato de Carvalho, 1992; Gadsen *et al.*, 2001).

Statistical analysis was done using SPSS (version for Windows); all tests were two tailed and alpha was set at 5 %. Non-parametric tests were used for non-normally distributed data and both univariate and multivariate analyses were employed to look for differences in trophic ecology between species and between sexes (within species) (cf. Digby & Kempton, 1987). For assessing whether taxonomic diet composition of each species was reliably assessed (i.e. to avoid that inter-specific comparisons may be spurious and biased by the effect of the sample size), species-specific cumulative-diversity curves were elaborated (see Magurran, 1988).

## RESULTS

### INTER-SPECIFIC COMPARISONS

In total, we examined the stomach contents of 177 specimens, but 25 of these had empty stomachs (17 *P. oxyrhynchus*, 5 *P. aequiplicata* and 3 *B. maculatus*). The frequency of specimens with empty stomachs was significantly greater for *P. oxyrhynchus* than for *P. aequiplicata* or *B. maculatus* ( $\chi^2$  test with  $df = 2$ ,  $P < 0.02$ ); this comparison was not done with *H. occipitalis*, because of the small sample for this species. There were 152 specimens that contained at least one identified prey item, which comprised 67 (36 males, 31 females) *P. oxyrhynchus*, 50 (29 males, 21 females) *P. aequiplicata*, 32 (18 males, 14 females) *B. maculatus* and 3 (2 males, 1 female) *H. occipitalis*. It is likely that the numbers of specimens examined reflect the relative abundance of the four species in the field. Indeed, local people sell *H. occipitalis* for a much higher price than the other three species, due to

their larger size and their relative scarcity (which makes them an attractive delicacy).

Considering the four species together, we found a total of 32 different prey type categories. *P. oxyrhynchus* consumed 28 out of the 32 prey types, while *P. aequiplicata* consumed 17, *B. maculatus* 15 and *H. occipitalis* consumed only 10 different types of prey. For the first three species, the cumulative-diversity curves indicated that a plateau phase was reached, i.e. that the prey composition was reliably assessed (Fig. 1). For *H. occipitalis* the same analysis was not done due to the too small sample examined. The frequency of consumption of the various prey types differed significantly from an equal sample in the four species ( $\chi^2$  test with  $df = 3, P < 0.005$ ), with *P. oxyrhynchus* clearly being the most generalist of the four predators. A breakdown of the data into prey type categories eaten by each predator species is presented in Table I. It shows the number of specimens of each species of predator that was recorded having eaten each prey item. It also shows the total number of specimens (combining the four predator species) in which each prey item was recorded. In this table, for each prey category, the data are independent, but one individual predator may contribute data to more than once because it ate more than one category of prey. The list of prey categories which were not eaten by each of the four anuran species are presented in Table II. Common prey items, which were consumed by all four predator species, were: Formicoidea, Coleoptera adults, Araneidae, Isopoda, Oligochaeta, and Pulmonata. Common prey items, which were consumed by three of the four predator types, were: Dermaptera, Hemiptera, Odonata adults, and Orthoptera. If we consider the nine most frequent prey types (across species) and apply Fisher exact tests to the proportion of stomachs containing a given prey type (Table III), and we then put these nine categories into a PCA, we can use the scores as a diet summary. The first row axes summarise 33.6 % of the overall variance; looking at the factor pattern, high scores on PCA 1 describe stomachs tending not to contain Diptera or Formicoidea, whereas high scores on factor 2 mean Formicoidea and Araneidae. The resulting plot (Fig. 2) shows quite a nice distinction between the two species of *Ptychadena* and *Bufo maculatus* on factor 1, and between both of these and the other one on factor 2 (the latter is not statistically significant).

The data in Table II clearly show the much wider choice of prey items consumed by *P. oxyrhynchus* compared to *P. aequiplicata*, even though the sample sizes of the two predators were similar (see above). Moreover, it is also clear that the extra prey categories consumed by *P. oxyrhynchus* and not by *P. aequiplicata* are not an artefact of the sample examined, i.e. not the result of one aberrant *P. oxyrhynchus* individual that consumed a lot of different prey species. This is shown by the data in parentheses in column two of the table, which indicates how many *P. oxyrhynchus* individuals were recorded as having eaten each prey type not consumed by *P. aequiplicata*.

Based on the similarity in taxonomic dietary composition (i.e., proportions of prey types found in a given stomach), a multivariate cluster analyses (Un-weighted Pair-Group Analysis based on Arithmetic Means) tree-diagram, with percent disagreement as linkage distances, demonstrated that the two species of *Ptychadena* are very different from one another despite their similarity in size, morphology, and systematic position (Fig. 3). Nonetheless, one of the two species, *P. aequiplicata*, was similar to *H. occipitalis*, which may be related to the fact that they are both highly aquatic species. The two species of *Ptychadena* were also classified as very different from each other in a PCA factorial plan (standardized VARIMAX rotated

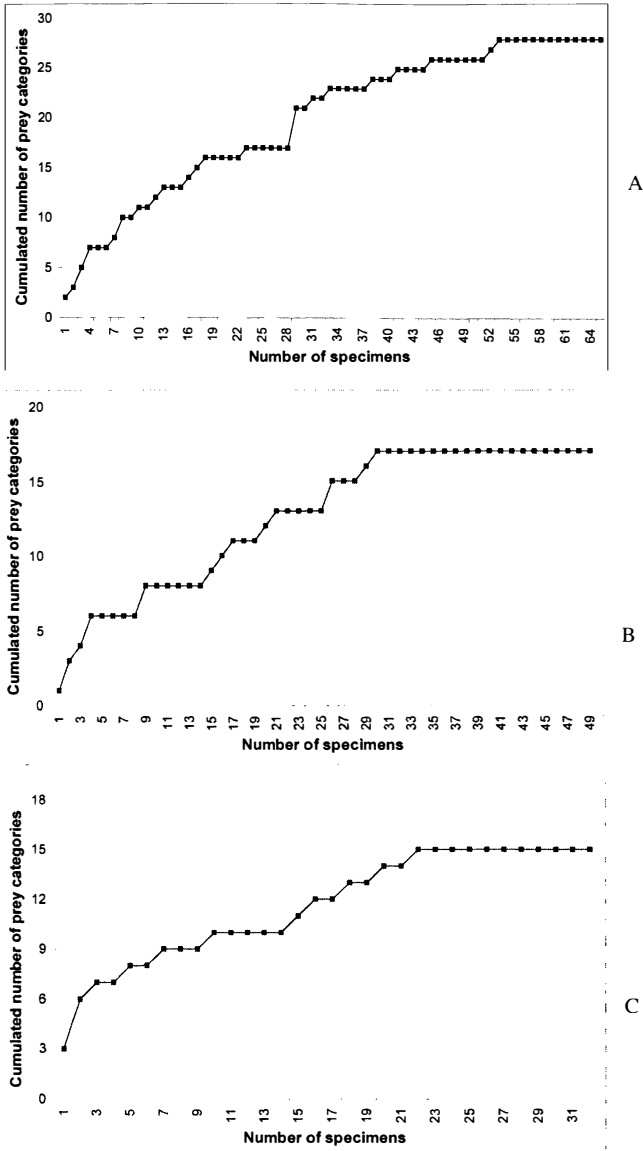


Figure 1. — Plot showing numbers of frog specimens from which stomachs were examined against cumulative number of prey categories identified from their stomachs. Note that a plateau phase was obtained for all the three species. Graphic A = *Ptychadena oxyrhynchus*; Graphic B = *P. aequiplicata*; Graphic C = *Bufo maculatus*.

TABLE I

Summary of the diet composition of the four predator species at the study area. Numbers represent the number of predator specimens that ate each prey type, and not the total number of prey items in the stomachs

Prey Type	Number of Predators Containing Each Prey Item				
	<i>Ptychadena oxyrhynchus</i>	<i>Ptychadena aequiplicata</i>	<i>Bufo maculatus</i>	<i>Hoplobatrachus occipitalis</i>	Total
INVERTEBRATES					
Oligochaeta	4	2	8	2	16
Pulmonata	2	1	6	1	10
Scorpiones	1	0	1	0	2
Opilionida	3	0	3	0	6
Lithobiidae	0	0	1	0	1
Miriapoda	1	1	0	0	2
Chilopoda	2	0	1	0	3
Araneidae	4	3	4	1	12
Salticidae	2	0	0	0	2
Formicoidea	10	4	11	1	26
Apoidea	2	3	0	0	5
Vespoidea	2	2	0	0	4
Coleoptera (larvae)	1	2	0	0	3
Coleoptera (adults)	9	29	9	1	48
Collembola	1	0	0	0	1
Dermaptera	5	4	1	0	10
Diptera	18	4	0	0	22
Hemiptera	5	4	1	0	10
Ephemeroptera	2	0	0	0	2
Gastropoda	1	0	0	0	1
Gerridae	1	2	0	0	3
Homoptera	1	0	0	0	1
Isoptera	7	4	3	1	15
Lepidoptera (adults)	3	0	0	0	3
Lepidoptera (larvae)	1	0	1	0	2
Odonata (adults)	8	1	0	1	10
Orthoptera	4	3	1	0	8
VERTEBRATES					
Anuran tadpoles	0	0	0	2	2
<i>P. oxyrhynchus</i>	0	0	0	1	1
Anuran eggs	0	0	0	1	1

model) based on the similarities between species in terms of prey taxa which were not eaten, despite being available in the field (Fig. 4). In this analysis, *P. aequiplicata* was classified as similar to *B. maculatus*, whereas the other two species were arranged in completely separate positions. This is relatively surprising because *B. maculatus* is a ground-dwelling terrestrial species, whereas *P. aequiplicata* is highly aquatic (Lamotte, 1998). The scores of preys on factors are presented in Table IV.

Computing a discriminant analysis on dietary features of the three anurans, we obtained two statistically significant functions (Function 1: eigenvalue: 0.412; canonical correlation: 0.586; Wilk's  $\lambda$ : 0.919;  $\chi^2 = 39.143$ ,  $P < 0.0002$ ; Function 2: eigenvalue: 0.178; canonical correlation: 0.399; Wilks'  $\lambda$ : 0.802;  $\chi^2 = 15.82$ ,

TABLE II

Summary of the data on the prey categories which were NOT consumed by each predator type. Numbers in parentheses in the second column indicate how many *P. oxyrhynchus* individuals were recorded as having eaten each prey type not consumed by *P. aequiplicata*. Based on these numbers, it can be seen that the extra prey categories consumed by *P. oxyrhynchus* and not by *P. aequiplicata* are not an artefact of the sample examined, i.e. not the result of one aberrant *P. oxyrhynchus* individual that simply consumed a lot of different prey species

<i>Ptychadena oxyrhynchus</i> did not consume...	<i>Ptychadena aequiplicata</i> did not consume... (# of <i>P. oxyrhynchus</i> individuals that ate the prey item)	<i>Bufo maculatus</i> did not consume...	<i>Hoplobatrachus occipitalis</i> did not consume...
		Apoidea	Apoidea
	Chilopoda (2)		Chilopoda
		Coleoptera larvae	Coleoptera larvae
	Collembola (1)	Collembola	Collembola
			Dermoptera
		Diptera	Diptera
		Hemiptera	Hemiptera
	Ephemeroptera (2)	Ephemeroptera	Ephemeroptera
	Gastropoda (1)	Gastropoda	Gastropoda
		Gerridae	Gerridae
	Homoptera (1)	Homoptera	Homoptera
	Isoptera (1)		Isoptera
	Lepidoptera adults (3)	Lepidoptera adults	Lepidoptera adults
	Lepidoptera larvae (1)		Lepidoptera larvae
Lithobiidae	Lithobiidae (0)		Lithobiidae
		Miriapoda	Miriapoda
		Odonata adults	
	Opilionida (3)		Opilionida
			Orthoptera
	Salticidae (2)	Salticidae	Salticidae
	Scorpiones (1)		Scorpiones
		Vespoidea	Vespoidea
Anuran tadpoles	Anuran tadpoles (0)	Anuran tadpoles	
<i>P. oxyrhynchus</i>	<i>P. oxyrhynchus</i> (0)	<i>P. oxyrhynchus</i>	
Anuran eggs	Anuran eggs (0)	Anuran eggs	



TABLE III

Statistical details of Fisher exact test applied on the proportion of stomachs of the four anuran species containing a given prey type. This analysis is made across species, and after ignoring the very rare food items.

PREY TYPE		KW TEST	FISHER
	$\chi^2$	P	P
OLIGOCHAETA	11.6	0.003	0.001
PULMONATA	11.6	0.003	0.001
ARANEIDAE	1.7	0.43	0.47
ISOPODA	0.2	0.90	1.00
FORMICOIDEA	11.8	0.003	0.001
COLEOPTERA	25.4	0.001	0.001
DIPTERA	15.3	0.001	0.001
ODONATA	7.6	0.022	0.03
DERMAPTERA	0.77	0.68	0.77

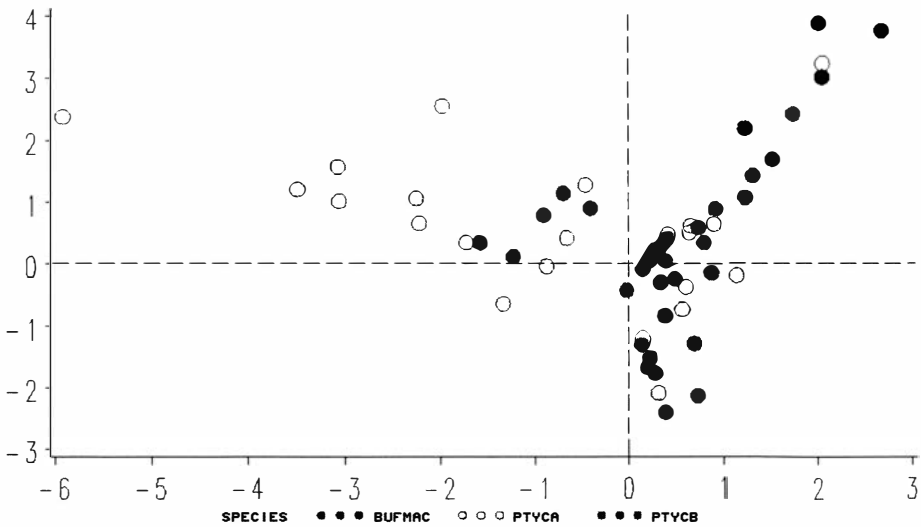


Figure 2. — Factorial plan of a Principal Component Analysis (PCA) on the similarities across anuran species, based on the proportion of specimens containing a given prey type, including in the analysis only the nine most abundant prey types, selected after Fisher exact test across species. Abbreviations: *PtycA* = *P. oxyrhynchus*; *PtycB* = *P. aequiplicata*.

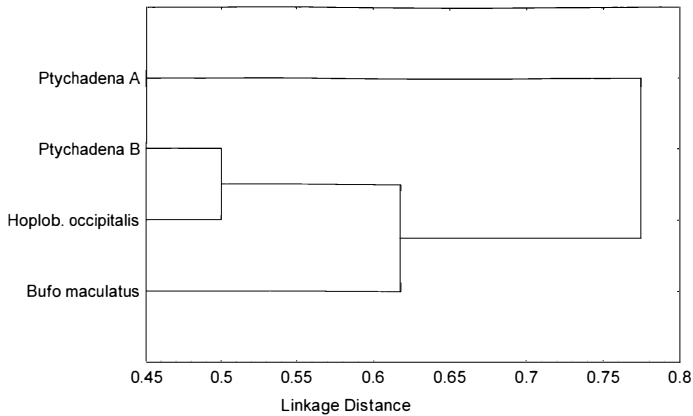


Figure 3. — UPGMA tree-diagram, with percent disagreement as linkage distances, of the similarity between sympatric frog species in terms of taxonomic dietary composition. Note that the two species of *Ptychadena* were very different from each other despite similarities in size, morphology, and systematic position. Abbreviations: *Ptychadena A* = *P. oxyrhynchus*; *Ptychadena B* = *P. aequiplicata*.

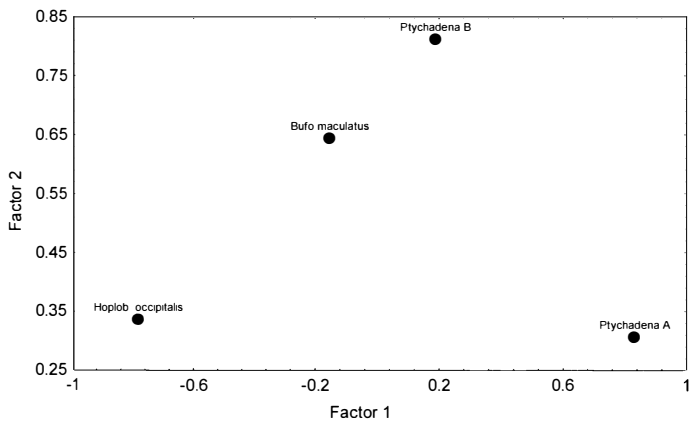


Figure 4. — Factorial plan of Principal Component Analysis (standardized VARIMAX rotated model) on the similarities between sympatric frog species in terms of prey taxa which were not eaten, despite being available in the field. Note that, also in this case, the two species of *Ptychadena* were classified as very different from each other despite similarities in size, morphology, and systematic position. Abbreviations: *Ptychadena A* = *P. oxyrhynchus*; *Ptychadena B* = *P. aequiplicata*.

$P < 0.03$ ). On the other hand, stepwise discriminant function analysis indicated that the dietary compositions for males and females were not significantly different in any species (*P. oxyrhynchus*: eigenvalue: 0.088; canonical correlation: 0.128; Wilks'  $\lambda$ : 0.097;  $\chi^2 = 2.006$ ,  $df = 1$ ,  $P = 0.236$ ; *P. aequiplicata*: eigenvalue: 0.096; canonical correlation: 0.133; Wilks'  $\lambda$ : 0.102;  $\chi^2 = 2.326$ ,  $df = 1$ ,  $P = 0.07$ ; *B. maculatus*: eigenvalue: 0.092; canonical correlation: 0.129; Wilks'  $\lambda$ : 0.092;  $\chi^2 = 1.998$ ,  $df = 1$ ,  $P = 0.08$ ).

Mean head widths (mm) were: *P. oxyrhynchus* = 10.9, *P. aequiplicata* = 11.0, *B. maculatus* = 26.8, *H. occipitalis* = 27.5. Head width varied significantly between species (ANOVA:  $F_{3,148} = 473.3, P < 0.001$ ), but there was no statistical difference between the two *Ptychadena* species (ANOVA:  $F_{1,115} = 0.18, P > 0.05$ ). Head width was significantly correlated with prey volume in the stomach in each of three species (in all the three species, Spearman's  $r > 0.456, P < 0.01$ ); *H. occipitalis* was excluded from this analysis due to the small sample size.

TABLE IV

*Scores of prey types on factors of a Principal Component Analysis (standardized VARIMAX rotated model) on the similarities between sympatric frog species in terms of prey eaten*

Prey type	Factor 1	Factor 2
Formicoidea	2.17617	0.68897
Apoidea	0.31511	-1.24100
Araneidae	0.81962	0.15572
Chilopoda	0.11909	-1.05764
Coleoptera (larv.)	0.02534	-1.07318
Coleoptera (ad.)	3.36298	0.99975
Collembola	-0.19685	-0.98382
Dermaptera	0.48708	-0.85016
Diptera	1.53533	-1.09698
Orthoptera	0.24106	-0.73631
Ephemeroptera	-0.28063	-0.78312
Gastropoda	-0.41557	-0.71396
Gerridae	-0.32461	-0.64140
Miriapoda	-0.43570	-0.59672
Homoptera	-0.54680	-0.55204
Isoptera	0.31366	0.62970
Scorpiones	-0.54078	-0.34080
Lepidoptera (ad.)	-0.49564	-0.42050
Lepidoptera (larv.)	-0.62826	-0.23285
Lithobiidae	-0.76320	-0.16369
Odonata	-0.11174	0.63471
Oligochaeta	0.28700	2.54506
Opilionida	-0.43384	0.15924
Pulmonata	-0.22907	1.50755
Vespoidea	-0.80209	0.04506
Anuran tadpoles	-1.09177	1.92282
<i>Ptychadena</i>	-1.17109	1.07080
Anuran eggs	-1.21483	1.12477

#### INTRA-SPECIFIC (INTER-SEXUAL) COMPARISONS

*H. occipitalis* was excluded from all intra-specific (i.e. inter-sexual) analyses due to the small sample size. For the other three species, taxonomic diet composition was similar between the sexes ( $P > 0.211$  in all cases,  $\chi^2$  test with  $df = 1$ ) and there were no significant inter-sexual differences in terms of prey categories which were not consumed by each sex ( $P > 0.186$  in all cases,  $\chi^2$  test with  $df = 1$ ).

## DISCUSSION

The study of community organization and the interaction between species has been a prominent issue of modern ecology for some time. Many studies have, however, been plagued by an “epistemological misdirection” towards equilibrium hypotheses (*sensu* Barbault, 1991), where snapshots in space and time of given assemblages have been considered as reliable indicators of that community's organization. That is to say, the role of physical factors and of spatial and temporal variability in the dynamics of natural communities has been underestimated (e.g., see Wiens, 1977; Schoener, 1986; Barbault, 1991). The present study is certainly affected by the same shortcomings, and these theoretical limitations should be taken into account when interpreting our results. One other limitation of this study is the lack of data concerning the availability of the various prey types in the field, and so we cannot say anything about whether our study species consume insects (and other invertebrates) in the proportions in which they occur in the environment. Nonetheless, our study has certainly revealed some remarkable patterns in the relationships between the trophic niches of the frogs of our study area.

The main patterns emerging from our study are that the various species clearly partition the available food sources, but there is no obvious resource partitioning between the sexes (within species). So, while intra-specific competition has probably no notable influence, inter-specific competition appears to play a major role in maintaining the structure of this community (this is assuming that food resource partitioning occurs as a direct consequence of competition, i.e. as a result of the pressure to reduce inter-specific overlap). Nonetheless it is obvious that these general statements may be partially inaccurate without prey-availability data, and thus more research is needed on this issue. It is particularly noteworthy that the two *Ptychadena* species, which are theoretically the greatest competitors due to similarities in morphology, size, and ecology (Lamotte, 1998), show the most obvious resource partitioning. *P. oxyrhynchus* is much more of a generalist feeder than *P. aequiplicata* (Table I) and is seen to consume many prey items which were rarely or never eaten by *P. aequiplicata* (Table II). It is indeed remarkable that, considering many variables in our multivariate analyses, each of the two *Ptychadena* species was more similar to one of the unrelated species (*Bufo* and *Hoplobatrachus*, which differ in morphological and eco-ethological traits) than to their congener. We consider this to be further indirect evidence of a strong divergence between the two *Ptychadena*, thus giving support to the hypothesis that inter-specific resource partitioning plays a major role in maintaining the structure of this anuran community. Considering that one species (*P. oxyrhynchus*) is known to occupy a wider variety of habitats (from forests to farmbrush, including also savannas and forest clearings) than the other (*P. aequiplicata*) (forest areas, mostly with closed canopy), it may be suggested that the wider variety of habitats in which *P. oxyrhynchus* may be found could, in turn, provide a wider variety of prey than for *P. aequiplicata*, with a more restricted habitat selection. Thus rather than a pattern of food resource partitioning, the coexistence of these two species might be regulated instead by a pattern of different habitat selection. Although this latter hypothesis is interesting, we are led to think it is wrong. Indeed, at the study area these species inhabit exactly the same micro-habitat, are obviously semi-aquatic, are active at the same hours of day, and thus certainly cannot have a different habitat selection pattern (Politano, 1998).

As to why there appears to be no major inter-sexual differences in diet composition in any of the four studied species, we can give no firm answers. One might

expect to find such differences in species where there is a great disparity in nutrient requirements between the sexes (e.g. cheap sperm and nutritious eggs) or, as a result of any differences in body size or microhabitat selection between the sexes (e.g. see Barbault, 1981). Presumably, therefore, none of these factors play an important role in our anuran community, although the females of our study species are often larger than the males (e.g. in *Bufo maculatus*).

Barbault's studies (1974a, b, 1976, 1991) demonstrated that factors other than competition are important in organizing Afrotropical communities of frogs, e.g. predation pressure, which is certainly high in our study area given the relative abundance of anuran-eating snakes (Luiselli *et al.*, 1998). These additional factors were not, however, investigated in the present paper. Our data are clearly only a "snap-shot" of the frogs' diets in space and time, and there is probably much individual variation that we have not accounted for. We are therefore not certain that the significant inter-specific differences observed here represent resource partitioning as a mechanism of coexistence and community structure. Indeed, even random differences among individuals and species may produce this type of diet differentiation. We therefore require additional data on behavioural interactions, and surveys from other field sites, to help confirm or refute our hypothesis. Our study did demonstrate, however, that prey volume is positively correlated with predator head size, and this can be taken as further indirect evidence that body size differences might reduce competition intensity among sympatric species (Pianka, 1986).

Finally, we suggest that future studies on Afrotropical amphibian communities should account for variation among prey categories in their relative volume contribution to the diet, this is because all competition models are based on energy harvest data and not on numerical diet data. Moreover, even in the presence of good volumetric data, the development of some sort of null model would be of great analytical benefit (Winemiller & Pianka, 1990).

## ACKNOWLEDGEMENTS

LL is gratefully indebted to the following companies for supporting his long-term ecological research in Nigeria: "AGIP S.p.A." (Rome), "T.S.K.J. Nigeria Ltd." (Port Harcourt and Lagos), "Ecosystem s.r.l." (Bari), "Aquater s.p.a." (Rome and San Lorenzo in Campo), "Amertex Oil and Gas Ltd." (Lagos), "Demetra s.r.l." (Rome and Fano), and "F.I.Z.V." (Rome). Part of this research was also helped by grants received by LL from "Chelonian Research Foundation" (Linnaeus Funds, years 1999 and 2000) and "IUCN/SSC Declining Amphibian Populations Task Force" (Annual Seed Grant, years 2000-2001). We are gratefully indebted to Dr. Paul Johnson (WildCRU, Zoology Dept. Oxford University) for having also contributed to the data analysis, to Prof. Philippe Lebreton (Claude Bernard University, Lyon), Prof. Christian Erard (MNHN, Brunoy), and anonymous referees, for helpful critical comments on the submitted draft.

## REFERENCES

- AKANI, G.C., BARIENE, I.F., CAPIZZI, D. & LUISELLI, L. (1999). — Snake communities of moist rainforest and derived savannah sites of Nigeria: biodiversity patterns and conservation priorities. *Biodiversity and Conservation*, 8: 629-642.
- AMIET, J.-L. (1986). — La batrachofaune sylvoicole d'un secteur forestier du Cameroun: la région de Yaoundé. *Mém. Mus. Nat. Hist. Nat. Paris, Zool.*, 132 : 29-42.

- BARBAULT, R. (1972). — Les peuplements d'Amphibiens des savanes de Lamto (Côte d'Ivoire). *Ann. Univ. Abidjan, sér. E*, 5 : 61-142.
- BARBAULT, R. (1974a). — Le régime alimentaire des Amphibiens des savanes de Lamto (Côte d'Ivoire). *Bull. IFAN, sér. A*, 36 : 952-972.
- BARBAULT, R. (1974b). — Observations écologiques dans la savane de Lamto (Côte d'Ivoire) : structure de l'herpétocénose. *Bull. Ecol.*, 5 : 7-25.
- BARBAULT, R. (1976). — Structure et dynamique d'un peuplement d'Amphibiens en savane protégée du feu (Lamto, Côte d'Ivoire). *Rev. Ecol. (Terre Vie)*, 30 : 246-263.
- BARBAULT, R. (1981). — *Ecologie des populations et des communautés*. Masson, Paris.
- BARBAULT, R. (1991). — Ecological constraints and community dynamics: linking community patterns to organismal ecology. The case of tropical herpetofaunas. *Acta Oecol.*, 12 : 139-163.
- BOWKER, R.G. & BOWKER, M.H. (1979). — Abundance and distribution of anurans in a Kenyan pond. *Copeia*, 1979: 278-285.
- DIGBY, P.G.N. & KEMPTON, R.A. (1987). — *Multivariate analysis of ecological communities*. Chapman & Hall, London.
- ENIANG, E.A. & LUISELLI, L. (2002). — Ikpan wetland rainforest: an area of high biodiversity importance in south-eastern Nigeria. *Rev. Ecol. (Terre Vie)*, 57: 19-28.
- GADSEN, H., PALACIOS-ORONA, L.E. & CRUZ-SOTO, G.A. (2001). — Diet of the Mexican Fringe-Toed Lizard (*Uma exsul*). *J. Herpetol.*, 35: 493-496.
- GUIBÉ, J. & LAMOTTE, M. (1958). — Les *Ptychadena* (Batraciens, Ranidés) du Cameroun. *Bull. IFAN, sér. A*, 20 : 1448-1463.
- HEYER, W.R. (1973). — Ecological interactions of frog larvae at seasonal tropical location in Thailand. *J. Herpetol.*, 7: 337-372.
- HEYER, W.R. (1974). — Niche measurements of frog larvae from a seasonal tropical location in Thailand. *Ecology*, 55: 651-656.
- HEYER, W.R. (1976). — Notes on the frog fauna of the Amazon Basin. *Acta Amazonica*, 6: 369-378.
- HEYER, W.R. & BELLIN, M.S. (1973). — Ecological notes on five sympatric *Leptodactylus* (Amphibia, Leptodactylidae) from Ecuador. *Herpetologica*, 29: 66-72.
- JONES, K.L. (1982). — Prey patterns and trophic niche overlap in four species of Caribbean frogs. Pp. 49-55, in: N.J. Scott Jr. (ed.), *Herpetological communities*. U.S. Department of the Interior, Fish and Wildlife Service, Washington D.C.
- LAMOTTE, M. (1998). — Panorama d'une faune ouest-africaine d'amphibiens : le peuplement du mont Nimba. *Bull. Soc. Herp. France*, 87-88 : 5-23.
- LAWSON, D.P. (1993). — The reptiles and amphibians of the Korup National Park Project, Cameroon. *Herpetol. Nat. Hist.*, 1: 27-90.
- LUISELLI, L. & AKANI, G.C. (2002). — An investigation into the composition, complexity and functioning of snake communities in the mangroves of south-eastern Nigeria. *Afr. J. Ecol.*, 40: 220-227.
- LUISELLI, L., AKANI, G.C. & CAPIZZI, D. (1998). — Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria. *J. Zool., London*, 246: 125-133.
- LUISELLI, L., AKANI, G.C. & CAPIZZI, D. (1999). — Is there any interspecific competition between dwarf crocodiles (*Osteolaemus tetraspis*) and Nile monitors (*Varanus niloticus ornatus*) in the swamps of central Africa? A study from south-eastern Nigeria. *J. Zool., London*, 247: 127-131.
- MAGURRAN, A.E. (1988). — *Ecological diversity and its measurement*. Croom Helm, London.
- NECKEL-OLIVEIRA, S., MAGNUSSON, W.E., LIMA, A.P. & ALBERNAZ, A.L.K. (2000). — Diversity and distribution of frogs in an Amazonian savanna in Brazil. *Amphibia-Reptilia*, 21: 317-326.
- PERRET, J.-L. (1966). — Les Amphibiens du Cameroun. *Zool. Jahrb. (Abt. Syst. Ökol. Geogr. Tiere)*, 93 : 289-464.
- PIANKA, E.R. (1986). — *Ecology and natural history of desert lizards*. Princeton University Press, Princeton.
- POLITANO, E. (1998). — *A study of the fauna (Amphibia, Reptilia, Aves, Mammalia) of the eastern Niger Delta and environmental assessment of LNG Bonny project*. Aquater Press, San Lorenzo in Campo.
- REID, J.C., OWENS, A. & LANEY, R. (1990). — Records of frogs and toads from Akwa Ibom State. *Nigerian Field*, 55: 113-128.
- RÖDEL, M.-O. (1999). — *The Amphibians of West African Savanna*. Editions Chimaira, Frankfurt-am-Main.
- ROMER, J.D. (1953). — Reptiles and amphibians collected in the Port-Harcourt area of Nigeria. *Copeia*, 1953: 121-123.

- SANDERSON, I.T. (1936). — The amphibians of the Mamfe Division, Cameroons. II. Ecology of the frogs. *Proc. zool. Soc. Lond.*, 1936: 165-208.
- SCHIOTZ, A. (1963). — The amphibians of Nigeria. *Vidensk. Medd. Dansk. Naturh. Foren. Kbh.*, 125: 1-92.
- SCHIOTZ, A. (1964). — The voices of some West African amphibians. *Vidensk. Medd. Dansk. Naturh. Foren. Kbh.*, 127: 35-83.
- SCHIOTZ, A. (1999). — *Treefrogs of Africa*. Editions Chimaira, Frankfurt-am-Main.
- SCHOENER, T.W. (1986). — Mechanistic approaches to community ecology: a new reductionism? *Am. Nat.*, 126: 633-641.
- TOFT, C.A. (1976). — *Partitioning of food in a community of tropical frogs*. Ph.D. Thesis, University of Princeton, New Jersey.
- VITT, L.J. & MORATO DE CARVALHO, C. (1992). — Life in the trees: the ecology and life history of *Kenotropyx striatus* (Teiidae) in the Lavrado area of Roraima, Brazil, with comments on the life histories of tropical teiid lizards. *Can. J. Zool.*, 70: 1995-2006.
- WIENS, J.A. (1977). — On competition and variable environments. *Am. Sci.*, 65: 590-597.
- WINEMILLER, K.O. & PIANKA, E.R. (1990). — Organization in natural assemblages of desert lizards and tropical fishes. *Ecol. Monogr.*, 60: 27-55.