FOOD HABITS AND RESOURCE PARTITIONING OF CARNIVORES (HERPESTIDAE, VIVERRIDAE) IN THE RAINFORESTS OF SOUTHEASTERN NIGERIA: PRELIMINARY RESULTS

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RÉSUMÉ

Le régime alimentaire de quatre espèces de Carnivores (*Herpestes ichneumon, Atilax paludinosus, Civettictis civetta, Genetta maculata*) a été étudié dans la zone de forêt continue du sud du Nigéria. Les contenus stomacaux de 29 *H· ichneumon*, 29 *A. paludinosus*, 27 *C. civetta* et 22 *G. maculata* ont été analysés. La proportion de tubes digestifs vides a varié entre 9 et 17 %, sans différence significative entre les espèces. *H· ichneumon* est apparu essentiellement comme un consommateur de mammifères, *A. paludinosus* comme un mangeur d'invertébrés tandis que *C. civetta* et *G. maculata* basent leur alimentation à la fois sur les mammifères et les invertébrés. En termes de largeur de niche écologique, *C. civetta* et *G. maculata* apparaissent fort similaires ; en revanche, *H. ichneumon* et *A. paludinosus* diffèrent à la fois entre eux et des deux autres espèces. En particulier, *A. paludinosus* s'avère plus spécialisé que les autres prédateurs. Cela reflète la position phylogénétique des espèces : les deux premières étant des Viverridés, les deux autres des Herpestidés. L'analyse en composantes principales des données du régime alimentaire montre que *H. ichneumon* et *G. maculata* sont très proches sur la dimension alimentaire de leur niche mais sont séparés des deux autres qui diffèrent entre eux. Le contexte écologique général de la coexistence de ces espèces au sein de l'écosystème forestier ombrophile d'Afrique tropicale est également discuté.

SUMMARY

The diets of four carnivores species (*Herpestes ichneumon, Atilax paludinosus, Civettictis civetta, Genetta maculata*) were studied in the continued forest zone of southern Nigeria. 29 stomachs of *H. ichneumon,* 29 of *A. paludinosus,* 27 of *C. civetta*, and 22 of *G. maculata* were examined. The numbers of empty stomachs varied from 9 % to 17 %, and did not differ significantly amongst species. *H· ichneumon* proved to be primarily mammalophagous. *A. paludinosus* was an "invertebratophagous" species, whereas *C. civetta* and *G. maculata* fed essentially on both invertebrates and mammals. The niche breadths of *C. civetta* and *G. maculata* were quite similar, whereas the niche positions of *H. ichneumon* and *A. paludinosus* were very different from those of the two former species and from each other. In particular, *A. paludinosus* was more specialized than any other predator. This evidence mirrors the phylogenetic position of the various species, as the former two *taxa* are Viverridae and the latter two species are Herpestidae. From Principal Component Analysis of the dietary data, it resulted that *H. ichneumon* and *G. maculata* are very similar in terms of

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dietary niche, and differ from the other two species which are also very different from each other. The general ecological context of the coexistence of these species in the rainforest ecosystem of tropical Africa is also discussed.

INTRODUCTION

Rainforest habitats in tropical Africa are no doubt the richest of all the African habitats in terms of biological diversity at the levels of either carnivorous or herbivorous species communities (Barbault, 1991). Thus, it is generally recognized that the complexity of coexisting animal communities tends to be very high in these Afrotropical environments (e.g. see Ricklefs, 1979). During the recent years, a considerable effort has been done to understand the mechanisms of coexistence among sympatric African forest predators, e.g. snakes, monitor lizards, and crocodiles (Luiselli *et al.*, 1998, 1999). However, the mechanisms of coexistence of other crucial predators, e.g. the small sized forest carnivores, remained much less investigated (but see MacDonald & Nel, 1986; Ray, 1997, 1998).

The rainforests of southern Nigeria are still characterized by a remarkable carnivore diversity (Angelici *et al.*, 1998, 1999, in press a), and thus could represent ideal field laboratories to study the food relationships between these species which could be possibly competitors. However, most of the carnivorous mammals of Nigeria are nearly unknown in terms of ecology and natural history (e.g. see Happold, 1987; Angelici *et al.*, 1998, 1999), and nothing of quantitative is known to date. In particular, species of the families Herpestidae, Mustelidae, and Viverridae are very little known even in terms of distribution, habitat preferences, and taxonomic status (cf. Angelici *et al.*, 1999). In contrast, knowledge of the natural history of these small to medium sized carnivores in other regions of the African continent is relatively good (cf. Skinner & Smithers, 1990; Ray, 1997, and references therein), although information available on foraging behaviour and feeding tactics is still scant and anecdotal (Estes, 1991).

In this paper I present data on the food habits of four species of carnivores in the rainforest region of southern Nigeria. In particular, I examine the food preferences of two species of Viverridae (*Civettictis civetta* and *Genetta maculata*) and of two species of Herpestidae (*Herpestes ichneumon* and *Atilax paludinosus*), with emphasis on their food niche breadth, dietary overlap, and potential for competition. Although other species of Viverridae and Herpestidae are present in the study region (Angelici *et al.*, 1999), I confined the present analysis to only these four species because they are common in the area, and thus I was able to collect a reliable amount of field data.

MATERIAL AND METHODS

STUDY AREA

The study was conducted during five field expeditions (for a total of 213 days in the field) between September 1996 and May 1998 in four regions of southeastern Nigeria (see Fig. 1): eastern Niger Delta (Port Harcourt region,

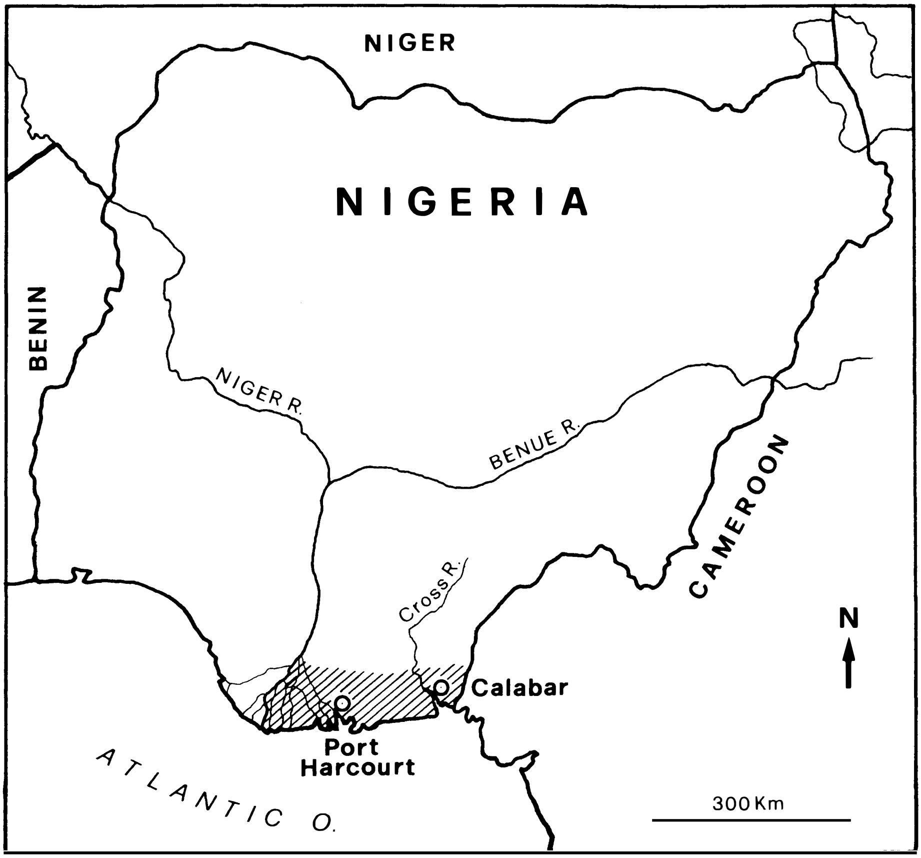

Figure 1. — Map of Nigeria showing the study area.

Rivers State, approx. 04° 45' N, 07° 01' E), and regions of Aba (Abia State, 04° 47' N, 07° 35' E), Eket (Akwa-Ibom State, 04° 50' N, 07° 59' E), and Calabar (Cross River State, 04° 48' N, 08° 21' E). These areas, which are heavily populated with hundreds of villages interspersed by patches of forests and cultivated lands, are especially important for the economy of Nigeria because of the big oil extraction and liquefied natural gas transmission installations. The forest patches may be dryland or swamp rainforest type. Mangrove forests (*Avicennia* spp., *Rhizophora racemosa*) are the dominant vegetation types in the areas of the fluvial systems influenced by salt-water or brackish-water. The climate of the study regions is tropical sub-Saharan, with well-marked dry and wet seasons and relatively little monthly fluctuations in maximum and minimum temperatures (Griffiths, 1972).

METHODS

Food data given here were collected from specimens killed in the field. No specimen was specifically killed for the purposes of this study. I used: (i) specimens shot and trapped by hunters, and (ii) specimens examined in small village markets (for the methodology employed, cf. Akani *et al.*, 1998; Angelici *et al.*, in press b).

Dietary records were collected by stomach dissection. Before analysis, all food remains were washed in a fine sieve, teased apart and sorted. Remains of mammals were identified by teeth, claws, or by microscopic examination of guard hair; birds by feathers or beaks; lizards by feet or tails; crabs by exoskeletons; invertebrates by mandibles, head capsules, hind legs, or shell remains (molluscan). In estimating the number of prey items per gut, a single prey item was assumed for mammal or bird categories, unless there was evidence to the contrary (i.e. for mammals a commonly occurring tooth or bone). Smaller prey items such as lizards or invertebrates could often be counted from distinctive parts. Food items were identified to the lowest taxon possible, by using reference collections for specimens, hairs, feathers, and bones of both mammals and birds (Angelici, unpubl. data). Fish remains were identified by Godfrey C. Akani (Port Harcourt University). Reptiles and amphibians were identified by using the reference collections of Luca Luiselli (F.I.Z.V., Rome).

Data were expressed as (i) number of occurrence of a given food category in the various stomachs examined (PNS), and (ii) number of occurrence of a given food category in relation to the total numbers of collected food items (PNF).

Food niche breadth was calculated by means of Simpson's (1949) diversity index, and food niche overlap was calculated by means of a Pianka's (1986) symmetric equation, with values ranging from 0 (no overlap) to 1 (total overlap).

Factor analysis (Principal Component Analysis on log-transformed data) was used to classify the various carnivore species in terms of their relative similarity as to feeding habits (taxonomical diet composition).

Statistical analyses were performed by SPSS (version 4.5 for Windows). All tests used were two-tailed with α set at 5 %. Systematics of the carnivore species followed Wozencraft (1993).

RESULTS

We examined stomachs of 29 *Herpestes ichneumon,* 29 *Atilax paludinosus,* 27 *Civettictis civetta,* and 22 *Genetta maculata.* The numbers of empty stomachs were: three for *H. ichneumon* (10.34 %), five for *A. paludinosus* (17.24 %); four for *C. civetta* (14.81 %), and two for *G. maculata* (9.09 %). These frequencies did not differ significantly amongst species (χ^2 with *d.f.* = 3, $P > 0.1$).

The list of prey eaten by these species is presented in Table I. Based on the frequency of occurrence of the various prey types in the stomachs, *H. ichneumon* is primarily a mammalophagous species, *A. paludinosus* is primarily invertebratophagous (most of the invertebrates eaten were aquatic, including Gastropoda, Bivalvia, and Crustacea), whereas *C. civetta* and *G. maculata* fed on both invertebrates and mammals.

Looking at the data in more detail, all species foraged on a wide range of food types, including reptiles, amphibians, fish, plants, and even garbage. In particular, amphibians represented the second most important food source for *A. paludinosus,* whereas birds and invertebrates were frequently preyed upon by *H. ichneumon,* reptiles were the second prey source for *C. civetta,* and birds and reptiles were important prey types for *G. maculata.*

TABLE I

Summary of the dietary data recorded from four species of carnivores in southeastern Nigeria. Data were expressed as (i) number of occurrence of a given food category in the various stomachs examined (PNS), and (ii) number of occurrence of a given food category in relation to the total numbers of collected items (PNF). H.i. = Herpestes ichneumon, *A.p.* = Atilax paludinosus, *C.c.* = Civettictis civetta, *G.m.* = Genetta maculata.

	H.i.		*A.p.*		*C.c.*		*G.m.*	
PREY TYPE	(PNS)	(PNF)	(PNS)	(PNF)	(PNS)	(PNF)	(PNS)	(PNF)
MAMMALS								
Crocidura nigeriae	2	2					1	1
Crocidura poensis	1	1			2	2		
Insectivora tot.	3	3			2	2	1	1
Cricetomys sp.	5	6	2	2	6	7	3	3
Mus musculoides	5	12	1	2	3	8	2	4
Lemniscomys striatus	2	2			3	4	2	2
Praomys tulbergi	3	4	2	4	3	7	4	10
Hybomys univittatus	1	5					2	3
Muridae indet.	5	6	1	1			2	3
Thryonomys swinderianus					2	2		
Rodentia tot.	21	35	6	9	17	28	15	25
BIRDS								
Streptopelia semitorquata	1	1					2	2
Corvus albus					1	1		
Passeriformes indet.							1	1
Eggs	4	10	1	4	3	6	2	4
Domestic fowl (adult or juv.)	3	5			2	5		
AMPHIBIANS								
Ptychadena sp.			6	11				
Bufo maculatus	3	3			2	3		
Hoplobatrachus occipitalis			1	1				
REPTILES								
Crotaphopeltis hotamboeia	1	1	2	2	1	1		
Afronatrix anoscopus	2	2						
Naja nigricollis					1	1		
Serpentes tot.	3	3	2	2	2	2		
Agama agama					3	4	1	1
Mabuya sp.	3	5			5	7	3	4
Mochlus fernandii					1	1		
Sauria tot.	3	5			9	12	4	5
OSTEICHTHYES								
Periophthalmus sp.	3	4	3	7				
Osteichthyes indet.			1	1				
INSECTA								
Orthoptera	2	10			8	13	9	17
Coleoptera	3	11	4	8	10	21	4	10
Other insects					6	8	4	13
MYRIAPODA indet.	3	5			5	11	2	3
ARANEAE indet.			1	1			1	4
MOLLUSCA								
Gastropoda indet. (freshwater)	3	10	7	26				
Gastropoda indet. (terrestrial)	2	6	1	3	2	3		
Bivalvia indet.			11	34				
CRUSTACEA								
Decapoda indet.	2	4	4	10	1	3		
VASCULAR PLANTS								
Fruits, berries or seeds	3	5	2	3	6	9	3	5
GARBAGES	4				9			

From a quantitative point of view, the food niche breadth of the various species is shown in table II. Food niche breadth differed significantly among species (one-way Kruskal-Wallis ANOVA, $P < 0.05$), and a Tukey Honest Significant *post-hoc* test indicated that *A. paludinosus* had the narrowest niche breadth, and that *H. ichneumon* and *G. maculata* were not significantly different from each another. *C. civetta* had intermediate niche breadth.

TABLE II

Values of food niche breadth and food niche overlaps for the four carnivore species, measured according to Simpson's (1949) diversity index (niche breadth) and according to Pianka's (1986) symmetric equation (niche overlap). Symbols: H.i. = Herpestes ichneumon, *A.p.* = Atilax paludinosus, *C.c.* = Civettictis civetta, *G.m.* = Genetta maculata.

Parameter	*H·i.*	*A.p.*	*C.c.*	*G.m.*
Niche Breadth	6.67	4.32	5.08	6.51
Niche Overlap				
H·i.	***	0.32	0.31	0.37
A.p.		***	0.59	0.61
C.c.			***	0.70
G.m.				***

Food niche overlap values calculated between the various species (Table II) suggested that there were significant differences among species (Kruskal-Wallis ANOVA, $P < 0.01$), and a Tukey Honest Significant *post-hoc* test indicated that (i) the highest potential for competition occurs between *C. civetta* and *G. maculata,* with approximately 70 % of the diet in common; (ii) *H. ichneumon* showed a low overlap with all of the other sympatric species.

A set of Principal Component Analysis (unrotated model, after log-transformation of the data) on PNS data permitted to classify the four studied species within a two-dimension space (Fig. 2; eigenvalues: 2.28263 and 1.36643). Based on this multivariate analysis, it appears that *H. ichneumon* and *G. maculata* are very similar in terms of dietary niche, whereas the other two species are very different from each another and from the group of the two above-mentioned species.

DISCUSSION

From the quantitative point of view, my data suggest that the diets of *C. civetta* and *G. maculata* were quite similar, whereas the niche positions of *H. ichneumon* and *A. paludinosus* were very different from those of the two former species and also between them. This evidence mirrors the phylogenetic position of the various species: Viverridae *versus* Herpestidae. Both Viverridae species, are

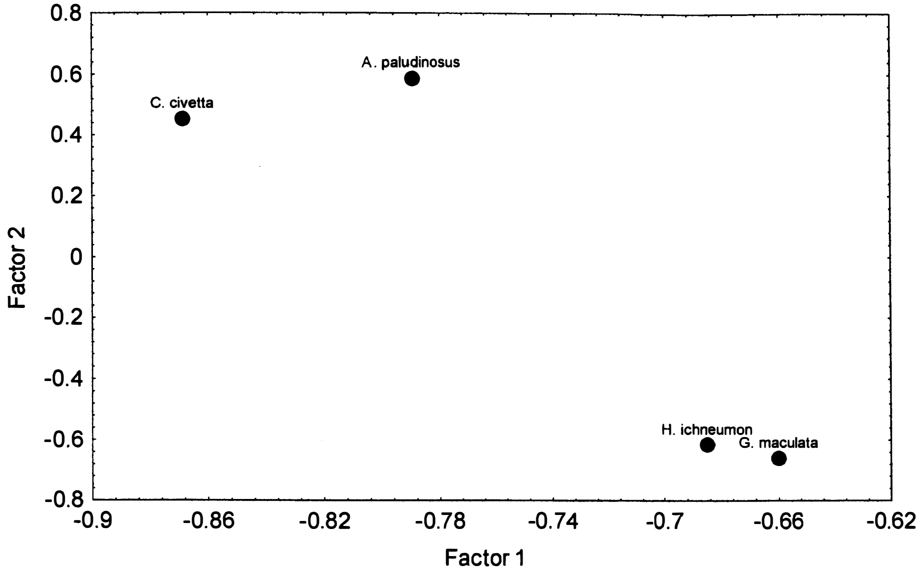

Figure 2. — Plot of loadings of a Principal Component Analysis on the diet composition of the four studied carnivores from south-eastern Nigeria. For more details, see text.

active and versatile predators, which will alternatively lie in ambush and dash at their prey (Estes, 1991). Thus, they are relatively similar in general trends of predatory behaviour, although *C. civetta* usually does not stalk or chase prey like a genet (Estes, 1991). In general, my dietary data on these species are quite in agreement with data from conspecifics elsewhere in showing that both *C. civetta* and *G. maculata* are omnivorous feeding upon small vertebrates, invertebrates, and even plant matter (Rosevear, 1974; Lack, 1977; Randall, 1977; Smithers & Wilson, 1979; Skinner & Smithers, 1990). In particular cases *C. civetta* can forage substantially on fruits and berries (Pendje, 1994). I am led to think that the comparatively lesser frugivory of my *C. civetta* sample could depend on a lesser availability of this kind of food in the environment.

With regard to the two Herpestidae species, the situation is different. *H. ichneumon* is broadly distributed across Africa and also introduced in southern Europe, and thus should expectably be characterized by a very versatile diet to adapt itself to the very different environmental conditions of its range. Available information from studies published on sub-Saharan African populations (Smithers & Wilson, 1979; Stuart, 1983) are in good agreement with my own data, which confirmed predation on domestic poultry (cf. also Happold, 1987).

The semiaquatic *A. paludinosus* was the most specialized species in my sample. This result is in agreement with available literature, collected primarily in southern African populations (Smithers & Wilson, 1979; Du Toit, 1980; Louw & Nel, 1986). The fact that most of the prey eaten by this mongoose was aquatic is quite predictable and consistent with the general habits of this species (Baker, 1989). It is noteworthy that, contrary to Baker's (1989) findings, Nigerian *A. paludinosus* ate crabs entirely, without discarding their carapace. The fact that several prey items are nocturnal (e.g. the colubrid snake *Crotaphopeltis hotamboeia*) is a further demonstration of the nocturnal habits of this mongoose (Estes, 1991). However, it should be noted that the activity rhythm of this species tends to vary geographically: for instance, it is nocturnal in the Gabon forests and diurnal on the Mount Kenya (e.g., see Estes, 1991).

In general, shrews and rodents were quite important in the diet of all the species, as already observed in small African forest carnivores from elsewhere (Ray, 1998). It is noteworthy that these small mammals could play a major role in the dynamics of the forest ecosystems of southern Nigeria, as they are also prominent prey for other phylogenetically unrelated predators, e.g. snakes (Luiselli & Angelici, 1998; Luiselli *et al.*, 1998, 2000). The coexistence of a relatively diversified predator fauna eating partly or mainly upon small mammals suggests that the density of forest predators is limited by the amount of food available (see also Barbault, 1991; Luiselli & Angelici, in press). However, long term fluctuations in the availability and the temporal distribution of the food resources, due to strong inter- and intra- annual climatic changes (wet and dry seasons, see Griffiths, 1972; White, 1983) can maintain variability (e.g. see Cézilly *et al.*, 1991).

With regard to the coexistence of these several predators situated at the intermediate levels of the trophic chain, it should be noted that the progressive impoverishment of the higher level predators (e.g. leopards, giant snakes, monitor lizards, crocodiles, raptors) due to human hunting pressure (Akani *et al.*, 1998; Angelici *et al.*, 1998; in press a, b) is likely to have produced a slight increase in the frequency of herpestids, viverrids, and snakes (Angelici, unpublished data) as a consequence of the newly opened niches available (cf. Pianka, 1978). For instance, the intermediate trophic level predators *H. ichneumon* and the spitting cobra *Naja nigricollis* are now expanding over wetter areas than in the recent past (i.e. in the Niger Delta, cf. Powell, 1997; Luiselli & Akani, 1999).

In any case, comparisons of my data with those of previous authorities should be taken with some caution, given the fact that some previous sources based their analyses on scats and not on stomach dissection, and so could have presented some quantitative differences just because of methodology distortion.

Concerning the eventual competition between these species, it should be noted that other niche parameters should be considered, including the species-specific times of activity, the species body size and their relative hunting techniques, other than their habitat preferences. With regard to habitat preferences, all these species showed relatively similar habitat preferences in the rainforest area of Nigeria (see Angelici *et al.*, 1999), although *A. paludinosus* is more linked to marshes and swamp forests, and *C. civetta* is more plastic in habitat requirements. This relative habitat similarity would be considered as a factor potentially in favour of the existence of competition. However, the size difference between species (in particular between the two Herpestidae and the two Viverridae species) should obviously act against such an eventual interspecific competition, as it is well known that major size differences between potential competitors could reduce effective competition potential (Ricklefs, 1973).

The results of the multivariate statistical model on the diet composition suggest that the highest potential for interspecific competition should be between *G. maculata* and *H. ichneumon.* These species are relatively similar also in terms of habitat selection, and show a pronounced adaptability to altered habitats (Angelici *et al.*, 1999; in press a). Thus, the comparative ecology of these two species should be carefully monitored in the future, as it can highlight some unexpected patterns in the process of colonization and competition in the tropical forest-plantation mosaic.

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REFERENCES

AKANI, G.C., LUISELLI, L., ANGELICI, F.M. & POLITANO, E. (1998). — Bushmen and herpetofauna: Notes on Amphibians and Reptiles traded in bush-meat markets of local people in the Niger Delta (Port Harcourt, Rivers State, Nigeria). *Anthropozoologica,* 27: 21-26.

ANGELICI, F.M., AKANI, G.C. & LUISELLI, L. (1998). — The leopard (*Panthera pardus*) in southeastern Nigeria: status, ecological correlates of occurrence, and conservation implications. *Ital. J. Zool.,* 65: 307-310.

ANGELICI, F.M., GRIMOD, I. & POLITANO, E. (in press a). — Mammals of the eastern Niger Delta (Rivers and Bayelsa States, Nigeria). *Folia Zoologica,* in press.

ANGELICI, F.M., LUISELLI, L. & POLITANO, E. (1999). — Distribution and habitat of some carnivores (Herpestidae, Mustelidae, Viverridae) in the rainforests of southeastern Nigeria. *Z. Säugetierkunde,* 64: 116-120.

ANGELICI, F.M., LUISELLI, L., POLITANO, E. & AKANI, G.C. (in press b). — Bushmen and mammal fauna: A survey of the mammals traded in bush-meat markets of local people in the rain forests of south-eastern Nigeria. *Anthropozoologica,* in press.

BAKER, C.M. (1989). — Feeding habits of water mongoose (*Atilax paludinosus*). *Z. Säugetierkunde,* 54: 31-39.

BARBAULT, R. (1991). — Ecological constraints and community dynamics: linking community patterns to organismal ecology. The case of tropical herpetofaunas. *Acta Oecol.,* 12: 139-163.

CEZILLY, F., BRUN, B. & HAFNER, H. (1991). — Foraging and fitness. *Acta Oecol.,* 12: 683-696.

DU TOIT, C.F. (1980). — The yellow mongoose *Cynictis penicillata* and other small carnivores in the Mountain Zebra National Park. *Koedoe* 23: 179-184.

ESTES, R.D. (1991). — *The behavior guide to African mammals.* University of California Press, Berkeley & Los Angeles.

GRIFFITHS, J.F. (1972). — *Climates of Africa.* Elsevier Publ. Co., New York.

HAPPOLD, D.C.D. (1987). — *The Mammals of Nigeria.* Clarendon Press, Oxford.

LACK, A. (1977). — Genets feeding on nectar from *Maranthes polyandra* in Northern Ghana. *E. Afr. Wildl. J.,* 15: 233-234.

LOUW, C.J. & NEL, J.A.J. (1986). — Diets of coastal and inland-dwelling water mongoose. *S. Afr. J. Wildl. Res.,* 16: 153-156.

LUISELLI, L. & AKANI, G.C. (1999). — Habitats of snakes in the rainforests of Eket (Akwa-Ibom State, south-eastern Nigeria). *Herpetozoa,* 11: 99-107.

LUISELLI, L. & ANGELICI, F.M. (1998). — Sexual size dimorphism and natural history traits are correlated with intersexual dietary divergence in royal pythons (*Python regius*) from the rainforests of southeastern Nigeria. *Ital. J. Zool.,* 65: 183-185.

LUISELLI, L. & ANGELICI, F.M. (in press). — Coexistence of pythons and leopards: A ghost of past competition. *In:* L. Luiselli (ed.). *Snake Ecology and Natural History in the Rainforests of Southern Nigeria.* Krieger Publishing Co., Tampa.

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 Nile monitors (*Varanus niloticus ornatus*) and dwarf crocodiles (*Osteolaemus tetraspis*) in the swamps of central Africa? A study from south-eastern Nigeria. *J. Zool. London,* 247: 127-131.

LUISELLI, L., ANGELICI, F.M. & AKANI, G.C. (2000). Large elapids and arboreality: The ecology of Jameson's green mamba, *Dendroaspis jamesoni* in an Afrotropical forested region. *Contributions to Zoology,* in press.

MACDONALD, J.T. & NEL, J.A.J. (1986). — Comparative diets of sympatric small carnivores. *South African Journal of Wildlife Research,* 16: 153-156.

PENDJE, G. (1994). — La frugivorie de *Civettictis civetta* (Schreiber) et son rôle dans la dispersion des graines au Mayombe. *Rev. Ecol. (Terre et Vie),* 49: 107-116.

PIANKA, E.R. (1978). — *Evolutionary ecology.* 2nd edition. Harper & Row, New York.

PIANKA, E.R. (1986). — *The ecology and natural history of desert lizards.* Princeton University Press, Princeton.

POWELL, C.B. (1997). — Discoveries and priorities for mammals in the freshwater forests of the Niger Delta. *Oryx,* 31: 83-85.

RANDALL, R.M. (1977). — *Aspects of the ecology of the civet* Civettictis civetta *(Schreber, 1778).* M. Sc. thesis, University of Pretoria, Republic of South Africa, 250 pp.

RAY, J.C. (1997). — Comparative ecology of two African forest mongooses, *Herpestes naso,* and *Atilax paludinosus. Afr. J. Ecol.,* 35: 237-253.

RAY, J.C. (1998). — Temporal variation of predation on rodents and shrews by small African forest carnivores. *J. Zool. London,* 244: 363-370.

RICKLEFS, R.E. (1973). — *Ecology.* Chiron Press, Philadelphia.

ROSEVEAR, D.R. (1974). — *The Carnivores of West Africa.* British Museum (Natural History), London.

SIMPSON, E.H. (1949). — Measurement of diversity. *Nature,* 163: 688.

SKINNER, J.D. & SMITHERS, R.H.N. (1990). — *The Mammals of the Southern African Subregion (new edition).* University of Pretoria, Pretoria.

SMITHERS, R.H.N. & WILSON, V.J. (1979). — Check list and atlas of the mammals of Zimbabwe, Rhodesia. *Mus. Mem. Natl. Mus. Monum. Rhod.,* 9: 1-147.

STUART, C.T. (1983). — Food of the large grey mongoose *Herpestes ichneumon* in the south-west Cape Province. *S. Afr. J. Zool.,* 18: 401-403.

WHITE, F. (1983). — *The vegetation of Africa.* Unesco Press, Paris.

WOZENCRAFT, W.C. (1993). — Order Carnivora. Pp. 279-348, *in:* D.E. Wilson & D.A.M. Reeder (eds). *Mammal Species of the World. A Taxonomic and Geographic Reference.* 2e éd. Smithsonian Institution Press. Washington & London.