HABITAT ASSOCIATIONS AND DIETARY RELATIONSHIPS BETWEEN TWO GENETS, *GENETTA MACULATA* AND *GENETTA CRISTATA*

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RÉSUMÉ. — *Associations d'habitat et relations alimentaires entre deux genettes*, Genetta maculata *et* Genetta cristata. — La zone de forêt humide du sud du Nigéria est habitée par deux espèces de genettes, la Genette à crête (*Genetta cristata*) et la Genette pardine (*Genetta maculata*). La première est une espèce menacée alors que la seconde est répandue et relativement abondante. Afin d'identifier les caractéristiques environnementales et paysagères qui influeraient sur la présence ou l'absence de ces espèces, nous avons construit un modèle de régression logistique (procédure conditionnelle pas à pas pour valeurs discrètes) à partir de toutes les localités de capture. Nous avons établi que la présence de *G. cristata* est statistiquement corrélée de manière positive à la forêt primaire sèche et aux plantations de manguiers en forêt, ainsi que dans une moindre mesure à la forêt secondaire sèche et à la forêt primaire inondée. De son côté, *G. maculata* était négativement influencée par les divers types de forêt. *G. cristata* était négativement influencée par les zones suburbaines, les plantations d'ananas, le bush et les formations de palmiers à huile qui affectaient *G. maculata* de manière positive. Le régime alimentaire a été étudié par dissection d'estomacs ; les chevauchements de niche ont été estimés à l'aide des formules de Pianka et de Czechanowski et comparés à des hypothèses nulles basées sur des simulations de type Monte Carlo. Pour les deux espèces, les restes d'insectes dominaient dans le régime ; toutefois, en termes de biomasse, les petits mammifères constituaient la majorité du régime et les arthropodes représentaient la seconde source de proies en termes d'importance. Le régime alimentaire de la Genette à crête était similaire à celui de *G. maculata* sympatrique et les valeurs de recouvrement des régimes indiquaient une forte compétition interspécifique. Cela a été confirmé par les procédures de Monte Carlo.

SUMMARY. — The rainforest zone of southern Nigeria is inhabited by two species of genets, the Crested Genet (*Genetta cristata*) and the Common large-spotted Genet (*Genetta maculata*). The former species is threatened, whereas the latter is widespread and quite abundant. In order to identify the environmental and landscape characteristics which may influence the presence/absence of both *Genetta* species, we run all the localities of capture for the two species into a logistic regression model (forward stepwise conditional procedure for discrete values). We found that the presence of *G. cristata* was statistically positively correlated to the presence of primary dry forest and bush-mango plantations inside the forest, and to a less extent secondary dry forest, and primary flooded forest. On the other hand, *G. maculata* was negatively influenced by the various types of forest. The presence of *G. cristata* was negatively influenced by the presence of suburban areas, pineapple plantations, bushlands, and oil palm plantations, which had a positive effect on *G. maculata*. Diet habits were studied by dissection of genet stomachs, and current niche overlaps were evaluated by using Pianka and Czechanowski formulas, and compared with "null models" based on Monte Carlo simulations. Insect remains were dominant in the diet of both species. However, in terms of biomass of the prey items, small mammals accounted for the majority of the diet, and arthropods the second prey source in terms of importance, in both

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species. The diet of the Crested Genet was similar to that of sympatric *Genetta maculata*, and the overlap values indicated that there is likely a strong interspecific competition for food among them. This was confirmed by Monte Carlo randomisations procedures.

It is now well established that accurate natural history information serves as a factual basis for the life sciences, and for reliable nature conservation strategies (Greene, 1986; 1993). A main problem is that, for many (most?) species we know so little about, and our scarce knowledge of the various species' habits may impede the establishment of accurate conservation measures with a consequent high risk of extinction. This is especially true for species which are both extremely elusive and inhabiting poorly developed areas in logistically difficult countries.

An example of the above-mentioned problem is certainly represented by the genets (genus *Genetta*, Viverridae), which have one of their "species richness hotspots" in the biafreen forests of southern Nigeria and western Cameroon (Kingdon, 1989). The systematic status of the biafreen genets is quite confused (Crawford-Cabral, 1980-81; Happold, 1987; Wozencraft, 1994; Powell & Van Rompaey, 1998), but there are at least two species that occur in sympatry inside the forest-plantation mosaic of southern Nigeria: i.e. the Crested Genet *Genetta cristata* and the Common large-spotted Genet *Genetta maculata*. The latter species is by far the most common among the two species (Angelici *et al.*, 1999a, 1999b), and some data on its feeding ecology and distribution have already been published (Angelici *et al.*, 1999a, 1999b; Angelici, 2000). On the other hand, the coexistence ecology of *G. maculata* and *G. cristata* is particularly important not only in an ecological perspective, but also in a biogeographical perspective. Indeed, the Crested Genet, which is nocturnal and extremely elusive (Heard & Van Rompaey, 1990), is endemic of a small area of tropical Africa at the border between south-eastern Nigeria and western Cameroon (Heard & Van Rompaey, 1990), where scientific research has traditionally been impeded by endemic poverty, unstable socio-political problems and corruption of the institutions (De Montclos, 1994), despite the whole areas has been subjected to a mass deforestation in the last forty years and is considered a minor centre of endemism for many faunal and floral groups (Kingdon, 1989).

The Crested Genet was originally described as *Genetta servalina cristata* Hayman, 1940 (in Sanderson, 1940). Its systematic position is still unsettled, mainly because it was considered just as a subspecies of *Genetta servalina* Pucheran 1855 by some authorities (Coetzee, 1977; Wozencraft, 1993), whereas it was considered a distinct species by others (Rosevear, 1974; Crawford-Cabral, 1980-81; Corbet & Hill, 1986). These latter authorities based their opinion on the presence of a morphological character which is unique among African genets, i.e. a dorsal erectile crest which is clearly seen in all the skins available to date. More recently, the distinctness to the species level of *G. cristata* from the other genets was supported also by molecular biology data, which however confirmed a close relationship of this taxon with *G. servalina* (Gaubert *et al.*, 2004).

The Crested Genet is apparently rare, and, because of the restricted distribution range, is listed as Endangered (EN) by IUCN (2003). Apart from its reduced range and the few records available, another reason for classifying this species as Endangered is that most of its forest habitats are currently under serious threats, due to habitat pollution, deforestation, and overpopulation (De Montclos, 1994). *G. cristata* was recorded at the border between Nigeria and Cameroon, east of the River Cross, and the westernmost limit of its range was considered to be the River Cross, whereas the easternmost limit was the River Sanaga (Sanderson, 1940; Eisentraut, 1963; Heard & Van Rompaey, 1990). Very recently, however, Powell & Van Rompaey (1998) added to the known range of this species also several records (confirmed by the presence of deposited vouchers) from the Niger Delta, i.e. a mainly wet area situated west of the River Cross, in southern Nigeria. However, Boitani *et al.* (1999) wrongly presented a potential distribution map for *G. cristata* where the Niger Delta area was considered uncertain for the presence of this species, but failed to give any detail for their opinion.

On the other hand, *G. maculata* is a widespread species, which occurs in a great part of sub-Saharan Africa, and is not necessarily linked to the forest biota, but also occurs in thickets inside savannas, as well as in semicultivated and altered areas (Kingdon, 1997; Angelici & Gaubert, in press).

As it is usual for many other rare carnivores from tropical Africa, nearly to nothing is known on the ecology of forest genets (particularly of *G. cristata*) in the wild, including their feeding habits. With regard to the Crested Genet there are only a few comments available on this matter, which however are based mostly on suppositions and generalizations from data available for other closely-related species of the genus *Genetta*. Some anecdotal but noteworthy observations were done by Heard & Van Rompaey (1990) on captive animals. These authors suggested that insects, frogs and lizards are the main preys of semi-domesticated Crested Genets from the Cross River State, and also concluded that lizards are likely the preferred type of prey for these viverrids.

Our aim in this paper is to convey detailed data on the ecological distribution and feeding habits of free-ranging Crested Genets, and to compare these data with data available for sympatric populations of Common large-spotted Genets.

More in particular, we respond to the following key-questions:

(i) Are there, and if yes, what are, the habitat types which are positively/negatively related to the presence of the Crested Genet and of the Common large-spotted Genet in southern Nigeria?

(ii) Are there different responses (in terms of its presence/absence) of the Crested Genet and of the Common large-spotted Genet to the various types of cultivations/plantations which are spread in the study region? If yes, what are the ecological reasons that may explain the non random distribution of the two genet species?

(iii) What are the feeding habits of these ecologically little-known species?

(iv) Are the feeding habits of the Crested Genet different from those of sympatric *G. maculata*, which may be a potential competitor inside the study region?

MATERIALS AND METHODS

STUDY AREA

The study was conducted during several field expeditions conducted between September 1996 and June 2004, in the ecological "macro-region" of the Niger Delta till the Cameroon border. We conducted our surveys in the territories of eight states of the Federal Republic of Nigeria, i.e., from West to East, Delta, Bayelsa, Anambra, Imo, Rivers, Abia, Akwa-Ibom, and Cross-River. Thus, although irregularly, we surveyed a surface of approximately 400 × 250 km. The study area, which is heavily populated with hundreds of villages interspersed by patches of forests and cultivated lands, is especially important for the economy of Nigeria because of the big oil extraction and liquefied natural gas transmission installations (De Montclos, 1984). 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). The pluviometric regime of a site where Crested and Common large-spotted Genets were found is given in figure 1.

PROTOCOL

Food data given here were collected from specimens killed in the field. No specimen was specifically killed for the purposes of this study. We used: (i) specimens shot or trapped by local hunters, and (ii) specimens examined in village markets (for the methodology employed see Angelici *et al.*, 1999a; Angelici, 2000). We used for our analyses only those specimens for which the exact locality of capture was known.

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, and hind legs. 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 a lizards or invertebrates could often be counted from distinctive parts. Food items were identified to the lowest possible taxon, by using reference collections for specimens, hairs, feathers, and bones of both mammals and birds (Angelici, unpubl. data). Reptiles and amphibians were identified by using the reference collections of one of us (Luiselli, unpubl. data).

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

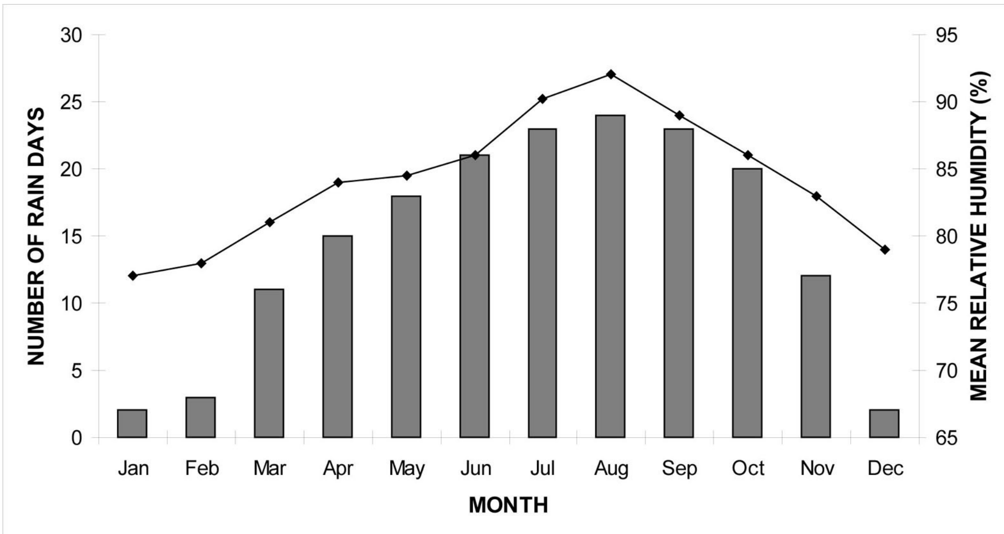

Figure 1. — Frequency of rainy days per month (bars) and mean monthly relative humidity (line) at a locality of southern Nigeria where the presence of Crested Genets and Common large-spotted Genets was ascertained (Akpabouyo; data from the Department of Geography, University of Calabar, Nigeria).

(iii) biomass contributions of the prey types to the diet (% B). Biomass of the various prey types was the cumulative biomass of the various items recorded in the field, which was the direct measurement of the biomass of the items found in stomachs for those prey types which were not too much damaged by the masticatory and digestive processes (i.e. lizards, most of the insects, etc). For the other items, we calculated the mean biomass of the prey item *in vivo*, based on personal reference collections by the authors, or following the indications of Rosevear (1969), and Happold (1974, 1987).

In order to identify the environmental and landscape characteristics which may influence the presence/absence of both *Genetta* species, we run all the localities of capture for the two species in both literature and original data into a logistic regression model (forward stepwise conditional procedure for discrete values; Hosmer & Lemeshow, 1989). To do it, for each capture point we considered a 5 km radius, and determined the habitats available inside that surface by using a map databank of vegetation and landscape (scale 1:10,000; Federal Government of Nigeria or Aquater s.p.a., prepared for environmental impact assessments). We chose the radius size of 5 km taking into account the movement radius within each home range of 6 males of *G. maculata* which were radiotracked during our study period, and which reached about 4.7 linear km (Angelici *et al.*, in prep.). We assumed that only habitats which occupied at least 5% of the surface around each genet site of capture were relevant for the presence of the species in question, and hence we processed only those habitats which met with this assumption. We decided to exclude the marginal habitats because they were either clearly inappropriate (e.g., urban centres, etc.) or just not-influent for the model (i.e., they were too splitted for giving significance to the model). Although it is possible that a rare habitat type may be critical for providing a limited resource to the genets (e.g., den sites, water, etc), in any case it would not have been possible to discover it by means of our statistical model, because the scale size was inappropriate for such a finer analysis. We also selected for comparisons several random sites (25 for both species), situated inside the potential range of the Crested Genet and of the Common large-spotted Genet, where their absence was ascertained by careful unpublished research by ourselves (years 1996-2004), and by the absence of literature records. For these sites we employed the same procedure as that described above, i.e. we considered a 5 km radius around each random site, and then determined the habitats available inside that surface. Then, we applied a logistic regression model to the dataset, by using the presence/absence of *G. cristata* and *G. maculata* as dependent variable and the various study areas (with their various landscape characteristics) as covariates.

Fifteen landscape variables were considered for our logistic regression model. These were: (i) primary dry forest, (ii) secondary dry forest, (iii) primary flooded forest, (iv) secondary flooded forest, (v) arboreal mangroves, (vi) altered mangroves, (vii) suburban areas, (viii) pineapple plantations, (ix) bush-mango plantations, (x) yam plantations, (xi) cassava plantations, (xii) banana and plantain plantations, (xiii) derived savanna, (xiv) oil palm plantations, and (xv) bush re-growth.

Locality of captures were estimated by occasional direct sightings of free-ranging specimens, or by interviews with hunters. In this latter case, we always asked the hunters to accompany us in the exact spot of capture. Then, the GPS coordinates of the exact spot of capture were recorded. The margin of error of each capture locality can be evaluated approximately as no more than 200 m.

For calculating the similarity of trophic niche between the two genet species, we calculated the overlap indices of Pianka (1973) and Czechanowski (Feinsinger *et al.*, 1981). Pianka's formula for species *j* and *k*, with resource utilizations p_{1i} and p_{2i}, is:

$$O_{j,k} = O_{2,1} = \Sigma\, p_{2i} \times p_{1i} / \Sigma \sqrt{(p_{2i}^2 \times p_{1i}^2)}$$

In this formula the values range from 0 (no overlap) to 1 (total overlap). Czechanowski's formula for species *1* and *2*, with resource utilizations p_{1i} and p_{2i}, is:

$$O_{1,2} = O_{2,1} = 1.0 - 0.5 \times \Sigma | p_{1i} - p_{2i} |$$

Graphically, this index corresponds to the intersection of the utilization histograms of the two species, and also ranges from 0 (no overlap) to 1 (total overlap) (Gotelli & Entsminger, 2000). We calculated these indices using the program "EcoSym 700" (Gotelli & Entsminger, 2000). We performed a cross-tabulation on those frequencies to determine where differences in food types used existed for each species. By means of the "EcoSym" package, we performed Monte Carlo simulations to create "pseudo-communities" (Pianka, 1986) and statistically compared the derived patterns with those in the actual data matrix. We used the RA3 model to evaluate the similarity in food use (= overlap); this model randomises particular resource states used by each species while retaining niche breadth. This model has been shown to have robust statistical properties for detecting non-random niche overlap patterns (or, as in our study case, similarity in resource use between species; Winemiller & Pianka, 1990). As we did not have a static measure of food type availability at the study area, therefore we used the default setting of equiprobable resource states available in "Ecosym". The assumption of equiprobability of resource states means in our study case that the various prey type states (= resource states) are equally usable (= abundant) by all species in each of the two survey periods.

All other statistical analyses were done by "Statistica version 6.0" or "SPSS 8.0" for Windows PC packages, with all tests being two-tailed and alpha-set at 5%. When χ^2 test had $df = 1$, the Yates' correction factor was applied.

RESULTS

Ecological distribution

The list of the specimens of both genets examined during the present study, with a gazetteer of all the localities of capture, is given in tables I (*G. cristata*) and II (*G. maculata*). In total, 25 different localities of presence for the Crested Genet are known in south-eastern Nigeria. With regard to *G. cristata*, based on our original data, five specimens were recorded from localities situated east of the River Cross, and six from west of the River Cross. A single individual was even recorded from a locality situated west of the River Niger (Patani). Another record (Azumini riverine forest) demonstrated the presence of the Crested Genet in the extensively deforested region situated between the central axis of the River Niger Delta and the River Cross, where the species had never been recorded before. For *G. maculata*, 33 localities of capture were recorded (Tab. II), but all of the data mirror the distribution patterns already known for this species.

Table I

Localities of capture of Genetta cristata *examined in the present study*

Specimen and sex	Date and origin of capture specimen	Locality of capture
Adult male	May 1998, Itu local market	near Ndom-Nwong (05°12' N, 08°10' E) (Cross River State)
Sub-adult male	June 2000, shot by a local hunter	Ikpan (05°01'N, 08°39' E) (Cross River State)
Adult male	August 2001, local market	Adagbabiri (04°56' N, 6°16' E) (Bayelsa State)
Adult female	August 2001, for sale along the road	Patani, surroundings of (05°13'N, 06°11' E) (Delta State)
Adult male	August 2001, for sale along the road	Akpabouyoh (04°51' N, 08°22' E) (Cross River State)
Adult male	October 2001, for sale along the road	Azumini River, surroundings of (04°57' N, 07°29' E) (Abia State)
Adult female	December 2001, local market	Akamkpa (05° 20' N, 08° 21' E) (Cross River State)
Adult female	March 2003, shot by a local hunter	between Ogbia town (04°43'N, 06°20' E) and Nembe (04°32'N, 06°25' E) (Bayelsa State)
Adult male	September 2003, for sale along the road	Igbofia (05°22' N, 08°17' E)(Cross River State)
Adult male	October 2003, local market	Ogbia village (04°74' N, 06°43' E) (Rivers State)
Adult female	October 2003, for sale along the road	Stubbs Creek (04°50' N, 08°01' E) (Akwa Ibom State)

TABLE II

Localities of capture of Genetta maculata *examined in the present study*

Specimen and sex	Locality of capture
2 adult males	Orubiri (04° 42' N, 07° 01' E)
1 adult male, 1 adult female	Elem-Sangama (04° 40' N, 06° 40' E)
1 adult female, 1 sub-adult male	Otari (04° 53' N, 06° 41' E)
1 sub-adult female	Kreigeni (05° 17' N, 06° 37' E)
1 adult female	Bonny island (04° 25' N, 07° 15' E)
1 adult male	Rumuji (04° 57' N, 06° 57' E)
2 adult females	Awarra (05° 21' N, 06° 49' E)
1 adult female, 2 adult males, 1 sub-adult male	Calabar (04° 48' N, 08° 21' E)
1 adult female	Itu (05° 12' N, 07° 59'E)
1 sub-adult male, 1 adult female	Abarikpo (05° 08' N, 06° 37' E)
1 adult female	Tombia (04° 46' N, 06° 53' E)
2 adult males	Orashi (04° 53' N, 06° 47' E)
2 adult females	Omoku (05° 21'N, 06° 39'E)
1 adult male	Amassoma (04° 59'N, 06° 07'E)
2 adult females	Adagbabiri (04° 56' N, 6° 16' E)
3 adult males	Ahoada (05° 04' N, 06° 38' E)
1 adult male	Bori (04° 40'N, 07° 22' E)
1 adult male	Etinan (04° 51'N, 07° 51' E)
2 adult females, 1 adult male	Ikot-Ubo (04° 44'N, 08° 02' E)
1 sub-adult male	Abraka (05° 47'N, 06° 06'E)
1 adult female, 1 adult male	Okoroba (04° 38'N, 06° 11'E)
2 adult females	Onitu (05° 04'N, 06° 28'E)
1 sub-adult female, 1 adult male	Yae (04° 45'N, 07° 29'E)
1 adult male	Owelli (06° 11'N, 07° 28'E)
2 adult males	Arocuchkwu (05° 24' N, 07°56' E)
1 adult female	Atimbo (04° 55' N, 08° 22' E)
2 adult females	Akampka (05° 20' N, 08° 21' E)
1 adult male	Bomadi (05° 09' N, 05° 56' E)
1 adult female	Evwremi (05° 22'N, 06° 02'E)
1 adult male, 1 adult female	Chokochoko (04° 59'N, 06° 56' E)
1 adult male, 1 sub-adult female	Amarata (04° 59' N, 06° 18' E)
3 adult females	Brass (04° 29' N, 06° 17'E)

In order to predict what factors may influence the local distribution of these species, we run a logistic regression model on the presence/absence of *G. cristata* and *G. maculata* against the fifteen habitat parameters listed in the methods, for 25 (*G. cristata*) and 33 (*G. maculata*) localities of presence and 25 localities of absence of each species. We got a statistically significant model (–2 log likelihood = 50.835; intercept only = 66.208; $\chi^2 = 15.373$, $df = 14$, $P = 0.011\,9$), which predicted that (see Tab. III):

(i) the presence of *G. cristata* was statistically positively correlated to the presence of primary dry forest and bush-mango plantations inside the forest, and to a less extent secondary dry forest, and primary flooded forest;

(ii) the presence of *G. cristata* was negatively influenced by the presence of suburban areas, pineapple plantations, bushlands, and oil palm plantations;

(iii) the presence of *G. maculata* was statistically positively correlated to the presence of derived savanna and oil palm plantations, and to a less extent banana plantations, and both types of mangroves;

(iv) the presence of *G. maculata* was negatively influenced by the presence of primary dry forest, secondary dry forest, primary flooded forest, and secondary flooded forest.

TABLE III

Results of a logistic regression analysis predicting what habitat factors are positively or negatively correlated to the presence/absence of the two species of Genetta *in southern Nigeria. Significant correlations are in boldface (positive scores), and in boldface + italic (negative scores)*

Habitat type	Logistic regression score of *Genetta cristata*	Logistic regression score of *Genetta maculata*
Primary dry forest	**1.208**	***–1.103***
Secondary dry forest	0.256	***–1.407***
Primary flooded forest	0.396	***–1.383***
Secondary flooded forest	0.065	***–1.109***
Arboreal mangroves	0.143	0.446
Altered mangroves	– 0.087	0.417
Suburban areas	***–1.682***	0.303
Pineapple plantations	***–1.406***	0.108
Bush-mango plantations	**0.668**	0.116
Yam plantations	–0.244	0.088
Cassava plantations	–0.273	0.328
Banana and plantain plantations	–0.134	0.622
Derived savanna	–0.076	**1.043**
Oil palm plantations	***–0.599***	**0.864**
Bush re-growth	***–0.753***	0.374

The logistic regression model showed that for 13 out of 15 environmental variables there were opposite scores for the two species; for two variables (i.e. primary dry forest and oil palm plantations) the scores were significantly opposite, and for 8 variables the opposite scores were significant for one species but not for the other (Tab. III).

DIET

We examined stomachs of 11 Crested Genets (6 were adult males, one subadult male, and 4 adult females) and 56 Common large-spotted Genets (23 adult males, 26 adult females, 4 subadult males, and 3 subadult females). Adult sex-ratio was not significantly different in either species (in both cases, P = n.s. at Fisher exact test).

With regard to *G. cristata*, one stomach was empty (9.1% of the total sample examined). The list of prey eaten by this species is presented in table IV. Insect remains were dominant in the diet (51.4% of the total number of prey items), and arthropods accounted for about 60%. In addition, some groups of insects (i.e. Coleoptera and Orthoptera) were the most frequently found prey taxa in relation to the number of stomachs examined (n = 11), which confirmed that the amount of preyed insects did not come from a single aberrant genet eating on a disproportionate number of insects, but from several specimens regularly foraging on these arthropods. Mammals accounted for 20%, reptiles for 8.6%, and vegetal matters for 5.7% of the total number of prey items, and all of these prey groups were just occasionally consumed by genets as confirmed by their low frequency of occurrence in relation to the number of stomachs examined (Tab. IV). Birds and frogs were more marginal in terms of percent composition of the diet. In terms of frequency of occurrence, insect remains were eaten significantly more often than any other type of prey by the Crested Genets (in every pairwise comparison, at least $P < 0.001$ at Yates' corrected χ^2 test with df = 1). Analysis of biomass contributions to the diet of *G. cristata* indicated that the giant rat (*Cricetomys* sp.) was the most important prey type, and that *Praomys tulbergi* was the second most important prey type (Tab. V).

TABLE IV

Summary of the dietary data recorded from 11 specimens of Genetta cristata *in southeastern Nigeria. Data were expressed as (i) number of genet stomachs in which a given food category was found (PNS), and (ii) number of occurrences of a given food category in relation to the total numbers of collected items (PNF).*

Prey type	PNS		PNF	
	n	%	*N*	%
Cricetomys sp. (juv.)	1	9.1	1	1.64
Mus musculoides	3	27.3	5	8.20
Lophuromys sikapusi	1	9.1	1	1.64
Praomys tulbergi	2	18.2	3	4.92
Passeriformes indet. *(pulli)*	1	9.1	4	6.56
Trychobatrachus robustus	1	9.1	2	3.28
Mabuya sp.	2	18.2	3	4.92
Panaspis togoensis	1	9.1	1	1.64
Orthoptera indet.	7	63.6	12	19.67
Goliathus goliathus	1	9.1	1	1.64
Arcon centaurus	1	9.1	2	3.28
Coleoptera indet.	7	63.6	14	22.95
Other insects	2	18.2	4	6.56
Myriapoda indet.	2	18.2	3	4.92
Pandinus imperator	1	9.1	2	3.28
Vascular plants	2	18.2	3	4.92
Fruits, berries or seeds	2	18.2	3	4.92

The list of preys for *G. maculata* is presented in table VI, whereas the biomass contribution of the various items is given in table VII. The dietary spectrum was relatively broad, and qualitatively similar to that of *G. cristata* in terms of PNS, PNF, and biomass (compare Tab. IV & V with Tab. VI & VII). Analysis of biomass contributions indicated that, exactly as in the previous species, the giant rat (*Cricetomys* sp.) was the most important prey type, and *Praomys tulbergi* was the second most important prey type. Hence, the two species were also very similar in terms of diet habits when biomass is taken into account.

TABLE V

Summary of the dietary data recorded from 11 specimens of Genetta cristata *in southeastern Nigeria, in terms of biomass contribution of the various prey taxa. In this table, the biomass is calculated as the total biomass contributions in g of the various items (n B) and as their relative percentage to the total biomass (% B)*

Prey type	*n B*	*% B*
Cricetomys sp. (juv.)	310.3	37.8
Mus musculoides	45.7	5.6
Lophuromys sikapusi	63.1	7.7
Praomys tulbergi	114.1	13.9
Total Mammals		65.0
Passeriformes indet. (*pulli*)	36	4.4
Total Birds		4.4
Trychobatrachus robustus	37.2	4.5
Total Amphibians		4.5
Mabuya sp.	11.6	1.4
Panaspis togoensis	3.5	0.4
Total Reptiles		1.8
Orthoptera indet.	52.3	6.4
Goliathus goliathus	21.1	2.6
Arcon centaurus	14.6	1.8
Coleoptera indet.	33.4	4.1
Other insects	10.2	1.2
Myriapoda indet.	33.6	4.1
Pandinus imperator	26.2	3.2
Total Arthropods		23.4
Vascular Plants	7.8	0.9
Total (g)	820.7	

Results of Monte Carlo simulations (1 000 iterations) for PNS, PNF, and biomass are given in table VIII. Simulations done by comparing randomised versus actual matrix data for two different equations (Pianka and Czekanowski) showed that the distribution of the two species across the niche categories was not random ($P < 0.045$). High interspecific overlaps were found in terms of both PNS and PNF, whereas there were statistically significant differences ($P < 0.01$; Kruskal-Wallis test) between the overlap value for biomass and those for PNF and PNS; that is, the interspecific overlap value for biomass was comparatively lower than that of both PNF and PNS (Tab. VIII). In other words, the two species appeared to partition more efficiently the prey resource in terms of biomass than in terms of taxonomic prey frequency.

DISCUSSION

ECOLOGICAL DISTRIBUTION

A first evidence of our study is that, in agreement with data presented by Powell & Van Rompaey (1998), the Crested Genet is confirmed to be present also in the territories of southern Nigeria situated west of the River Cross, and even west of the River Niger (see the record of Patani given in this paper, and the previous record by Powell & Van Rompaey,

TABLE VI

Summary of the dietary data recorded from 56 specimens of Genetta maculata *in southeastern Nigeria. Data were expressed as (i) number of genet stomachs in which a given food category was found (PNS), and (ii) number of occurrence of a given food category in relation to the total numbers of collected items (PNF)*

Prey type	PNS		PNF	
	n	%	*n*	%
Crocidura nigeriae	4	7.1	4	3.5
Crocidura poensis	1	1.8	1	0.9
Crocidura sp.	2	3.6	2	1.8
Cricetomys sp. (juv.)	4	7.1	5	4.3
Mus musculoides	2	3.6	3	2.6
Lemniscomys striatus	4	7.1	6	5.2
Praomys tulbergi	8	14.2	12	10.4
Dendromus sp.	1	1.8	1	0.9
Hybomys univittatus	4	7.1	4	3.5
Streptopelia semitorquata	2	3.6	2	1.8
Passeriformes indet. (*pulli*)	2	3.6	3	2.6
Bird eggs	3	5.3	6	5.2
Agama agama	4	7.1	4	3.5
Mabuya sp.	5	8.9	7	6.1
Psammophis phillipsi	1	1.8	1	0.9
Lamprophis fuliginosus	2	3.6	2	1.8
Orthoptera indet.	11	19.6	17	14.8
Coleoptera indet.	8	14.2	12	10.4
Arcon centaurus	3	5.3	3	2.6
Other insects	5	8.9	7	6.1
Myriapoda indet.	2	3.6	2	1.8
Araneae	1	1.8	1	0.9
Fruits, berries or seeds	6	10.7	9	7.8

1998). Furthermore, our new records also demonstrate for the first time the occurrence of the Crested Genet in the extensively deforested region situated between the central axis of the River Niger Delta and the River Cross, i.e. in the area currently assigned to the states of Abia and Akwa-Ibom.

Our logistic regression model is particularly important because it is the first attempt to link the presence/absence of the African genets with the habitat features of their range at a quantitative level, and not just at a merely descriptive way (as done in other previous studies, e.g. see Heard & Van Rompaey, 1990; Powell & Van Rompaey, 1998; Angelici *et al.*, 1999b). Interestingly, our model shows that the two species are differently influenced by the various environmental factors. To begin with, our model not only shows statistically that the Crested Genet is a species of forest habitats (as empirically supposed by previous authorities, i.e. Happold, 1987; Heard & Van Rompaey, 1990; Angelici *et al.*, 1999a, 1999b, 1999c), but it also allows to understand (i) the type of forest required by the species (the undisturbed dry forest), (ii) a type of forest-derived habitat which appears very important (bush-mango plantations inside the forest), and (iii) a list of types of plantation (other than

TABLE VII

Summary of the dietary data recorded from 56 specimens of Genetta maculata *in southeastern Nigeria, in terms of biomass contribution of the various prey taxa. In this table, the biomass is calculated as the total biomass contributions in g of the various items (n B) and as their relative percentage to the total biomass (% B)*

Prey type	*n B*	*% B*
Crocidura nigeriae	92.1	2.4
Crocidura poensis	16.8	0.4
Crocidura sp.	32.2	0.8
Cricetomys sp. (juv.)	1 550.8	41.1
Mus musculoides	27.3	0.7
Lemniscomys striatus	249.7	6.6
Praomys tulbergi	456.1	12.1
Dendromus sp.	7	0.2
Hybomys univittatus	248	6.6
Total Mammals		70.9
Streptopelia semitorquata	410	10.8
Passeriformes indet. (*pulli*)	21.1	0.6
Bird eggs	30	0.8
Total Birds		12.2
Agama agama	108.7	2.9
Mabuya sp.	57.4	1.5
Psammophis phillipsi	187	4.9
Lamprophis fuliginosus	134.5	3.6
Total Reptiles		12.9
Orthoptera indet.	74.1	2.0
Coleoptera indet.	28.9	0.8
Arcon centaurus	12.7	0.3
Other insects	9.1	0.2
Myriapoda indet.	18.4	0.5
Araneae	3.1	0.1
Total Arthropods		3.9
Fruits, berries or seeds	1.8	0.05
Total	3 776.8	

suburban areas) which negatively affect the presence of this species (pineapple and oil palm). On the other hand, the presence of *G. maculata* is positively correlated with two habitat categories (derived savanna and oil palm plantations) and negatively with four types of forest (secondary as well as primary dry and flooded forests). Hence, our model shows the existence of a distinct interspecific difference in terms of factors influencing species' presence at the regional scale. We suppose that the different habitat requirements may allow the two genets to partition efficiently their spatial niche, especially in consideration of the fact that forest habitats which are important for *G. cristata* are negatively influencing *G. maculata*. If we consider that southern Nigeria has been environmentally devastated during the last 40 years (with more than 98% of the original forest being felled), it is likely that the newly created forest-derived savanna habitats has favoured the diffusion of the one species (*G. maculata*) to the detriment of the other (*G. cristata*). Hence, we predict that *G. cristata* may be extremely threatened, and we would urge the international community

TABLE VIII

*Monte Carlo simulations of niche overlap analysis, according to indices of Pianka and of Czekanowski applied to PNS, PNF (data in tables IV (*Genetta cristata*) and VI (*Genetta maculata*)) and biomass (Tab. V and VII). The model assumptions of the simulations are given in the table.*

	PNS	PNF	Biomass
Niche breadth	retained	retained	retained
Zero states	reshuffled	reshuffled	reshuffled
Resource use	equiprobable	equiprobable	equiprobable
Iterations	1 000	1 000	1 000
Pianka's overlap	0.909 9	0.884 2	0.714 5
Random seed	–13 751	26 294	14 394
P of indices being less than exp.	0.12	0.15	0.22
P of indices being more than exp.	0.88	0.85	0.78
Czekanowski's overlap	0.778	0.755	0.679 8
Random seed	–12 524	18 667	11 596
P of indices being less than exp.	0.09	0.18	0.34
P of indices being more than exp.	0.91	0.82	0.66

to establish high priority conservation plans for this species. In particular, a most interesting emergence of our study is that *G. cristata* responds differently to the various types of plantations: these genets are negatively affected especially by pineapples and oil palms, but also by bananas, yam, cassava, etc, as well as by the re-growing bush of the fields which have been abandoned after deforestation and cultivation. However, they are positively influenced by the presence of bush-mango plantations. We suppose that the positive link between this latter type of cultivation and the Crested Genet is in that bush-mango plantations are often small-scale cultivations, interspersed in forest areas. These cultivations may provide clearings inside the continuous forest-cover, and important food supply for the genets, which can find insects and lizards (which are particularly abundant in this type of plantation; Angelici *et al.*, unpublished data), and that may on occasion eat also the mango fruits (this study). On the other hand, it is likely that the other types of plantations are avoided by the genets because they are correlated with an *a priori* extensive deforestation: for instance, the oil palm plantations cover usually much larger surfaces than bush-mango plantations, and they usually occur in areas which have been strongly deforested. For instance, in the extensively deforested area situated east of the Orashi River course in Rivers State, the dominant landscape is oil-palm plantations, and the presence of the Crested Genet there has not been confirmed since long time (Heard & Van Rompaey, 1990). It is evident from these results that, if we are to protect the remnant populations of the Crested Genet, we need to put special attention to habitat conservation, by privileging the keeping of patches of mature dry forest with bush-mango plantations, which proved to be an ideal habitat for this species. Conversely, at least for this species, the other types of natural habitats of the region (e.g., mangroves and deltaic flooded forests) appeared quite negligible.

Concerning the local status of *G. maculata*, it should be noted that this is certainly the commonest genet species in southern Nigeria. However, this species is also certainly subjected to over-hunting, and may be locally at risk also in consideration of the continuing rates of habitat loss in this part of Africa.

DIET

Our data indicate that the two genet species are grossly similar in terms of their dietary preferences, with arthropods being the main prey type in terms of both the total number of prey items recorded and the number of stomachs containing a given prey type. However, when we take into account the biomass contributions of the various prey species, it is obvious that the mammal resource (and more generally the vertebrate resource) accounts for the major part of the diet of the two genet species. Hence, our data are quite consistent with those collected in Central African Republic from some species of medium-sized rainforest carnivores (Ray & Sunquist, 2001), but not for the Crested Genet whose feeding habits had never been previously studied. Our simulation analyses suggest that the competition for food should be relatively strong between the two genet species, because about 3/4 of the quantitative diets of the two species were identical under each of the three dietary descriptor parameters used in this study (PNS, PNF, or biomass). However, it is noteworthy that the similarity between species was proportionally less evident when biomass is considered than when the other two diet descriptors used are considered. Indeed, Schoener (1983) has demonstrated that high overlap values are likely positively correlated with an intense competition process when the food niche dimension is considered, whereas the same is not always true as for other niche dimensions, including e.g. macrohabitat and spatial use.

CONCLUSIONS

Our study has demonstrated that the two genet species differ significantly in terms of habitat use, whereas they are extremely similar in terms of dietary habits. These evidences were confirmed by all types of analyses performed, including descriptive analyses of current data as well as simulation studies. Therefore, we conclude that the two species partition the available habitat resource to reduce interspecific competition, as already seen in other carnivores (e.g. Chuang & Lee, 1997; Ray, 1997; Ray & Sunquist, 2001).

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REFERENCES

Angelici, F.M. (2000). — Food habits and resource partitioning of carnivores (Herpestidae, Viverridae) in the rainforests of southeastern Nigeria: Preliminary results. *Rev. Ecol. (Terre et Vie)*, 55: 67-76.

Angelici, F.M. & Gaubert, P. (in press). — *Genetta maculata* Common large-spotted Genet. *In*: J. Kingdon, D. Happold & T. Butynski (eds.), *The Mammals of Africa: Carnivora, Pinnipedia, Pholidota, Tubulidentata, Hyracoidea, Proboscidea, Sirenia, Perissodactyla*. Academic Press, London.

Angelici, F.M., Grimod, I. & Politano, E. (1999a). — Mammals of the Eastern Niger Delta (Rivers and Bayelsa States, Nigeria): An environment affected by a gas-pipeline. *Folia Zool.*, 48: 249-264.

Angelici, F.M., Luiselli, L. & Politano, E. (1999b). — Distribution and habitat of selected carnivores (Herpestidae, Mustelidae, Viverridae) in the rainforests of southeastern Nigeria. *Zeitschr. f. Säugetierk.*, 64: 116-120.

Angelici, F.M., Luiselli, L., Politano, E. & Akani, G.C. (1999c). — Bushmen and mammal-fauna: A survey of the mammals traded in bush-meat markets of local people in the rainforests of South-Eastern Nigeria. *Anthropozoologica*, 30: 51-58.

Boitani, L., Corsi, F., De Biase, A., D'Inzillo Carranza, I., Ravagli, M., Reggiani, G., Sinibaldi, I. & Trapanese, P. (1999). — *A databank for the conservation and management of the African Mammals*. Istituto di Ecologia Applicata, Rome.

Chuang S.A. & Lee L.L.(1997). — Food habits of three carnivore species (*Viverricula indica, Herpestes urva*, and *Melogale moschata*) in Fushan Forest, northern Taiwan. *J. Zool.*, 243: 71-79.

Coetzee, C.G. (1977). — Part 8. Order Carnivora. Pp. 1-42, *in*: J. Meester & H.W. Setzer (eds.), *The mammals of Africa. An identification manual*. Smithsonian Inst. Press, Washington, D.C.

Corbet, G.B. & Hill, J.E. (1986). — *A world list of mammalian species*. Second edition. British Museum (Natural History), London.

CRAWFORD-CABRAL, J. (1980-81). — The classification of the genets (Carnivora, Viverridae, genus *Genetta*). *Bol. Socied. Portug. Ciênc. Nat.*, 20: 97-114.

DE MONTCLOS, M.-P. (1994). — *Le Nigéria*. Kurthala, Paris.

EISENTRAUT, M. (1963). — *Die Wirbeltiere des Kamerungebirges*. Paul Parey, Hamburg.

FEINSINGER, P., SPEARS, E.E. & POOLE, R.W. (1981). — A simple measure of niche overlap. *Ecology*, 62: 27-32.

GAUBERT, P., FERNANDES, C.A., BRUFORD, M.W. & VÉRON, G. (2004). — Genets (Carnivora, Viverridae) in Africa: An evolutionary synthesis based on cytochrome *b* sequences and morphological characters. *Biol. J. Linn. Soc.*, 81: 589-610.

GOTELLI, N.J. & ENTSMINGER, G.L. (2000). — *EcoSym: null model software for ecology*. Acquired Intelligence Inc., New York.

GREENE, H.W. (1986). — Natural history and evolutionary biology. Pp. 99-108, *in*: M.E. Feder & G.V. Lauder (eds.), *Predator-prey relationships*. University of Chicago Press, Chicago.

GREENE, H.W. (1993). — What's good about *good* natural history. *Herp. Nat. Hist.*, 1: 3.

GRIFFITHS, J.F. (1972). — *Climates of Africa*. Elsevier, Paris.

HAPPOLD, D.C.D. (1974). — The small rodents of the forest-savanna-farmland association near Ibadan, Nigeria, with observations on reproduction biology. *Rev. Zool. Afr.*, 88: 814-836.

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

HEARD, S. & VAN ROMPAEY, H. (1990). — Rediscovery of the Crested Genet. *Mustelid and Viverrid Conservation*, 3: 1-4.

HOSMER, D.W. & LEMESHOW, S. (1989). — *Applied logistic regression*. Wiley, New York.

IUCN (2003). — *2003 IUCN Red List of Threatened Species*. The IUCN Species Survival Commission, Gland.

KINGDON, J. (1989). — *Island Africa. The evolution of Africa's rare animals and plants*. Princeton University Press, New Jersey.

KINGDON, J. (1997). — *The Kingdon field guide to African mammals*. Academic Press, London.

PIANKA, E.R. (1973). — The structure of lizard communities. *Ann. Rev. Ecol. Syst.*, 4: 53-74.

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

POWELL, C.B. & VAN ROMPAEY, H. (1998). — Genets of the Niger Delta, Nigeria. *Mustelid and Viverrid Conservation*, 19: 1-7.

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. & SUNQUIST, M.E. (2001). — Trophic relations in a community of African rainforest carnivores. *Oecologia*, 127: 395-408.

ROSEVEAR, D.R. (1969). — *The Rodents of West Africa*. British Museum (Natural History), London.

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

SANDERSON, I.T. (1940). — The mammals of North Cameroon Forest Area. Being the results of the Percy Sladen Expedition to the Mamfe Division of the British Cameroons. *Trans. Zool. Soc. London*, 24: 623-725.

SKINNER, J.D. & SMITHERS, R.H.N. (1990). — *The mammals of the southern African subregion*. New edition. University of Pretoria, Pretoria.

WINEMILLER, K.O. & PIANKA, E.R. (1990). — Organization in natural assemblages of desert lizards and tropical fishes. *Ecol. Monogr.*, 60: 27-55.

WOZENCRAFT, W.C. (1994). — Order Carnivora. *In*: D.E. Wilson & D.A.M. Reeder (eds.), *Mammal species of the world. A taxonomic and geographic reference*. Second edition. Smithsonian Institution Press, Washington and London.