

ARE THERE SHARED GENERAL PATTERNS OF SPECIFIC DIVERSITY, ABUNDANCE, AND GUILD STRUCTURE IN SNAKE COMMUNITIES OF TROPICAL FORESTS OF MADAGASCAR AND CONTINENTAL AFRICA?

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RÉSUMÉ

Une étude comparative de la composition des communautés de serpents de 45 sites forestiers tropicaux est présentée, appuyée sur des données originales ou prises dans la littérature. Douze sites sont localisés au Nigéria, un au Cameroun et 30 à Madagascar. Deux sites forestiers de Panama sont également utilisés dans les comparaisons. Les comparaisons inter-régionales montrent une remarquable constance entre les sites du nombre moyen d'espèces observées par minute ; les plus fortes similitudes s'observent entre les sites nigériens et malgaches ainsi qu'entre les sites nigériens et camerounais ; en revanche, les similitudes sont plus faibles entre tous ces sites africains et malgaches et les panaméens. L'altitude et la distance entre sites n'influent pas de manière significative sur la détection et l'estimation de l'abondance des espèces. Les sites nigériens présentent davantage de taxa semi-aquatiques que les malgaches. Au Nigéria comme à Madagascar, la guildes des terrestres est dominante et la guildes des arboricoles constituée d'une remarquable diversité d'espèces. La diversité des espèces fouisseuses syntopiques est très faible tant au Nigéria qu'à Madagascar (1 à 2 espèces seulement dans chacun des 22 sites étudiés). Sur les sites nigériens on observe en général une dominance des espèces spécialisées dans la consommation de lézards et de mammifères, mais les batracophages et les ornithophages sont eux aussi abondants. Sur les sites malgaches, on observe une prévalence significative des consommateurs de lézards, suivis par les chasseurs de batraciens, les autres spécialistes (p.e. les prédateurs de mammifères) étant bien moins représentés. Les abondances des espèces généralistes et des espèces se nourrissant d'invertébrés sont semblables dans les deux régions géographiques alors que les piscivores n'ont été rencontrés qu'au Nigéria. La rareté à Madagascar des espèces consommatrices de mammifères, de poissons et d'oiseaux pourrait s'interpréter comme un patron biogéographique général en termes de disponibilité des types de proies (en considérant la rareté relative de certains types de proies dans les forêts et rivières malgaches) ainsi que de distribution des tailles des serpents. Pour ce qui concerne cette distribution de la taille des serpents au sein des divers peuplements étudiés, il apparaît que le milieu forestier peut héberger autant d'espèces de moins de 2 m de long au Nigéria qu'à Madagascar mais que seul le Nigéria héberge des espèces géantes ou du moins de très grande taille (de 2 à 9 m de long). Les patrons écologiques qui émergent de cette étude comparative sont discutés dans le cadre des théories actuelles de l'écologie des peuplements et de la biogéographie.

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SUMMARY

A comparative study of snake community composition of 45 tropical forest patches, including both original and literature data, is presented. Twelve study areas are situated in Nigeria, one in Cameroon, and 30 in Madagascar. Two forest sites from Panama were also used as outgroups. There was a remarkable consistency among sites in inter-regional comparisons in terms of mean number of species observed \times min.⁻¹. The highest similarities were between Nigerian and Malagasy sites and between Cameroon and Nigerian sites, whereas similarities between all these African sites and Panama sites were lower. Altitude and linear distances among sites did not influence significantly the snake species detection and abundance. Nigerian sites had comparatively higher numbers of semi-aquatic taxa than Malagasy sites. The terrestrial guild was the dominant one, and the arboreal guild was constituted by a remarkable diversity of species, in nearly all sites of both Nigeria and Madagascar. There was a very low diversity of syntopic fossorial species in both Nigeria and Madagascar (in all 22 study plots, only 1 or 2 fossorial species were found). In Nigerian sites there was a general prevalence of primarily lacertophagous and mammalophagous species, but batracophagous and ornithophagous species were also quite abundant. In the Malagasy sites lacertophagous species were significantly prevalent, followed by batracophagous species, whereas species with other dietary preferences (e.g., mammalophagous) were much under-represented. The abundance of species feeding on invertebrates and of generalist species was similar in the two geographic regions, whereas piscivorous species were found only in the Nigerian sites. The scarcity of mammalophagous, piscivorous and ornithophagous species in Madagascar could be interpreted as a general biogeographic pattern in terms of food type availability (taking into account the scarcity of some types of prey in Malagasy forests and freshwater streams) as well as in terms of snake size distributions. With regard to snake body size distributions in the various examined communities, it appeared that forest environments of both Nigeria and Madagascar can house a similar snake community as for numbers of species < 2 m in length, but Nigerian environments can harbour numbers of giant and very large species (from 2 to 9 m in length) that cannot be held in Malagasy forests. The ecological patterns emerged in this comparative study are discussed in the light of current community ecology theory and biogeography.

INTRODUCTION

The study of community structure has received much impulse since the age of Hutchinson and MacArthur in the period 1960-1970, and, with regard to herpetological communities, has considerably revived since Scott's (1982a) miscellaneous contribution, and a series of later literature (e.g., Ortega *et al.*, 1982; Barbault *et al.*, 1985; Schoener, 1985; Toft, 1985; Pianka, 1986; Hairston, 1987; Auffenberg & Auffenberg, 1988; Medel *et al.*, 1988; Gonzales-Romero *et al.*, 1989; Henle, 1989a, b; Fitch, 1999).

Afrotropical herpetological communities have been considerably less studied, and the most complete bulk of work currently available is no doubt that of Barbault (1974, 1975, 1977, 1987, 1991) who worked in a wet savanna of Ivory Coast. Barbault's work demonstrated that predation by snakes influences significantly the abundance and population dynamics of their preys, mainly lizards and frogs (Barbault, 1977, 1991). Considering it is generally admitted that an increase in species variety from poles to equator goes together with a diversification and intensification of the predatory process (Barbault, 1991), and that the snake communities in African tropical forests are very diversified (e.g., Butler & Reid, 1989), it is likely that these predators can considerably affect the population dynamics of fish, amphibians, lizards, mammals, and birds. Thus, the understanding of the general patterns of community composition of Afrotropical forest snakes is an essential step to assess the general ecosystem structure and function of these nowadays endangered environments.

Despite the importance of snake communities in ecosystem dynamics of tropical forests is well established, it is still quite difficult to gather quantitative data from the literature. Thus, since some years we are studying the community ecology of the herpetofauna in the tropical forest ecosystems of Madagascar and southern Nigeria, in the aim to learn more about the general functioning of these ecosystems and the relative role of their diversified reptile and amphibian fauna. With regard to Nigeria, some papers have already been published (Akani *et al.*, 1999a, 1999b; Luiselli *et al.*, 1998; Luiselli & Akani, 1999). Concerning Madagascar, some information on the ecology and taxonomy of the herpetofauna is provided, among others, by Andreone (1991a, b), Raxworthy & Nussbaum (1994b, 1996), Raxworthy *et al.* (1998), Andreone & Randriamahazo (1997), and Andreone *et al.* (in press). Anyway, excepting for the works by Andreone and collaborators, almost all the recent field studies deal with the species presence-absence (with a range of ecological and biogeographic considerations), without furnishing information about the exact numbers of observed specimens. This is indeed a limiting factor, since, either for ecological or conservation considerations, quantitative data are strongly needed.

In this paper we present data on the snake-fauna community composition of several study sites in southern Nigeria and Madagascar, and compare them with available information for other tropical forest snake communities. In particular, we compare (when possible and when data are available) in each study site:

- (1) the abundance of snakes in terms of number of species observed \times min.⁻¹ of sampling effort and number of specimens observed \times min.⁻¹ of sampling effort;
- (2) the specific diversity index;
- (3) the effects of altitude and linear distance among sites on the snake abundance;
- (4) the structure of the various communities in terms of habits;
- (5) the structure of the various communities in terms of dietary preferences;
- (6) the structure of the various communities in terms of body sizes.

Finally, we search for any general pattern shared among the various communities or for any remarkable difference among them, and try to interpret the emerging patterns in function of the global theories of community ecology.

MATERIALS AND METHODS

STUDY AREAS

A total of 45 forest patches were surveyed, including both original and literature data (Table I). Twelve study areas came from Nigeria, one from Cameroon, 30 from Madagascar, and two, used as "outgroups" in our analyses, from Panama. Some literature sources were lacking of some data-sets (e.g., frequency of observations of snakes in relation to effort unity) (see Table I), and so our comparative analyses have been carried out to the best precision possible. A list of sites and related references is given as follows. Furthermore, for Malagasy sites, information about latitudes and longitudes (taken by means of a Global Positioning System GPS, or by consulting the relative bibliographic reference) is given in Table III.

Madagascar: the sites are situated in the typical low- (< 800 m a.s.l.), mid- (800 < h < 1,200 m a.s.l.) and high-altitude (> 1,200 m a.s.l.) eastern evergreen rainforest belt (Parc National d'Andohahela: Andreone & Randriamahazo, 1997; Réserve Spéciale d'Anjanaharibe-Sud: Andreone & Raxworthy, 1998; Nussbaum *et al.*, 1998, Raxworthy *et al.*, 1998; Anjozorobe-Andranomay Forest: Raselimanana *et al.*, 1998; Parc National d'Andringitra: Raxworthy & Nussbaum, 1996; Parc National de la Montagne d'Ambre: Raxworthy & Nussbaum, 1994a; Ambolokopatrika Forest: Andreone *et al.*, in press; Tsararano Forest: Andreone *et al.*, in press; Parc National de Masoala: Andreone & Randrianirina, unpublished), evergreen eastern littoral forest (Tampolo Forest: Raselimanana *et al.*, 1998), north-western Sambirano evergreen forests (Réserve Naturelle Intégrale de Lokobe - Nosy Be: Andreone & Randrianirina, unpublished), central-southern deciduous forests (Parc National de Zombitse: Raxworthy *et al.*, 1994). It should be remembered that the eastern rainforest belt of Madagascar, once almost continuous from Vohémar (North-East) to Tolagnaro (South-East), is currently very fragmented, mainly due to the *tavy* practice (slush and burn agriculture), and today there is a mosaic of more or less pristine forests (in some occasions protected as natural reserves) and bare, secondary grassland formations (Green & Sussman, 1990). The same, anyway, can be said for almost all the forests of Madagascar, and the western and the littoral forests too are indeed among the most endangered habitats. A more in depth analysis of the vegetation and forest situation in Madagascar is reported elsewhere (e.g., Jenkins, 1987; Nicoll & Langrand, 1989).

Nigeria: we analysed data coming from twelve localities which have been subjected to careful research in the recent years (Akani *et al.*, 1999a, b; Luiselli *et al.*, 1998; Luiselli & Akani, 1999). All these localities are situated in the south-eastern part of the country, which lies within the continuous Guinea-Congolian rainforest zone (White, 1983, 1986). Details of the environmental characteristics of these study sites are presented elsewhere (e.g., Akani *et al.*, 1999a, b; Luiselli *et al.*, 1998, 2000b; Luiselli & Akani, 1999). In general, forest patches, either of the freshwater swamp-forest type or of the dryland type, are interspersed within a patchy mosaic of farmlands, plantations, and industrial areas, this region of Nigeria being one of the most developed of the whole African continent (De Montclos, 1994).

Cameroon: we used data from Scott (1982b); this author worked in the surroundings of Tissongo Lake, in the southern region of Cameroon. The study area was characterized by a lowland evergreen rainforest.

Panama: we used data available for Panama in Myers & Rand (1969), who made surveys in Barro Colorado Island and in Barro Colorado, where evergreen lowland rainforest was present.

STUDY METHODS

Details of field observational and capture methodologies employed are already presented in the original papers (e.g., Myers & Rand, 1969; Scott, 1982b; Luiselli *et al.*, 1998, 2000b; Raxworthy *et al.*, 1998; Akani *et al.*, 1999a, b; Luiselli & Akani, 1999; Andreone *et al.*, in press). Anyway, our data collecting in the field were relatively consistent among the various areas, and were based on (i) the recording of all the snake specimens encountered during random walks across the studied territories, and (ii) the recording of the total amount of minutes spent in

searching for snakes (field effort). Opportunistic searching and refuge examination were conducted in all natural habitats available. Secretive species were sought in their refuges (e.g., fallen logs, under bark, in leaf litter, soil, and leaf axils of palms). Night searches were made with the aid of head-lamps and flashlights. A second collecting method consisted in pitfall bucket traps and other trap devices, whose detailed description is given elsewhere (e.g., Andreone *et al.*, in press; Raxworthy *et al.*, 1998; Akani *et al.*, 1999a). Voucher specimens of Malagasy taxa were sacrificed (by means of a choroethanol injection) and fixed in 10 % buffered formalin and later transferred in 75° ethanol. The collected material has been deposited in the Malagasy Herpetological Collection at the Museo Regionale di Scienze Naturali, Torino (Italy), and the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo (Madagascar). Voucher specimens of Nigerian species are stored in the collections of the Department of Biological Sciences, Rivers State University of Science and Technology, Port Harcourt (Rivers State, Nigeria), and in the private collections of one of the authors and of his collaborators F.M. Angelici (Rome) and G.C. Akani (Port Harcourt).

To evaluate the taxonomic composition of the snake communities in every study sites, we took into account both the visual observations and the captures, done either by hands or by traps (e.g., Akani *et al.*, 1999a and Andreone *et al.*, in press). However, for estimating the relative abundance of snakes in the various study areas, we used only data gathered by visual observations and captures of snake specimens encountered during walks, excluding therefore trapping data.

GUILD AND STATISTICAL ANALYSES

To measure snake abundance in the study areas, we estimated the total effort in the field (intended as the total number of minutes spent in searching for snakes in each day and in the whole study period), then we divided the total number of snakes observed each day by the number of minutes spent in the field in each day. For this kind of analyses we took into account all the sites, as visited by us during our field surveys, or given in literature. Furthermore we calculated the linear distance (in km) between all the analysed sites. The composition of the snake communities was analysed in terms of “habits”, “dietary preferences” and “size”. For these analyses we pooled together all the data regarding a certain locality (e.g., the sites named in Table I Anjanaharibe-Sud W1-W2 and E1-E4 were pooled to give the general site “Anjanaharibe-Sud” of Tables III-VI).

The community in terms of “habits” was distinguished in the following types: (1) fossorial, (2) terrestrial, (3) semi-aquatic, and (4) arboreal snake species (see also Luiselli *et al.*, 1998).

Although little is known for the exact food habits of tropical snakes, they were analysed subdividing the taxa in nine guilds: species preying on 1) insects and other invertebrates; 2) fish; 3) amphibians; 4) lizards (including chameleons); 5) snakes; 6) birds; 7) mammals; 8) bird eggs; the last guild being species with a very generalist diet.

The composition of the snake communities in terms of “body size” (maximal total length) was then analysed taking into account five species categories: 1) snakes larger than 4,000 mm (giant species); 2) snakes between 4,000 and 2,000 mm (big species), 3) snakes between 1,500 and 2,000 mm (large species); 4) snakes between 800 and 1,500 mm (medium sized species); 5) snakes between 200 and 800 mm (small species).

TABLE I

Comparison of numbers of snake species per effort unit, snake specimens per effort unit, Margalef's diversity index, among several study areas situated in continental Africa (Nigeria and Cameroon), Madagascar, and Central America (Panama). Elevation (in meters above sea level) of each site, field effort (in minutes), and pertinent literature reference is also given. Numbers of species in each site presented in this table came only from quantitative surveys, and do not include additional presence records from qualitative surveys.

Country	Site	Altitude	Forest type	Field effort	Number of species	Number of specimens	Species / min	Specimens / min	Margalef's index	Literature source
Cameroon	Lac Tissongo	30	rainforest	3,960	6	6	0.001515	0.00152	2.971	Scott, 1982b
Nigeria	Abarikbo	< 20	rainforest	2,400	0	0	0	0	***	Akani <i>et al.</i> , 1999a
Nigeria	Ejule	150	derived savanna	12,475	18	51	0.001443	0.00409	4.324	Akani <i>et al.</i> , 1999a
Nigeria	Eket	< 10	rainforest	20,079	24	115	0.001195	0.00573	4.847	Akani <i>et al.</i> , 1999a
Nigeria	Kreigeni	< 10	rainforest	2,400	3	4	0.001250	0.00167	1.443	Akani <i>et al.</i> , 1999a
Nigeria	Orashi	< 10	rainforest	2,400	4	8	0.001667	0.00333	1.443	Akani <i>et al.</i> , 1999a
Nigeria	Orubiri	< 50	rainforest	2,400	0	0	0	0	***	Akani <i>et al.</i> , 1999a
Nigeria	Otari	< 30	rainforest	2,400	2	3	0.000833	0.00125	0.910	Akani <i>et al.</i> , 1999a
Nigeria	Peterside	0	rainforest	2,400	4	6	0.001667	0.00250	1.674	Akani <i>et al.</i> , 1999a
Nigeria	Rumuji	25	rainforest	2,400	1	3	0.000417	0.00125	0	Akani <i>et al.</i> , 1999a
Nigeria	Soku	40	rainforest	2,400	3	5	0.001250	0.00208	1.243	Akani <i>et al.</i> , 1999a
Nigeria	Tombia I	< 10	rainforest	2,400	3	7	0.001250	0.00292	1.028	Akani <i>et al.</i> , 1999a
Nigeria	Tombia II	0	rainforest	2,400	2	4	0.000833	0.00167	0.721	Akani <i>et al.</i> , 1999a
Madagascar	Ambolokopatrika I	800-900	rainforest	3,240	3	5	0.000926	0.00154	1.243	Andreone <i>et al.</i> in press
Madagascar	Ambolokopatrika II	950-1,300	rainforest	3,600	4	9	0.001111	0.00250	1.365	Andreone <i>et al.</i> in press
Madagascar	Andranomay	1,300	rainforest	2,880	5	not avail.	0.001736	not avail.	not avail.	Raselimanana, 1998
Madagascar	Andringitra I	650-800	rainforest	3,240	7	not avail.	0.002160	not avail.	not avail.	Raxworthy & Nussbaum, 1996
Madagascar	Andringitra II	750-860	rainforest	2,880	3	not avail.	0.001042	not avail.	not avail.	Raxworthy & Nussbaum, 1996
Madagascar	Andringitra III	1,100-1,350	rainforest	2,880	3	not avail.	0.001042	not avail.	not avail.	Raxworthy & Nussbaum, 1996
Madagascar	Andringitra IV	1,550-1,700	rainforest	2,520	1	not avail.	0.000397	not avail.	not avail.	Raxworthy & Nussbaum, 1996
Madagascar	Andringitra V	1,850-2,300	rainforest	720	0	not avail.	0	not avail.	not avail.	Raxworthy & Nussbaum, 1996
Madagascar	Anjanaharibe W1	1,000-1,100	rainforest	3,600	5	6	0.001389	0.00167	2.232	Raxworthy <i>et al.</i> (1998)
Madagascar	Anjanaharibe W2	1,200-1,600	rainforest	3,240	3	3	0.000926	0.00111	1.820	Raxworthy <i>et al.</i> (1998)
Madagascar	Anjanaharibe E1	800-950	rainforest	4,680	6	not avail.	0.001282	not avail.	not avail.	Raxworthy <i>et al.</i> (1998)
Madagascar	Anjanaharibe E2	1,100-1,350	rainforest	4,320	1	not avail.	0.000231	not avail.	not avail.	Raxworthy <i>et al.</i> (1998)
Madagascar	Anjanaharibe E3	1,500-1,700	rainforest	3,600	1	not avail.	0.000278	not avail.	not avail.	Raxworthy <i>et al.</i> (1998)
Madagascar	Anjanaharibe E4	1,850-2,000	rainforest	1,800	1	not avail.	0.000556	not avail.	not avail.	Raxworthy <i>et al.</i> (1998)

Country	Site	Altitude	Forest type	Field effort	Number of species	Number of specimens	Species / min	Specimens / min	Margalef's index	Literature source
Madagascar	Lokobe	0-100	Sambirano forest	2,880	5	6	0.001736	0.00208	2.232	Andreone & Randrianirina, unpublished
Madagascar	Masoala I	450-550	rainforest	3,600	6	15	0.001667	0.00417	1.846	Andreone & Randrianirina, unpublished
Madagascar	Masoala II	600-700	rainforest	2,880	4	8	0.001389	0.00278	1.443	Andreone & Randrianirina, unpublished
Madagascar	Masoala III	600-700	rainforest	3,240	8	14	0.002469	0.00432	2.652	Andreone & Randrianirina, unpublished
Madagascar	Tsararano I	700-850	rainforest	3,600	3	35	0.000833	0.00972	0.563	Andreone <i>et al.</i> , in press
Madagascar	Tsararano II	600-750	rainforest	3,240	6	23	0.001852	0.00710	1.595	Andreone <i>et al.</i> , in press
Madagascar	Zombitse I	700-900	deciduous	4,800	5	not avail.	0.001042	not avail.	not avail.	Raxworthy <i>et al.</i> (1994)
Madagascar	Zombitse II	700-900	deciduous	1,560	3	not avail.	0.001923	not avail.	not avail.	Raxworthy <i>et al.</i> (1994)
Madagascar	Zombitse III	700-900	deciduous	360	0	not avail.	0	not avail.	not avail.	Raxworthy <i>et al.</i> (1994)
Madagascar	Zombitse IV	700-900	deciduous	540	5	not avail.	0.009259	not avail.	not avail.	Raxworthy <i>et al.</i> (1994)
Madagascar	Zombitse V	700-900	deciduous	7,260	7	not avail.	0.000964	not avail.	not avail.	Raxworthy <i>et al.</i> (1994)
Madagascar	Andohahela I	200-700	rainforest	6,120	3	4	0.000490	0.00065	1.443	Andreone & Randriamahazo, 1997
Madagascar	Andohahela II	200-700	rainforest	4,680	5	14	0.001068	0.00299	1.516	Andreone & Randriamahazo, 1997
Madagascar	Tampolo	5-10	littoral	4,680	13	not avail.	0.002778	not avail.	not avail.	Raselimanana <i>et al.</i> , 1998
Madagascar	Montagne d' Ambre	900-1,500	rainforest	20,880	16	not avail.	0.000766	not avail.	not avail.	Raxworthy & Nussbaum, 1994a
Panama	Barro Colorado Isl.	< 50	rainforest	5,460	11	not avail.	0.00200	not avail.	not avail.	Myers & Rand, 1969
Panama	Barro Colorado	< 50	rainforest	3,240	6	not avail.	0.00190	not avail.	not avail.	Myers & Rand, 1969

Then, the community composition in terms of “habits”, “dietary preferences” and “body size” was compared among sites by means of χ^2 test. Statistical analyses were done with SPSS (version 6.0 for Windows) and STATISTICA software packages. All tests were two-tailed, and alpha was set at 5%. Relationships between log-transformed variables were assessed by the Pearson product-moment correlation coefficient. To compare variables among sites, we used non-parametric Kruskal-Wallis ANOVA followed by Tukey honest significance *post-hoc* test or Duncan’s multiple range *post-hoc* test. Species diversity was calculated using Margalef’s Diversity Index (Magurran, 1988).

The taxonomic status of some taxa (e.g., *Psammophis phillipsi*, *Crotaphopeltis hotamboeia*, *Dasypeltis* sp., *Naja nigricollis* for Nigeria, and those belonging to the genera *Typhlops*, *Geodipsas*, *Liophidium*, *Liopholidophis*, and *Pseudoxyrhopus* for Madagascar) is still confused and far from being totally established, and possibly will undergo modification and revision by systematic works in the future. While waiting for these revisions, we have followed the nomenclature given by Meirte (1992) in the case of mainland Africa species, and Glaw & Vences (1992, 1994), Raxworthy & Nussbaum (1994a, b), Cadle (1996a, b) for Malagasy taxa. The Malagasy boine species, attributed by Kluge (1991) to the genus *Boa* (classification as followed by some recent authors: e.g., Raxworthy *et al.*, 1998) are here maintained to the former classification (e.g., Glaw & Vences, 1992, 1994), basing upon recent, still unpublished genetic studies (M. Vences, 1999 pers. comm.), and therefore *Acrantophis dumerili* (= *Boa dumerili*), *A. madagascariensis* (= *Boa madagascariensis*), and *Sanzinia madagascariensis* (= *Boa manditra*).

RESULTS

FIELD EFFORT, SNAKE SPECIES NUMBER, ABUNDANCE AND DIVERSITY

The summary of the data on field efforts, snake abundance and specific diversity recorded from each study site is given in Table I.

Kruskal-Wallis ANOVAs showed that the mean number of species observed \times min.⁻¹ was very similar in the tropical forests of either southern Nigeria, Cameroon, Madagascar, or Panama ($F = 1.374$, $df = 3, 41$, $P = 0.264$; see Figure 1), and both Duncan’s multiple range and Tukey compromise *post-hoc* tests indicated that the highest similarities were between Nigerian and Malagasy sites ($P = 0.808$) and between Cameroon and Nigerian sites ($P = 0.984$), whereas the similarities of all these “African” sites with Panama sites were smaller (P values ranging between 0.200 and 0.344). MANOVA models (with number of species \times min.⁻¹ as the factor, individual forest, altitude, linear distance among sites, forest type, and categorized field effort as the covariates) showed that only individual forest could influence the studied factor ($P < 0.041$), whereas all the other factors were entirely irrelevant to the observed pattern (in all cases, at least $P > 0.211$). Kruskal-Wallis ANOVAs showed that the mean number of snake specimens observed \times min.⁻¹ was also very similar in the tropical forests of both Nigeria and Madagascar ($F = 1.498$, $df = 1, 26$, $P = 0.232$; see Figure 2). In this latter set of analyses we removed data from Cameroon and Panama because they were unsatisfactorily explained in the original papers (Myers & Rand, 1969; Scott, 1982b, and see Table I). MANOVA models (with number of specimens \times min.⁻¹ as

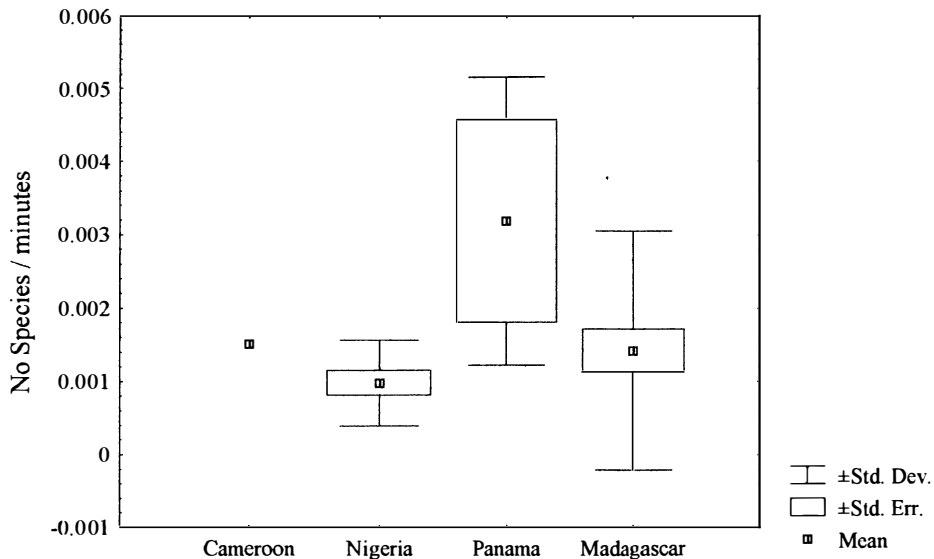


Figure 1. — Box-and-whisker plot showing the averages (and dispersion measures) of the mean number of species observed $\times \text{min.}^{-1}$ in the main Afrotropical and Malagasy study regions (Nigeria, Cameroon, and Madagascar). Panama is put as an outgroup for comparisons. For statistical details, see text.

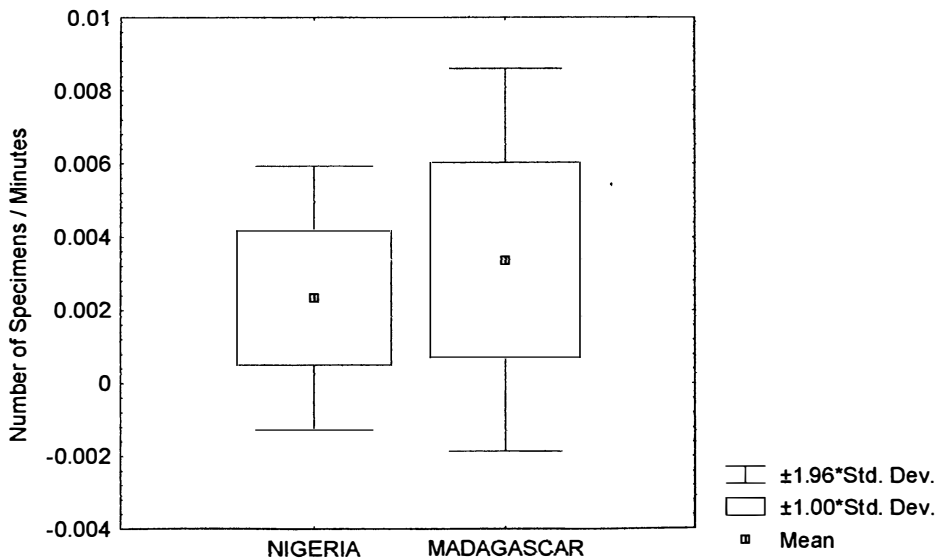


Figure 2. — Box-and-whisker plot with the averages (and dispersion measures) of the mean number of specimens observed $\times \text{min.}^{-1}$ in tropical forests of Nigeria and Madagascar. For statistical details, see text.

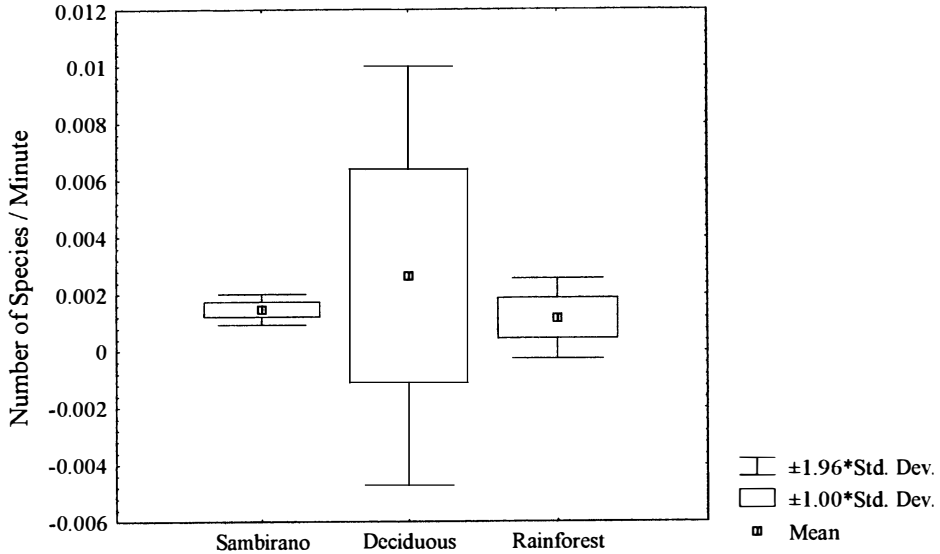


Figure 3. — Box-and-whisker plot showing the averages (and dispersion measures) of the mean number of species observed $\times \text{min.}^{-1}$ in three types of analysed forests in Madagascar. For statistical details, see text.

the factor, individual forest, altitude, linear distance among sites, forest type, and categorized field effort as the covariates) showed that not any correlates could influence significantly the studied factor (in all cases, at least $P > 0.131$).

With regard to Madagascar, the rainforest sites did not differ significantly from the Sambirano sites and from the deciduous forest sites in terms of mean number of species observed $\times \text{min.}^{-1}$ (Kruskal-Wallis ANOVA: $F = 1.800$, $df = 2, 27$, $P = 0.184$; see Figure 3), and Duncan's multiple range *post-hoc* test suggested that Sambirano sites were much closer to rainforest sites than to deciduous forest sites.

Values of Margalef's diversity index varied remarkably from site to site in each of the studied regions (ranges for continental Africa: from 0 to 4.837; for Madagascar: from 0.563 to 2.652). In this case, the ranges for continental Africa (Cameroon + Nigeria) were much higher than those for Madagascar (Figure 4). However, this turned out to be a mere artifact of the fact that in the Nigerian plots there was a much higher variation in terms of field effort (values ranging from 2,400 min to 20,079 min per site) than in Madagascar (values ranging from 2,400 to 7,800 per site). This evidence could be appreciated if we consider that field effort significantly affected the calculations of mean number of species observed $\times \text{min.}^{-1}$ and number of specimens $\times \text{min.}^{-1}$ as well as Margalef's index values (see Akani *et al.*, 1999a). If we correct Nigerian scores for field effort categories,

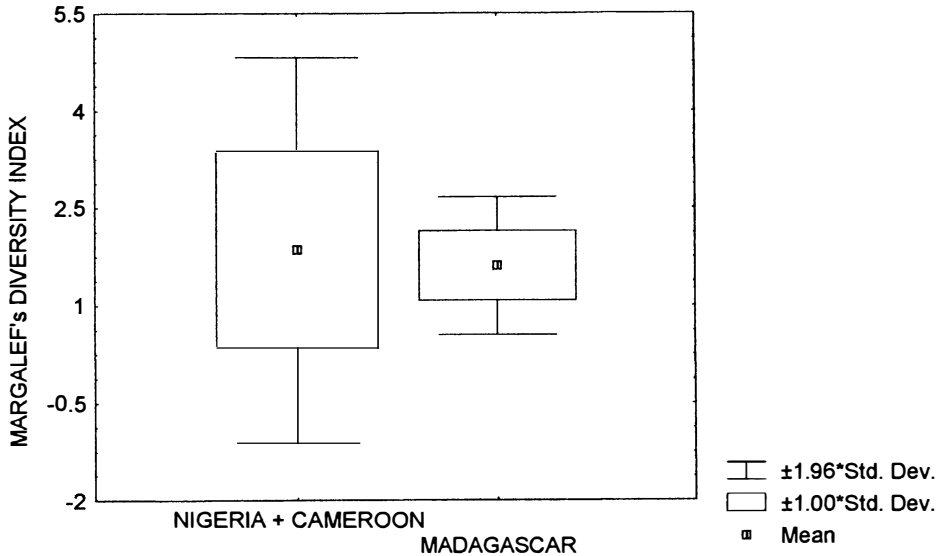


Figure 4. — Box-and-whisker plot showing the averages (and dispersion measures) of Margalef's diversity index calculated for study plots situated in the tropical forests of Nigeria and Madagascar. For statistical details, see text.

the application of a Kruskal-Wallis ANOVA model showed no significant difference between Nigeria and Madagascar in terms of Margalef's diversity index values ($F = 0.257$, $df = 1,20$, $P = 0.618$).

If we pool all the study sites in the analyses, altitude did not influence either the mean number of species observed $\times \text{min.}^{-1}$ ($r = 0.074$, adjusted $r^2 = -0.019$, ANOVA $F = 0.221$, $df = 1,40$, $P = 0.64$) or the mean number of specimens observed $\times \text{min.}^{-1}$ ($r = 0.265$, adjusted $r^2 = 0.070$, ANOVA $F = 1.736$, $df = 1, 23$, $P = 0.200$). However, if we consider single areas for which data in sites at different altitudes are available (e.g., Andringitra, Anjanaharibe-Sud, and Zombitse, all in Madagascar), there was a slight tendency for a reduction of species abundance and diversity with altitude increases.

STRUCTURE OF THE SNAKE COMMUNITIES IN TERMS OF "HABITS"

The list including all the snake species encountered in both Nigeria and Malagasy sites with data relative to their body size, habits, and feeding preferences is presented in Table II, whereas list of species found in each study site of Madagascar is given in Table III. Concerning species of Nigerian sites, the complete list could be found in the original literature sources (Akani *et al.*, 1999a, b; Luiselli *et al.*, 1998; Luiselli & Akani, 1999).

TABLE II

List of the snake species encountered in the various surveyed sites of both Nigeria and Madagascar, with indication of their "habits", dietary preferences, and average body size (length, mm). Only the main (first) prey category has been used to establish the dietary preferences of the analysed snakes. The species preying upon more than two prey categories were indicated as "generalists". Abbreviations: M = mammalophagous; E = feeding upon bird eggs; S = (mainly) ophiophagous; L = feeding upon (mainly) lizards (including chameleons); F = ichthyophagous; I = (mainly) invertebratophagous; G = generalist species.

Snake species	Country	Average body size (mm)	Habits	Diet	
BOIDAE					
<i>Acrantophis dumerili</i>	Madagascar	1,500-1,800	terrestrial	mammals	M
<i>Acrantophis madagascariensis</i>	Madagascar	1,500-1,800	terrestrial	mammals	M
<i>Sanzinia madagascariensis</i>	Madagascar	2,500	terrestrial, arboreal	mammals	M
<i>Calabaria reinhardtii</i>	Nigeria	800-1,000	fossorial	mammals	M
<i>Python regius</i>	Nigeria	800-1,300	terrestrial	mammals, birds	M
<i>Python sebae</i>	Nigeria	3,000-9,000	terrestrial	mammals	M
TYPHLOPIDAE					
<i>Rhamphotyphlops braminus</i>	Madagascar	175	fossorial	invertebrates	I
<i>Typhlops domerguei</i>	Madagascar	150	fossorial	invertebrates	I
<i>Typhlops microcephalus</i>	Madagascar	235	fossorial	invertebrates	I
<i>Typhlops mucronatus</i>	Madagascar	378	fossorial	invertebrates	I
<i>Typhlops ocellaris</i>	Madagascar	342	fossorial	invertebrates	I
<i>Typhlops</i> sp. 1	Madagascar	unknown (likely 150-400)	fossorial	invertebrates	I
<i>Typhlops</i> sp. 2	Madagascar	unknown (likely 150-400)	fossorial	invertebrates	I
<i>Typhlops</i> sp. 3	Madagascar	unknown (likely 150-400)	fossorial	invertebrates	I
<i>Typhlops congestus</i>	Nigeria	500-700	fossorial	invertebrates	I
<i>Rhinotyphlops crossii</i>	Nigeria	200-300	fossorial	invertebrates	I
VIPERIDAE					
<i>Bitis gabonica</i>	Nigeria	1,300-2,000	terrestrial	mammals	M
<i>Bitis nasicornis</i>	Nigeria	800-1,300	terrestrial	mammals, frogs	M
<i>Atheris squamiger</i>	Nigeria	450-650	arboreal	mammals, birds	M
<i>Causus maculatus</i>	Nigeria	300-600	terrestrial	frogs	F
<i>Causus lichtensteini</i>	Nigeria	300-600	terrestrial	frogs	F
<i>Echis ocellatus</i>	Nigeria	300-500	terrestrial	mammals, lizards	M
ELAPIDAE					
<i>Dendroaspis jamesoni</i>	Nigeria	1,800-3,200	arboreal	birds, mammals	B
<i>Pseudohaje goldii</i>	Nigeria	1,500-2,500	arboreal	mammals, frogs	M, F
<i>Elapsoidea semiannulata</i>	Nigeria	300-500	fossorial	snakes	S
<i>Naja melanoleuca</i>	Nigeria	1,800-3,500	terrestrial	frogs, fish, mammals	G
<i>Naja nigricollis</i>	Nigeria	1,500-2,300	terrestrial	lizards, mammals	L
COLUBRIDAE					
<i>Thelotornis kirtlandii</i>	Nigeria	900-1,200	arboreal	lizards	L
<i>Dispholidus typus</i>	Nigeria	1,000-1,400	arboreal	lizards	L
<i>Rhamnophis aethiopissa</i>	Nigeria	1,000-1,300	arboreal	lizards	L
<i>Boiga blandingii</i>	Nigeria	1,500-2,800	arboreal	lizards, birds	L

Snake species	Country	Average body size (mm)	Habits	Diet	
<i>Boiga pulverulenta</i>	Nigeria	1,200-1,800	arboreal	lizards	L
<i>Alluaudina bellyi</i>	Madagascar	240-447	terrestrial	lizards	L
<i>Brygophis coulangesi</i>	Madagascar	1,200	arboreal	lizards	L
<i>Dromycodryas bernieri</i>	Madagascar	1,100	terrestrial	lizards	L
<i>Dromycodryas quadrilineatus</i>	Madagascar	1,100	terrestrial	lizards	L
<i>Geodipsas boulengeri</i>	Madagascar	400	terrestrial	frogs, lizards?	F?
<i>Geodipsas infralineata</i>	Madagascar	800	terrestrial	frogs, lizards?	F?
<i>Geodipsas laphystia</i>	Madagascar	500	arboreal	frogs, frogs eggs	F
<i>Geodipsas</i> sp. 1	Madagascar	unknown (likely 500-800)	unknown	unknown (likely frogs and lizards)	
<i>Geodipsas</i> sp. 2	Madagascar	unknown (likely 500-800)	unknown	unknown (likely frogs and lizards)	
<i>Geodipsas</i> sp. 3	Madagascar	unknown (likely 500-800)	unknown	unknown (likely frogs and lizards)	
<i>Geodipsas</i> sp. 4	Madagascar	unknown (likely 500-800)	unknown	unknown (likely frogs and lizards)	
<i>Ithycyphus goudoti</i>	Madagascar	900	terrestrial	lizards	L
<i>Ithycyphus miniatus</i>	Madagascar	1,500	terrestrial, arboreal	lizards	L
<i>Ithycyphus oursi</i>	Madagascar	1,600	terrestrial, arboreal	lizards	L
<i>Ithycyphus perineti</i>	Madagascar	1,500	arboreal	lizards, frogs	L, F
<i>Langaha madagascariensis</i>	Madagascar	1,000	arboreal	lizards	L
<i>Leioheterodon madagascariensis</i>	Madagascar	1,500	terrestrial	Lizard eggs, mammals	G
<i>Liophidium rhodogaster</i>	Madagascar	600	terrestrial	lizards	L
<i>Liophidium torquatum</i>	Madagascar	700	terrestrial	unknown (likely lizards)	
<i>Liophidium</i> sp. 1	Madagascar	unknown (likely 600-800)	unknown	unknown (likely lizards)	
<i>Liophidium</i> sp. 2	Madagascar	unknown (likely 600-800)	unknown	unknown (likely lizards)	
<i>Liophidium</i> sp. 3	Madagascar	unknown (likely 600-800)	unknown	unknown (likely lizards)	
<i>Liopholidophis epistibes</i>	Madagascar	900	terrestrial	lizards, frogs	L
<i>Liopholidophis grandidieri</i>	Madagascar	900	terrestrial	lizards, frogs	L
<i>Liopholidophis infrasignatus</i>	Madagascar	900	terrestrial	lizards, frogs	L
<i>Liopholidophis lateralis</i>	Madagascar	900	terrestrial	lizards, frogs	L
<i>Liopholidophis rhadinæa</i>	Madagascar	749	terrestrial	frogs, frog eggs	F
<i>Liopholidophis sexlineatus</i>	Madagascar	1,100	semi-aquatic	frogs	F
<i>Liopholidophis stumpffi</i>	Madagascar	1,000	terrestrial	lizards, frogs	L
<i>Liopholidophis</i> sp. 1	Madagascar	unknown (likely 1,000)	terrestrial	lizards, frogs	L
<i>Liopholidophis</i> sp. 2	Madagascar	unknown (likely 1,000)	terrestrial	lizards, frogs	L
<i>Liopholidophis</i> sp. 3	Madagascar	unknown (likely 1,000)	terrestrial	lizards, frogs	L
<i>Madagascarophis citrinus</i>	Madagascar	900	terrestrial	frogs, lizards, snakes, birds	G
<i>Madagascarophis colubrinus</i>	Madagascar	700-1,000	terrestrial	frogs, lizards, snakes, birds, mammals	G
<i>Micropisthodon ochraceus</i>	Madagascar	700	terrestrial	unknown (likely lizards)	
<i>Mimophis mahfalensis</i>	Madagascar	1,000	terrestrial	lizards	L
<i>Pararhadinaea albignaci</i>	Madagascar	400	terrestrial	unknown	
<i>Pseudoxyrhopus ambreensis</i>	Madagascar	400	terrestrial	lizards	L
<i>Pseudoxyrhopus microps</i>	Madagascar	1,300	terrestrial	lizards, frogs	L
<i>Pseudoxyrhopus quinquelineatus</i>	Madagascar	600	terrestrial	lizards	L
<i>Pseudoxyrhopus sokosoko</i>	Madagascar	400	terrestrial	lizards	L
<i>Pseudoxyrhopus tritaeniatus</i>	Madagascar	1,000	terrestrial	lizards	L

Snake species	Country	Average body size (mm)	Habits	Diet	
<i>Pseudoxyrhopus</i> sp.	Madagascar	unknown	terrestrial	unknown (likely lizards)	
<i>Pseudoxyrhopus analabe</i>	Madagascar	300	terrestrial	lizards	L
<i>Pseudoxyrhopus heterurus</i>	Madagascar	600	terrestrial	lizards	L
<i>Stenophis arctifasciatus</i>	Madagascar	1,200	arboreal	lizards	L
<i>Stenophis betsileanus</i>	Madagascar	400	arboreal	lizards	L
<i>Stenophis granuliceps</i>	Madagascar	1,000	arboreal	lizards	L
<i>Stenophis gaimardi</i>	Madagascar	800	arboreal	lizards	L
<i>Stenophis</i> sp.	Madagascar	1,000	arboreal	lizards	L
<i>Grayia smithii</i>	Nigeria	1,000-1,600	semi-aquatic	fish, frogs	F
<i>Grayia tholloni</i>	Nigeria	1,000	semi-aquatic	fish, frogs	F
<i>Philothamnus heterodermus</i>	Nigeria	800-1,000	arboreal	lizards, frogs	L
<i>Philothamnus heterolepidotus</i>	Nigeria	800-1,000	arboreal	lizards, frogs	L
<i>Gastropyxis smaragdina</i>	Nigeria	1,000-1,300	arboreal	lizards, frogs	L
<i>Natriciteres fuliginoides</i>	Nigeria	300-400	semi-aquatic	tadpoles, invertebrates	G?
<i>Natriciteres variegata</i>	Nigeria	300-400	semi-aquatic	tadpoles, invertebrates	G?
<i>Hapsidophrys lineatus</i>	Nigeria	1,000	arboreal	lizards, frogs	L
<i>Afonatrix anoscopus</i>	Nigeria	800-1,000	semi-aquatic	frogs	L
<i>Mehelya crossi</i>	Nigeria	1,000-1,200	terrestrial	lizards, snakes, mammals	G?
<i>Mehelya guirali</i>	Nigeria	1,000-1,200	terrestrial	lizards, snakes, frogs	G?
<i>Mehelya poensis</i>	Nigeria	1,000-1,200	terrestrial	lizards, snakes, frogs	G?
<i>Aparallactus modestus</i>	Nigeria	300-400	terrestrial	invertebrates	I
<i>Lamprophis virgatus</i>	Nigeria	500-700	terrestrial	mammals	M
<i>Lamprophis lineatus</i>	Nigeria	500-700	terrestrial	mammals	M
<i>Lamprophis fuliginosus</i>	Nigeria	500-700	terrestrial	mammals	M
<i>Bothrophthalmus lineatus</i>	Nigeria	600-1,000	terrestrial	mammals	M
<i>Meizodon coronatus</i>	Nigeria	400-600	terrestrial	lizards	L
<i>Dipsadoboa duchesnii</i>	Nigeria	800	arboreal	frogs	F
<i>Crotaphopeltis hotambaeia</i>	Nigeria	500-800	semi-aquatic	frogs	F
<i>Psammophis</i> cf. <i>phillipsi</i>	Nigeria	800-1,300	terrestrial	lizards	L
<i>Polemon collaris brevior</i>	Nigeria	300-600	terrestrial	unknown	
<i>Dasypeltis scabra</i>	Nigeria	1,000	terrestrial	bird eggs	E
<i>Dasypeltis fasciata</i>	Nigeria	800-900	terrestrial	bird eggs	E
<i>Thrasops flavigularis</i>	Nigeria	1,300-2,000	arboreal	birds, mammals	B
ATRACTASPIDAE					
<i>Atractaspis aterrima</i>	Nigeria	300-500	fossorial	unknown	
<i>Atractaspis corpulenta</i>	Nigeria	500-600	fossorial	unknown	
<i>Atractaspis irregularis</i>	Nigeria	300-600	fossorial	mammals	M

Former studies have demonstrated that the structure of snake guilds tends to vary significantly in relation to the macrohabitat variation in tropical Africa. For instance, the number of arboreal and semi-aquatic snake species was much higher in a pristine rainforest site than in a derived anthropogenic site in southern Nigeria (Akani *et al.*, 1999a) Based on this evidence, a remarkable among-sites variation in the distribution of the numbers of snake species in relation to their “habits” should be expected.

In effect, this variation was indeed observed between the two main groups of localities (*i.e.* Madagascar and Nigeria, $P < 0.0001$ at χ^2 test; Table IV). Compared with Madagascar sites, the Nigerian ones were in general characterized by a higher number of semi-aquatic taxa (Table IV), which is likely to be correlated with the higher number of semi-aquatic taxa found in the whole of the Nigerian *versus*

TABLE III

List of all the snake species found, site-by-site, in Madagascar. With regard to Nigeria, the complete list of species of every localities is presented in Akani et al. 1999a, b, in Luiselli et al., 1998, and in Luiselli & Akani, 1999. Taxa provisionally given as "sp." are of doubtful determination and may represent new species. PN = Parc National (National Park); RS = Réserve Spéciale (Special Reserve); RNI = Réserve Naturelle Intégrale (Strict Nature Reserve). Coordinates are given taking into consideration the GPS information gathered during the field surveys (for sites visited by FA) and data from Nicoll & Langrand (1989).

Site	Coordinates	List of species
PN de la Montagne d'Ambre	12° 29'-12° 32' S / 49° 10' E	<i>Sanzinia madagascariensis</i> ; <i>Typhlops microcephalus</i> ; <i>T. mucronatus</i> ; <i>Alluaudina bellyi</i> ; <i>Geodipsas boulengeri</i> ; <i>G. infralineata</i> ; <i>Leioheterodon madagascariensis</i> ; <i>Liophidium rhodogaster</i> ; <i>L. torquatum</i> ; <i>L. sp. 3</i> ; <i>Liopholidophis lateralis</i> ; <i>L. sp. 2</i> ; <i>Pararhadinaea albignaci</i> ; <i>Pseudoxyrhopus ambrensis</i> ; <i>P. microps</i> ; <i>Stenophis arctifasciatus</i>
RNI de Lokobe	13° 25' S / 48° 20' E	<i>Typhlops mucronatus</i> ; <i>T. sp. 3</i> ; <i>Alluaudina bellyi</i> ; <i>Dromycodryas bernieri</i> ; <i>D. quadrilineatus</i> ; <i>Ithycyphus miniatus</i> ; <i>Langaha madagascariensis</i> ; <i>Leioheterodon madagascariensis</i> ; <i>Liophidium torquatum</i> ; <i>Liopholidophis stumpffi</i> ; <i>Madagascarophis citrinus</i> ; <i>M. colubrinus</i> ; <i>Pseudoxyrhopus microps</i> ; <i>Stenophis granuliceps</i>
RS d'Anjanaharibe-Sud	14° 44'-14° 46' S / 49° 25' -49° 30' E	<i>Sanzinia madagascariensis</i> ; <i>Typhlops mucronatus</i> ; <i>Brygophis coulangesi</i> ; <i>Geodipsas infralineata</i> ; <i>G. laphystia</i> ; <i>G. sp. 1</i> ; <i>Liophidium rhodogaster</i> ; <i>L. sp. 1</i> , <i>L. sp. 2</i> ; <i>L. epistibes</i> ; <i>L. infrasignatus</i> ; <i>Pseudoxyrhopus analabe</i> ; <i>P. microps</i> ; <i>P. tritaeniatus</i> ; <i>Stenophis betsileanus</i>
Forêt d'Ambolokopatrika	14° 31'-14° 32' S / 49° 25' -49° 26' E	<i>Typhlops mucronatus</i> ; <i>Geodipsas boulengeri</i> ; <i>G. laphystia</i> ; <i>Liopholidophis epistibes</i> ; <i>L. rhadinaea</i>
Forêt de Tsararano	14° 54' S / 49° 41' -49° 42' E	<i>Typhlops domerguei</i> ; <i>T. mucronatus</i> ; <i>Geodipsas laphystia</i> ; <i>Langaha madagascariensis</i> ; <i>Leioheterodon madagascariensis</i> ; <i>Liophidium rhodogaster</i> ; <i>Liopholidophis epistibes</i> ; <i>Pseudoxyrhopus microps</i> ; <i>Stenophis arctifasciatus</i>
PN de Masoala	15° 16'-15° 18' S / 49° 59' -50° 01' E	<i>Sanzinia madagascariensis</i> ; <i>Typhlops mucronatus</i> ; <i>Geodipsas boulengeri</i> ; <i>G. laphystia</i> ; <i>Liopholidophis epistibes</i> ; <i>L. infrasignatus</i> ; <i>L. rhadinaea</i> ; <i>Pseudoxyrhopus tritaeniatus</i> ; <i>Stenophis sp.</i>
Forêt de Andranomay-Anjozorobe	18° 28' S / 47° 57' E	<i>Typhlops mucronatus</i> ; <i>Liopholidophis infrasignatus</i> ; <i>L. lateralis</i> ; <i>L. sexlineatus</i> ; <i>Pseudoxyrhopus sp.</i>
Forêt de Tampolo	17° 17' S / 49° 25' E	<i>Acrantophis madagascariensis</i> ; <i>Sanzinia madagascariensis</i> ; <i>Rhamphotyphlops braminus</i> ; <i>Dromycodryas bernieri</i> ; <i>Ithycyphus goudoti</i> ; <i>I. miniatus</i> ; <i>Langaha madagascariensis</i> ; <i>Leioheterodon madagascariensis</i> ; <i>Liopholidophis lateralis</i> ; <i>Madagascarophis colubrinus</i> ; <i>Micropisthodon ochraceus</i> ; <i>Pseudoxyrhopus ambrensis</i> ; <i>P. heterurus</i>
PN d'Andringitra	22° 10'-22° 13' S / 45° 46' -47° 01' E	<i>Geodipsas boulengeri</i> ; <i>G. infralineata</i> ; <i>G. sp. 2</i> <i>G. sp. 3</i> , <i>G. sp. 4</i> ; <i>Liophidium rhodogaster</i> ; <i>L. sp. 4</i> ; <i>Liopholidophis grandidieri</i> ; <i>L. infrasignatus</i> ; <i>L. stumpffi</i> ; <i>L. sp. 3</i>
PN de Zombitse	22° 50'-22° 51' S / 44° 39' -44° 42' E	<i>Acrantophis dumerili</i> ; <i>Dromycodryas bernieri</i> ; <i>Ithycyphus oursi</i> ; <i>Leioheterodon madagascariensis</i> ; <i>Madagascarophis colubrinus</i> ; <i>Mimophis mahfalensis</i> ; <i>Pseudoxyrhopus quinquelineatus</i>
PN d'Andohahela	24° 45' S / 46° 51' E	<i>Sanzinia madagascariensis</i> ; <i>Liopholidophis epistibes</i> ; <i>L. infrasignatus</i> ; <i>L. rhadinaea</i> ; <i>Pseudoxyrhopus sokosoko</i> ; <i>Stenophis betsileanus</i>

TABLE IV

Structure of the snake communities of all the study plots in both Nigeria and Madagascar on the basis of species' "habits". In this table are included presence records coming from both quantitative and qualitative surveys in each study site. Symbols: NF = Number of fossorial species; NT = Number of terrestrial species; NAq = Number of semi-aquatic species; NAr = Number of arboreal species. Species which "habits" are unknown are excluded.

Country	Site	NF	NT	NAq	NAr
Nigeria	Abarikbo	0	3	1	0
Nigeria	Ejule	2	11	3	2
Nigeria	Eket	1	11	7	5
Nigeria	Kreigeni	0	4	2	3
Nigeria	Orashi	1	10	5	5
Nigeria	Orubiri	0	4	3	3
Nigeria	Otari	1	8	5	9
Nigeria	Peterside	0	5	3	4
Nigeria	Rumuji	1	6	5	6
Nigeria	Soku	2	9	5	7
Nigeria	Tombia I	0	6	1	3
Nigeria	Tombia II	0	4	1	5
Madagascar	Ambolokopatrika	1	3	0	3
Madagascar	Andranomay-Anjozorobe	1	3	1	0
Madagascar	Andringitra	0	5	0	2
Madagascar	Anjanaharibe	1	4	0	3
Madagascar	Lokobe	2	8	0	4
Madagascar	Masoala	1	3	0	4
Madagascar	Tsararano	1	2	0	4
Madagascar	Zombitse	0	6	0	1
Madagascar	Andohahela	0	4	0	2
Madagascar	Tampolo	2	8	0	3
Madagascar	Montagne d'Ambre	2	8	0	5

Malagasy territory (Table II). However, in most sites of both regions, the terrestrial guild was the dominant one, and the arboreal guild was also constituted by a remarkable diversity of species (Table IV). An interesting paralleling situation among sites in both Nigeria and Madagascar was the presence of a very little diversity of syntopic fossorial species, belonging to the genera *Rhamphotyphlops*, *Typhlops*, *Calabaria*, *Elapsoidea*, and *Atractaspis* (in all 22 study plots, only 1 or 2 fossorial species were found).

STRUCTURE OF THE SNAKE COMMUNITES IN TERMS OF DIETARY PREFERENCES

Analyses of the community structure in the various study sites in terms of feeding preferences is partially affected by the fact that, for many Malagasy species, lacking a solid background of ecological studies of snakes habits (taking anyway into considerations the recent contributions of Cadle, 1996a, b), it is not exactly known which dietary preferences they actually exhibit (e.g., species of the genera *Geodipsas*, *Liophidium*, *Microphistodon*, etc., see Table II). Nevertheless,

limiting our analyses to those well-known species, an interesting pattern could emerge. In the Nigerian sites there was a prevalence of primarily lacertophagous and mammalophagous species, although batracophagous and ornithophagous species too were quite abundant in the various communities (Table V). In the Malagasy sites there was a prevalence of lacertophagous species, followed by batracophagous species, whereas species with other dietary preferences were much under-represented (Table V). The abundance of the invertebratophagous and generalist species was similar in the two regions, whereas piscivorous, strictly ophidiophagous (such as the species *Elapsoidea semiannulata*), and egg-eating (such as those belonging to the genus *Dasypeltis*) snakes were found only in the Nigerian sites.

TABLE V

Structure of the snake communities of all the study plots in both Nigeria and Madagascar on the basis of species' dietary preferences. In this table are included presence records coming from both quantitative and qualitative surveys in each study site. Symbols for main prey types: I = number of species preying on insects and other invertebrates; P = number of ichthyophagous species; F = number of batrachophagous species; L = number of species preying on lizards (including chameleons); S = number of ophidiophagous species; B = number of species preying on birds; M = number of mammalophagous species; E = number of species preying on bird eggs; G = species with a very generalist diet. Species which diet composition is unknown are excluded from this table.

Country	Site	I	P	F	L	S	B	M	E	G
Nigeria	Abarikbo	0	0	1	2	0	0	1	0	0
Nigeria	Ejule	0	1	4	3	1	0	5	1	2
Nigeria	Eket	2	1	3	3	0	2	7	1	4
Nigeria	Kreigeni	0	1	1	3	0	1	2	0	1
Nigeria	Orashi	3	1	2	3	0	3	6	1	2
Nigeria	Orubiri	1	1	0	4	0	0	2	0	2
Nigeria	Otari	2	1	2	5	0	4	6	1	2
Nigeria	Peterside	0	1	2	4	0	0	2	0	2
Nigeria	Rumuji	2	1	2	3	0	4	4	0	2
Nigeria	Soku	3	1	3	3	0	3	6	0	2
Nigeria	Tombia I	0	1	2	3	0	1	1	0	1
Nigeria	Tombia II	0	0	1	5	0	1	2	0	1
Madagascar	Ambolokopatrika	1	0	3	1	0	0	0	0	0
Madagascar	Andohahela	0	0	1	4	0	0	1	0	0
Madagascar	Andranomay-Anjozorobe	1	0	1	2	0	0	0	0	0
Madagascar	Andringitra	0	0	2	4	0	0	0	0	0
Madagascar	Anjanaharibe	1	0	3	6	0	0	1	0	1
Madagascar	Lokobe	2	0	0	8	0	0	1	0	3
Madagascar	Masoala	1	0	2	5	0	0	1	0	0
Madagascar	Montagne d' Ambre	2	0	2	8	0	0	2	0	1
Madagascar	Tampolo	1	0	0	7	0	0	3	0	1
Madagascar	Tsararano	2	0	1	3	0	0	1	0	1
Madagascar	Zombitse	0	0	0	4	0	0	2	0	1

STRUCTURE OF SNAKE COMMUNITIES IN TERMS OF BODY SIZE

At a regional level, it should be noted that southern Nigeria houses more large sized species than Madagascar (Table II). In fact, only species of the genera *Acrantophis* and *Sanzinia* can attain large size in Malagasy sites, whereas in Nigerian sites such a large size can be attained by species of the genera *Naja*, *Pseudohaje*, and *Dendroaspis* (Luiselli & Angelici, 2000; Luiselli *et al.*, 2000a), with *Python sebae* which can attain a giant size (about 9 m). The largest snake specimen found was in fact a Nigerian *Python sebae*, about 5.5 m long (Luiselli *et al.*, 2001). This different distribution of large sizes in snakes was also reflected in the size-based community structure at the various sites. Indeed, giant species were totally lacking at Malagasy sites, and numbers of big species were higher in Nigerian than in Malagasy sites. However, in both Nigeria and Madagascar the majority of the species attained only medium to small size (Table VI).

A problem of this type of inter-regional comparison is that in many sites the actual snake composition could be higher than that pictured by our studies, due to the eventual escapes of some species. To overtake partially this problem, we pooled data from the Nigerian sites and compared them with pooled data from all the sites of Madagascar. It resulted therefore that the highest numbers of species in a given size category at each site were as follows: giant species: 1 in Nigeria and 0 in Madagascar; big species: 4 in Nigeria and 1 in Madagascar; large species: 3 in Nigeria and 3 in Madagascar; medium species: 9 in Nigeria and 8 in Madagascar; small species: 9 in Nigeria and 7 in Madagascar.

DISCUSSION

A main emerging issue of this paper is concerned with the estimates of snake abundances at the various sites in inter-regional comparisons. It should be noted that data of relative abundance of animals (including snakes) are often based on visual methods such as transect counts or, as in the present study, time-constrained searching (Campbell & Christman, 1982; Rodda, 1993). According to Rodda (1993), it is tacitly assumed that, when different searchers count animals in a given area, they do not vary among themselves in their ability to detect the target species. However, when different searchers try to estimate the abundance patterns of snakes in a given area, different results have to be expected because of strong individual effects on the data (e.g., Rodda & Fritts, 1992; Rodda, 1993, pers. comm.). This fact could be of course a very serious shortcoming to virtually any type of research on snake abundance, not only because of the problems in comparing data that are "intrinsically" different, but also because repeatability is a crucial component of any scientific research, and lack of repeatability is detrimental to the value of any scientific conclusion (e.g., Gould & Lewontin, 1979).

Thus, taking in mind these issues, we compared in the present paper all the studies which appeared similar in terms of applied methodology, and obtained as a consequence an interesting conclusion: wherever the study area was, the diversity and abundance patterns of the snake-faunas of the forest environment were quite consistent among geographically diverging areas, and this consistency was even more evident between studies applying nearly identical procedures of field data recording (those of F. Andreone and coworkers in Madagascar and those

of L. Luiselli and associates in Nigeria). Therefore, our comparative analysis revealed that researches on snake abundance and diversity, if done by applying standard and solid methodologies, are well feasible and may produce good results. In any case, it is crucial that, when publishing a paper, potential authors should explain their methodologies in full, and give details of true effort in the field and numbers of observed specimens (which are rarely found in such types of community studies).

Apart for the “methodological” issue, our comparative study also stressed some intriguing and broadly interesting ecological patterns.

The main emerging result is that the various studied rainforest patches, both in continental Africa and Madagascar, were extremely similar in terms of both snake species diversity and abundance, and that they were also well comparable with data available for Central America.

Did this general pattern emerge as an artifact of methodology? Probably not, as these similar results have emerged from studies conducted in many forest plots (see Table I) and by teams of scientists working separately and without any idea of later comparing their own data-sets when conducting their researches. So, if not a methodology artefact, what is the meaning of this consistency patterns among different study plots? At present it is not possible to give a definitive answer, but some hypotheses can surely be presented. We are led to think that the carrying capacity of the forest habitat, at the trophic level of snake communities (Kikkawa & Anderson, 1986), should be very similar among the different examined plots, whatever the geographic area is. As a consequence, the global availability of prey types (*i.e.* frogs, toads, lizards, mice, etc.) should be similar in the various geographic regions, thus permitting the subsistence of similar snake communities. Though our abundance data are apparently very interesting, nevertheless they need to be extended over longer periods covering the whole year before stressing firm conclusions. In fact, tropical forests of both Nigeria and Madagascar lie in regions characterized by seasonal variations in rainfall rates (White, 1983, 1986), and rainfall is known to play a leading role in the dynamics and organization of Afrotropical reptile communities (Barbault, 1974, 1977, 1991).

Indeed, some important inter-regional differences also emerged. The two major differences are that (i) Nigerian rainforest sites housed an higher number of very large or giant species than Malagasy rainforests, and that (ii) there was a considerable excess of semi-aquatic taxa in Nigerian than in Malagasy sites. With regard to point (i), it should be noted that this pattern could be well present in other tropical forests, *e.g.*, in India and SE Asia, where at least three giant snakes (*e.g.*, *Python molurus*, *P. reticulatus*, and *Ophiophagus hannah*) could be sympatric (Whitaker, 1978). It is likely that the coexistence of such large-species occurs in places where there is a good abundance of mammals which constitute their preys. In the Nigerian forests, in fact, there is still a considerable variety of medium and large sized mammals which could sustain the populations of these snakes (Angelici *et al.*, in press *b*). In particular, the giant rodent *Cricetomys gambianus* should be an essential prey type for both pythons and large elapids, as it is extremely common in the Nigerian rainforest and is a common prey for these predators (Luiselli *et al.*, 1998, 2001). The fact that mammalian prey should be a virtually unlimited resource in Nigerian environments is also confirmed by the diversified snake-fauna eating on it, which includes species belonging to as different phylogenetic lineages as pythons, viperids, elapids, and different groups of colubrids as well (Luiselli *et al.*, 1998, 2001; Luiselli & Angelici, 2000).

Conversely, the snake species feeding on small mammals are very few in the Malagasy environments, and this is consistent with a relative scarcity of mammals in this geographic region. As witnessed by recent studies on the mammal fauna of Madagascar a low number of rodents appears evident there, most likely due to biogeographic reasons and to competition with endemic lipotyphlans (Goodman & Jenkins, 1998). Indeed the lipotyphlan insectivores are in general small sized, and, excepting the spiny species *Tenrec ecaudatus* and *Setifer setosus* (which have a total size of 285-400 and 160-225 mm respectively; Garbutt, 1999), the other endemic tenrecids (such as those belonging to the genera *Microgale*, *Oryzorictes*) and introduced insectivores (such as *Suncus murinus* and, possibly, *S. etruscus*) have in general a much smaller size. And the general scarcity of mammal preys might be among the reasons for the occurrence of only a few « big » snakes (such as *Sanzinia madagascariensis* and *Acrantophis madagascariensis*). At this regard it is worth to stress that the boa *Sanzinia madagascariensis* appears to be more frequently encountered in anthropogenic environments (e.g., around villages, in degraded ecotonal savannas) than in pristine primary or fully regrown secondary rainforest (Andreone, 1991a, b). Most likely in these altered habitats they take advantage from the presence of anthropophilous introduced rodents, such as *Rattus rattus* and *R. norvegicus*, which indeed are introduced pests negatively affecting the indigenous rodent fauna (Goodman, 1995). Even in Nigeria, the giant snake *Python sebae* is commonly found in the suburbs, where it feeds mainly upon poultry, rats, and even dogs and goats (Luiselli *et al.*, 2001).

With regard to point (ii), we are led to think that the relative scarcity of semi-aquatic species in the Malagasy sites could be caused by two concurrent reasons: (1) a “topographic” reason, and (2) an “ecological reason”. The “topographic” reason could be the relative scarcity of permanent large water bodies in the eastern rainforest ecarpment of Madagascar (where fast rainforest streams are more common), which has not worked in favour of a selection for aquatic and piscivorous species. On the contrary, very wide areas of southern Nigeria (e.g., Niger Delta, Cross River Delta, etc.) are characterized by the presence of a complicated and diverse mosaic of large rivers, creeks and lakes where fish are abundant, and which could have favoured the evolution of aquatic snake species.

The “ecological” reason may lie in the fact that Malagasy amphibians are less linked to water bodies than Nigerian amphibians. For instance, the mantelline species (genera *Mantella* and *Mantidactylus*), which are the most common amphibians within Malagasy rainforests, lay their eggs out from water, and may have direct development (Andreone, 1999). This is also valid for cophylinae microhylids, which are independent from free water for their reproduction and larval development (Glaw & Vences, 1992, 1994; Andreone, 1999). As a consequence, batracophagous snakes can find their prey even far from water bodies, and could have not evolved any semi-aquatic behaviour as it has happened in most batracophagous snakes from elsewhere (including continental Africa, but also Europe, North-America, etc.), where amphibious species are much commoner, if not the predominant amphibians. Furthermore it is also worth quoting that the inland freshwater fauna of Madagascar is scanty, with only a few species (such as the bedotiids *Rheocles* spp. and *Bedotia* spp., eels (*Anguilla* spp.), and some native ciclids (such as those belonging to the genera *Paratilapia* and *Paretroplus*) being the original and natural inhabitants of the Malagasy rainforest water system (Reinthal & Stiassny 1991; Stiassny & Raminisoa, 1994; Rham, 1996). As for the mammalophagous snake species, also for the fish-eating snakes

this poorness (or, in some cases, totally absence) of fish may have been a limiting factor for the affirmation of a adaptive radiation in ichthyophagous species.

A common pattern in both Nigerian and Malagasy snake communities, as well as in other Afrotropical snake communities (e.g., Barbault, 1977), is that sympatric species tend to colonize every possible spatial niche, from the arboreal to the fossorial niche, with the majority of snakes belonging to the terrestrial guild. This type of habitat partitioning is a dominant feature of tropical lizard community organization (Pianka, 1966, 1986), and thus is not exclusively found in tropical snake assemblages. It is likely to result from substrate or micro-habitat specialization of species, and not necessarily a competitively induced phenomenon (Barbault, 1991). As for lizards, Barbault (1991) suggested that these reptiles may depend upon close substrate adaptation to avoid predators, to thermoregulate efficiently or to be successful in mating and defending territories, and thus substrate selection and specialization may be a response evolved to cope with a complex combination of various selective pressures. As for snakes, we suggest that the same could well be true, as they have similar evolutive stimuli as lizards, and may also depend upon a substrate adaptation to capture their prey. In fact, many species use an ambush foraging strategy, and have evolved livery and body shapes perfectly cryptic in their environment. Spectacular cases of such substrate adaptations are, for instance, the Gaboon viper (*Bitis gabonica*), which bizarre shape and livery is a perfect camouflage on forest litter substratum (which is its preferred substratum, see Angelici *et al.*, in press *a*), and the vine snake (*Thelotornis kirtlandii*) in the arboreal niche in Nigeria (Spawls & Branch, 1997), or the highly cryptic species of the colubrid genus *Langaha* in Madagascar (see Glaw & Vences, 1992, 1994).

With regard to the fossorial guild, it is noteworthy that the pattern of very few (one or two) coexisting species in all the study sites in both Nigeria and Madagascar mirrors data available for tropical fossorial lizard communities from arid environments (Huey *et al.*, 1974; Henle, 1989*a*). According to Barbault (1991), it is likely that in these communities, which are not strongly subjected to predation, the whole community organization is mainly related to competition for trophic resources. Thus, the very low number of coexisting species could depend on scarce food availability. It is possible that the same is valid also for the fossorial guilds of the surveyed sites of both Nigeria and Madagascar.

If we consider the remarkable variety of species observed in each site, and although quantitative information is lacking, it is likely that snake biomasses should be sufficiently large in forest environments of both regions to influence considerably the population dynamics of their preys, as already noted by Barbault (1974, 1977, 1991) in wet savannas of Ivory Coast. According to this author, the average biomass per hectare of batracophagous snakes remains throughout the year at a ratio of 1 to 10 with that of the amphibian community, and a similar relationships also exists between lacertophagous snakes and lizards. Thus, a further essential step of our research will be to evaluate the biomass per hectare of batracophagous, lacertophagous, and mammalophagous snakes in at least some of the surveyed sites of both Nigeria and Madagascar, the biomass per hectare of their prey types, and the relative predation rates month-by-month.

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