ARE THERE SHIFTS IN AMPHIBIAN FAUNAL COMPOSITION IN NIGERIAN LANDSCAPES UNDERGOING LONG-TERM DEGRADATION? A CASE STUDY FROM A MONTANE ENVIRONMENT

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RÉSUMÉ. — *Quelles variations subit la composition du peuplement d'Amphibiens dans les paysages nigériens subissant une dégradation sur le long terme ? Le cas d'un environnement de montagne.* — Les forêts tropicales mondiales subissent une importante altération anthropique. Les données recueillies au cours de diverses études dans les forêts du Nigéria montrent que l'herpétofaune subit ces modifications d'habitat. En particulier, quand les environnements forestiers tropicaux se dégradent et bien que la diversité globale reste stable ou voire même augmente, on remarque que l'on passe d'une dominance d'espèces spécialistes forestières à une dominance d'espèces généralistes capables d'utiliser une large gamme d'habitats. La même modification s'observe quels que soient le type d'habitat (*e. g.* forêt basse temporairement inondée ou forêt de montagne) ou le taxon (*e. g.* anoures ou serpents). Un inventaire des amphibiens a été conduit en 2002 sur le plateau d'Obudu au Nigéria, qui est une zone d'intérêt majeur pour la conservation, abritant beaucoup d'espèces endémiques et menacées. L'environnement y a été gravement dégradé et a souffert d'une forte déforestation dans les années récentes ; le tourisme de plaisance, en pleine extension, menace d'avoir un impact encore plus grand. En comparant les résultats de cet inventaire à divers jeux de données des années 1960 et 1980, nous sommes en mesure de décrire les changements dans la composition des peuplements intervenus après de nombreuses années de perturbation anthropique et nous discutons les raisons du succès ou de l'échec d'espèces spécialistes ou généralistes particulières.

SUMMARY. — Tropical forests worldwide undergo severe anthropogenic habitat alteration. We report here on various long-term studies in Nigerian rainforests and show that there appears to be a trend of change in herpetofaunal communities that follows this habitat change. Specifically, as rainforest environments become degraded there is a shift from a predominance of forest specialists to a predominance of generalists that are able to utilize a wide range of habitats (although overall species diversity may remain stable or even locally increase). The same shift is seen regardless of the type of habitat (e.g. seasonally flooded lowland forest or montane forest) or the taxa (e.g. anura or serpentes). An amphibian survey was conducted in 2002 in the Obudu plateau, Nigeria, which is an area of major conservation importance, containing many endemic and threatened species. The environment has been severely degraded and suffered heavy deforestation in recent years, and expanding leisure tourism threatens to have an even greater environmental impact. We compare the results from our current survey to other studies by previous authors conducted in the 1960's and 1980's to provide an insight into changes in community species composition after many years of anthropogenic disturbance. We discuss the reasons for the success and failure of particular specialist and generalist species.

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Tropical rainforest environments are intrinsically stable over time, which leads to high levels of specialization (narrow ecological niches) by organisms and consequently high rates of speciation. These habitats are therefore typically the richest biodiversity hotspots in the terrestrial world (reviewed in Wilson, 1992). However, in many regions of the world, pristine rainforests have undergone heavy anthropogenic exploitation and their vegetation structure has subsequently changed dramatically (e.g. savannah-like herbaceous vegetation is now widespread across former West African rainforest areas). It is well demonstrated that faunal species' assemblages have the potential to vary considerably over time (Wiens, 1977; Schoener, 1986; Barbault, 1991), and particularly so in areas with rapidly changing landscapes (Wiens, 1977; Cuellar, 1993). Given this, it is therefore quite likely that the faunal composition of these altered rainforest areas has also undergone important community changes. That is to say, the present day faunal species should be widely different from those that existed in the pristine environments.

Southern Nigeria offers an exceptional opportunity to explore changes in faunal community composition in environments with rapidly changing landscapes. This is because, since the 1960's, southern Nigeria has seen a massive expansion of the petrochemical industry and has consequently suffered wide-ranging disturbance to forest habitat (De Montclos, 1994; Politano, 1998). A main interest of our research group has been to study the long-term effects of forest habitat alterations on the herpetofauna of southern Nigeria. In previous studies we have documented that some savannah species of snakes (notably the spitting cobra, *Naja nigricollis*) are now invading formerly forested areas and exploiting the niches of their relatives who are more closely adapted to the rainforest habitats (i.e. the forest cobra, *Naja melanoleuca*). The spitting cobra is suboptimally adapted to the life in mature rainforest (Luiselli, 2001), yet each year it is more common in every habitat type. Conversely, the forest cobra is becoming increasingly rare and is clearly succumbing to this strong interspecific competition with the savannah invader (Luiselli, 2002). In another study, we (Lea *et al.*, 2003) documented that both amphibian and reptilian communities changed considerably after twenty years of development in a lowland area of the Niger Delta that suffered massive deforestation and increased human population, and that savannah species now tend to dominate over rainforest species.

Our aim in the current paper is to examine another case of community change by studying the amphibian biodiversity of a montane area in south-eastern Nigeria (Obudu Plateau, Cross River State), where faunal studies conducted over 40 years ago can be compared to current data from our original research. We will then compare any pattern that occurs to those observed in our previous study (Lea *et al.*, 2003) in order to determine if there are any general trends in anuran successions in the disturbed forested regions of this part of West Africa.

STUDY AREA AND METHODS

Study area

The Obudu Plateau (Nigeria) is an extension of the Bamenda highlands (Cameroon) and is an area of major conservation interest as it contains many endemic and threatened plant and animal species (Rodenkirchen, 2002). It is located in Ogoja province, Nigeria, 6º 21'N, 9º22'E. It has an elevation of 1 600 to 1 800 m. It has a relatively cool climate: mean annual rainfall of 4 280 mm and mean max. and min. temperatures of 22.2˚C (range: 18.5˚C in Aug to 24.5˚C in Feb/Mar) and 15.0˚C (range: 14.0˚C in Jul/Aug to 16.0˚C in Mar/Apr) (Tuley, 1966). It is covered predominantly by grassland and montane forest. The grassland is a *Loudetia-Hyparrhenia* association, with *Hyparrhenia diplandra, Andropogon auriculatus* and *Setaria anceps* dominant and *Loudetia camerunensis* and *Panicum hochstetteri* as "fillers" (Tuley, 1966).

Unfortunately, the environment has been severely degraded and has suffered high levels of deforestation in recent years. The building of a cattle ranch and hotel (in the late 1950's to early 1960's) attracted a great deal of immigration of people seeking employment who were subsequently left to eke out a living from the forest upon the hotel's closure (around 1980) (Rodenkirchen, 2002). The result has been massive forest clearance for subsistence farming and sand and other resource extraction. Additionally, uncontrolled grassland burning (often encroaching into remnant forest) and cattle grazing/trampling has destroyed understory vegetation, disturbed creek beds, eroded stream banks and contaminated water sources (Rodenkirchen, 2002). In 2002, as part of a large community investment project, the ranch hotel reopened and this expansion of leisure tourism currently threatens to have an even greater environmental impact (e.g. building of golf courses, etc).

Amphibian collections in the area were made by Schiøtz in 1959 and 1965 (Schiøtz, 1963, 1966, 1967) and Gartshore in 1980/81 and 1983/84 (Gartshore, 1986). The current survey was conducted for comparison and to provide an insight into the successional change in species composition after many years of anthropogenic disturbance. In addition, the survey will provide baseline data for monitoring recently initiated conservation programmes.

Methods

A ten-day survey (October 24th-November 2nd) was conducted during the rainy season of 2002. Each day, three independent people spent six hours actively searching for amphibians (three hours daylight/three hours night). Different routes encompassed central and edge forest, riverbanks, village streams, protected areas, permanent and temporary pools and fast flowing and still water environments. The various localities visited during the present survey are presented in Table I. Secretive species were sought in their refuges (e.g. under logs/rocks, beneath bark, in leaf litter, soil and leaf axils). Night searches were made with headlamps. Cryptic callers were spotted by triangulation. Local villagers were encouraged to bring amphibians for identification (done subsequently by comparing preserved specimens and photographs to reference material). Usually two males and two females of each species, together with specimens found dead or killed by local people, were preserved (in 75% ethanol). If species demarcation was unclear up to four additional specimens were collected and stored in the museum of the Cross-River National Park, Butatong, Nigeria. All other individuals were released unharmed at the site of capture after detailed photographic and written records had been taken. GPS reading were taken at survey locations.

There is no unequivocal nomenclature for West African amphibians, and the situation is especially confusing for several speciose genera e.g. *Hyperolius* and *Phrynobatrachus*. The taxonomy of Hyperoliidae and Rhacophoridae here follows Schiøtz (1999), and for all other species, for practical reasons, we follow LeBreton (1999) and Rödel (2000). Table II shows some of the key diagnostic features and references used to identify the anurans found at Obudu in 2002.

We classified the amphibians of Obudu and also the Etiope River (Niger Delta, Lea *et al*., 2003) according to their habitat tolerances by referring to the existing literature (Sanderson, 1936; Perret, 1959, 1966; Schiøtz, 1963; Amiet, 1986; Gartshore, 1986; Lawson, 1993; LeBreton, 1999; Rödel (2000) (see legends of Figs. 2 & 3).

RESULTS

A total of 12 anuran species from 10 genera and one caecilian *(Geotrypetes seraphini)* were caught in 180 hours of search time. This is the first report of a caecilian from Obudu; it was found at high densities under rocks and soft surface soil adjacent to shallow, slow moving streams at location 7 (Tables I, II and III). Ten individuals were counted in an area of less than 1m2 and their estimated size (snout-vent-length) range was 100 to 300 mm, indicating mixed cohorts. It is clearly an abundant species and only its fossorial nature prevents it being found more often.

The cumulative number of species found in 2002 levels off towards the end of the survey (Fig. 1), which indicates a good sampling (Magurran, 1988). In the 1960's there were 12 to 14 species from 9 genera (the uncertain species number is due to ambiguity about

TABLE I

Localities visited on Obudu plateau

Breeding location	GPS reading (N/E)	Site description
1. Becheve Nature Reserve	06º22.631 / 009º22.863	3,7
2. Community market	06º22.455 / 009º22.634	1,6
3. Grotto forest	06º22.264 / 009º22.926	4
4. Kejiku road stream	06º22.338 / 009º22.397	3,8
5. Government field forest	06º22.173 / 009º22.631	3,9
6. Apajili village	06º21.908 / 009º22.562	6
7. Banana village/Kejiku forest	06º22.397-538 / 009º22.279-229	5,8
8. Monkey face view forest	06º23.269 / 009º22.701	9
9. Imale village stream	06º20.098 / 009º20.256	6
10. Afundu valley river	06º23.831 / 009º23.963	2

Note. 1 = deep permanent pool > 1 m depth. 2 = fast flowing river. 3 = shallow, perennial, slow moving stream. 4 = shallow, seasonal, slow moving tributaries of fast flowing river; shaded area; leaf-litter covers ground. 5 = very rocky shallow, seasonal, slow moving stream; soft exposed soil. 6 = severely degraded environment; human habitation. 7 = small area of recently protected secondary forest. 8 = area occasionally disturbed. 9 = disturbed secondary forest.

exact location for two species) and in the 1980's there were 14 species from 8 genera found in the area. Therefore, the total number of species caught in each survey period remained relatively stable. Table III compares the species caught in 2002 with those from previous surveys.

TABLE II

Some diagnostic features and references used for the identification of anurans found at Obudu in 2002

Species	Main identifying characters & references
Bufo maculatus	Differs from *B. regularis* in: 1) smaller size (max. svl: *B. mac* ≅ 60 mm, *B. reg.* ≅ 130 mm); 2) numerous subdigital tubercles; 3) warty parotid glands — see Rödel (2000).
Arthroleptis variabilis	Males with lengthened 3rd finger; lack of webbing; light longitudinal stripe — see Schiøtz (1963) and Rödel (2000); highly variable genus but from this location the species is most likely to be *A. variabilis* (Rödel, pers. com.) — see also Euskirchen *et al.* (1999).
Astylosternus diadematus	Characteristic broad and wavy inter-orbital line; relative dimensions of front and rear limbs to the body; tubercle patterns on hands and feet; colouration and size — see figures and tables in Amiet (1977).
Cardioglossa melanogaster	2^{nd} finger twice as long as 1^{st}; vertical pupil; gold iris; v. distinctive dosal and lateral tan and black patterning — see figures and photos in Amiet (1972).
Leptodactylodon ovatus	Series of spines (4 + 3) on front feet in breeding males; dorsum orange/red; venter brown with blue-white spotted pattern (spots occasionally merge) — see Amiet (1980).
Trichobatrachus robustus	Dermal appendages on males; v. broad round head; distinctive tan and black markings esp. broad dark brown dorsal stripe and black canthal line extending over tympanum — see photograph in Euskirchen *et al.* (1999).
Hyperolius riggenbachi	Males uniform green (day) / yellow (night) with white dorso-lateral stripe; females black with yellow patterning and red toes — see photos in Schiøtz (1999).
Phrynobatrachus aelleni	Characteristic paired "zig-zag'dorsal ridges on every specimen — see figure in Lamotte (1998); dark pattern between angles on dorso-lateral folds above tympanum — see Schiøtz (1963); breeding males with yellow venter. (Note: *P. cricogaster* has similar dorsal ridges but also has a characteristic "bull's eye" pattern on the venter).
Phrynobatrachus wernei	No dorsal ridges; v. limited webbing; median subgular vocal sac with 2 deep lateral grooves surrounded by skin folds (inner and outer layers densely pigmented); throat and top of venter deep black in adult males; both sexes 24-28 mm svl — see figure in Schiøtz (1963).
Ptychadena oxyrhynchus	Large size with long hind legs; 3-4 shorter pairs of dorsal ridges; discontinuous dorsolateral ridges; no subdigital tubercles; nearly full webbing; small inner metatarsal tubercle — see figures, photos and tables in Rödel (2000).
Petropedetes parkeri	Very distinctive protrusion on (large) tympanum; femoral gland features; shape of toe discs; nuptial spines in breeding males — see figures in Amiet (1983).

There was generally a low diversity of species in all the habitats surveyed. The highest number of species at any location was six and the average (modal) number was three (Table IV). The sites with the highest diversity (4 to 6 species) were characterized by having small, protected forested areas and/or slow moving streams but did include disturbed sites around human habitation (cf. Tables I & IV). The species that predominated at each locality, and overall, are shown in Table V. By far the most abundant and widespread species was *Phrynobatrachus aelleni*, followed by *Hyperolius riggenbachi* and *P. wernei*. Other species were locally abundant. The calculated abundance values, however, are biased by species' tendencies to aggregate and/or call from semi-exposed positions and should be used only as a guide. The general low diversity of species and dominance of particular groups is discussed below.

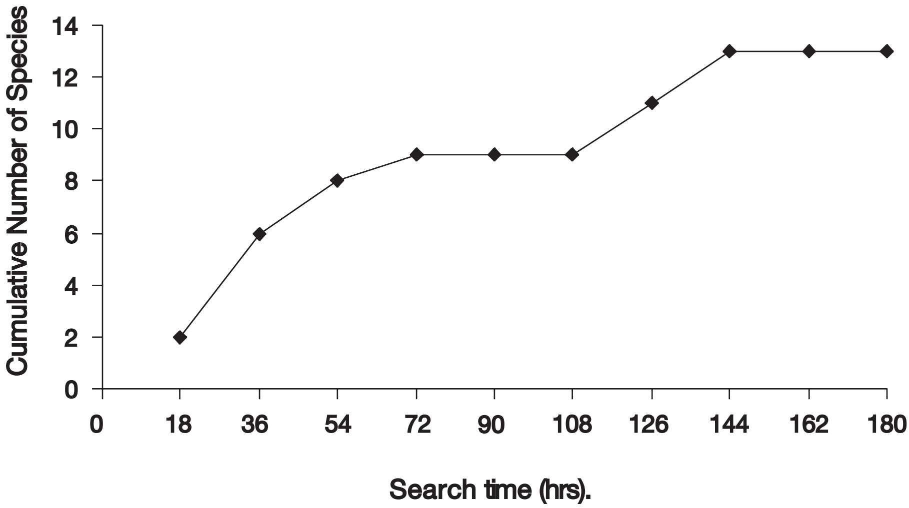

Figure 1. — Obudu Plateau — Species accumulation plot.

TABLE III

Obudu Plateau anurans

1960's species (collections 1959 & 1965) (Schiøtz 1963, 1966, 1967)	1980's species (collections 1980/81 & 1983/84) (Gartshore 1986)	Species found in 2002
Bufonidae:	Bufonidae:	Bufonidae*:*
Bufo regularis (Reuss, 1834) G *Woltersdorffina parvipalmata* (Werner, 1898) F	*Werneria mertensi* (*mertensiana*) * (Amiet, 1972b) F *Woltersdorffina parvipalmata* (Werner, 1898) F	*Bufo maculatus* (Hallowell, 1854) G
Arthroleptidae*:*	Arthroleptidae*:*	Arthroleptidae*:*
Arthroleptis spp. U *Astylosternus diadematus* (Werner, 1898) F *Cardioglossa gracilis* (Boulenger, 1905) F *C. pulchra* (type locality) (Schiøtz, 1963) F *Cardioglossa* spp.? (location ambiguous) U *Cardioglossa* spp.? (location ambiguous) U *Leptodactylodon albiventris* ** (Boulenger, 1905) F *Trichobatrachus robustus* (Boulenger, 1905) F	*Astylosternus montanus* (Amiet, 1978) F *Cardioglossa melanogaster* (Amiet, 1972a) F *C. pulchra* (type locality) (Schiøtz, 1963) F *C. schioetzi* (Amiet, 1981) F *C. trifasciata* (Amiet, 1972) F *Leptodactylodon bicolor* * (Amiet, 1971) F *L. polyacanthus* (Amiet, 1971) F	*Arthroleptis* cf. *variabilis* (Matschie, 1893) G *Astylosternus diadematus* (Werner, 1898) F *Cardioglossa melanogaster* (Amiet, 1972) F *Leptodactylodon ovatus* (Andersson, 1903) F *Leptodactylodon* spp. U *Trichobatrachus robustus* (Boulenger, 1905) F
Hyperoliidae:	Hyperoliidae:	Hyperoliidae*:*
Hyperolius (*r.*) *riggenbachi* *** (Nieden, 1910) E	*Hyperolius* (*r.*) *riggenbachi* (Nieden, 1910) E *Leptopelis modestus* (Werner, 1898) F	*Hyperolius* (*r.*) *riggenbachi* (Nieden, 1910) E
Ranidae*:*	Ranidae*:*	Ranidae*:*
		Phrynobatrachus aelleni (Guibé & Lamotte, 1963) G
Phrynobatrachus cricogaster (Perret, 1957) F *P. steindachneri* (Nieden, 1910) E *P. w. werneri* (Nieden, 1910) G	*Phrynobatrachus cricogaster* (Perret, 1957) F *P. steindachneri* (Nieden, 1910) E *P. w. werneri* (Nieden, 1910) G	*Phrynobatrachus* cf. *werneri* (Nieden, 1910) G *Ptychadena oxyrhynchus* (Smith, 1847) G *Petropedetes parkeri* (Amiet, 1983) G

Note. F, G, U & E refer to *forest*, *generalist*, *unknown* & *expected* — see fig. 2. * = probably, according to Amiet in Gartshore (1986). ** = possibly *L. polyacanthus*, Rödel, pers. com. *** = recorded by Shiøtz as two separate species: *H. r. hieroglyphicus* (Ahl, 1931) & *H. r. riggenbachi* — but here considered to be conspecific (following Gartshore, 1986).

TABLE IV

Community composition at each locality

Species / Localities	1	2	3	4	5	6	7	8	9	10
Bufo maculatus									4	
Arthroleptis variabilis	8			9						
Astylosternus diadematus	4		4							
Cardioglossa melanogaster	2		1							
Leptodactylodon ovatus							12	7		
Leptodactylodon spp.			3				7	4		
Trichobatrachus robustus			3							3
Hyperolius riggenbachi	8	12					9		9	
Phrynobatrachus aelleni	6	3	10	1	8	12	4	4	2	
Phrynobatrachus wernei		6			8	4	6			
Ptychadena oxyrhynchus					3*					
Petropedetes parkeri									4	
Geotrypetes seraphini							10			

Note. For description of localities see Table I. Figures give number of individuals sighted at that site. (* = Found in temporary roadside puddles, lacking vegetation).

TABLE V

Species overall abundance (# individuals sighted/180 hrs) in decreasing order, and relative abundance at each location (# sighted/18 hrs)

		Relative abundance at location									
	Overall abundance	1	2	3	4	5	6	7	8	9	10
Phrynobatrachus aelleni	0.28	0.33	0.17	0.56	0.06	0.44	0.67	0.22	0.22	0.11	
Hyperolius riggenbachi	0.21	0.44	0.67					0.50		0.50	
Phrynobatrachus wernei	0.13		0.33			0.44	0.22	0.33			
Leptodactylodon ovatus	0.11							0.67	0.39		
Arthroleptis variabilis	0.09	0.44			0.50						
Leptodactylodon spp.	0.08			0.17				0.39	0.22		
Geotrypetes seraphini	0.06							0.56			
Astylosternus diadematus	0.04	0.22		0.22							
Trichobatrachus robustus	0.03			0.17							0.17
Bufo maculatus	0.02									0.22	
Petropedetes parkeri	0.02									0.22	
Cardioglossa melanogaster	0.02	0.11		0.06							
Ptychadena oxyrhynchus	0.02					0.17					

Figure 2 shows that, although a similar number of species were caught in each survey, there has been a clear transition from a predominance of forest specialists in the 1960's and 1980's to a predominance of generalist species in 2002. The difference between numbers of forest specialists and numbers of generalists is statistically significant across the three survey periods ($\chi^2 = 7.35$, df = 2, $p < 0.05$) (analysis excludes the three unknown species in the 1960's). There is no difference, however, between the 1960's and 1980's either including ($\chi^2 = 0.38$, df = 1, $p > 0.05$) or excluding ($\chi^2 = 0.81$, df = 1, $p > 0.05$) the three unknown species in the 1960's. These results parallel the changes seen in Lea *et al.* (2003) where there was again a significant ($\chi^2 = 4.17$, df = 1, $p < 0.05$) shift from forest specialists to generalists (see Table VI and Fig. 3).

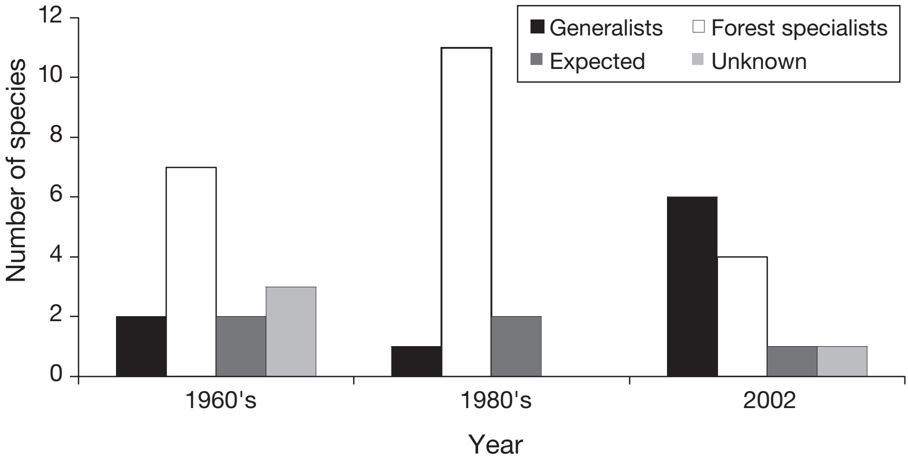

Figure 2. — Classification of species at Obudu according to whether they are: 1) *forest specialists*; 2) *generalists* (reported to occur in wide range of habitats); 3) species *expected* to occur at Obudu (i.e. preferred habitats include montane grassland/forest) or 4) unidentified species where habitat preference is *unknown*. Note that the three unknown species in the 1960's were two *Cardioglossa* spp. and one *Arthroleptis* spp. and these are likely to be forest specialists. The figure shows that there has been a transition from predominance of forest specialists (1960 to 1980) to a predominance of generalists (in 2002) (cf. numbers of forest species and generalists across survey periods: $\chi^2 = 7.35$, df = 2, $p < 0.05$; analysis excludes 3 unknown species in 1960's). (There is no difference between 1960's and 1980's either including ($\chi^2 = 0.38$, df = 1, $p > 0.05$) or excluding ($\chi^2 = 0.81$, df = 1, $p > 0.05$) the three unknown species).

TABLE VI

Etiope River anurans (adapted from Lea et al., *2003)*

Species found in 1982		Species found in 2002	
Bufonidae:		Bufonidae:	
Bufo maculatus	G	*Bufo maculatus*	G
Hyperoliidae:		Hyperoliidae:	
Acanthixalus spinosus	F	*Afrixalus dorsalis***	G
*Hyperolius fusciventris burtoni***	G	*A. vittiger ***	G
*H. guttulatus***	G	*Hyperolius fusciventris burtoni***	G
H. nasutus	S	*H. guttulatus***	G
H. sylvaticus nigeriensis	F	*Leptopelis viridis*	S
Ranidae:		Ranidae:	
Hoplobatrachus occipitalis	G	*Aubria subsigillata*	F
Phrynobatrachus cf. *latifrons*	G	*Hoplobatrachus occipitalis*	G
Ptychadena aequiplicata	F	*Phrynobatrachus* cf. *latifrons*	G
		*Ptychadena bibroni**	G
Pipidae:		*Pt. longirostris**	G
Silurana tropicalis	G	*Pt. mascareniensis*	G
		Pt. oxyrhynchus	G
Rhacophoridae:		*Pt. pumilio**	G
Chiromantis rufescens	F	*Pt. trinodis**	G
		Pipidae:	
		Silurana tropicalis	G

Note. F, G, & S refer to *forest specialists*, *generalist* and *savannah* species. (For evidence of habitat preferences see references cited in Lea *et al*., 2003). For this analysis, our "generalist" category includes species that commonly inhabit both savannah and farmbush (*) (Rödel, 2000) and those with habitat preferences listed as "bushland mosaic" (**) (Schiøtz, 1999).

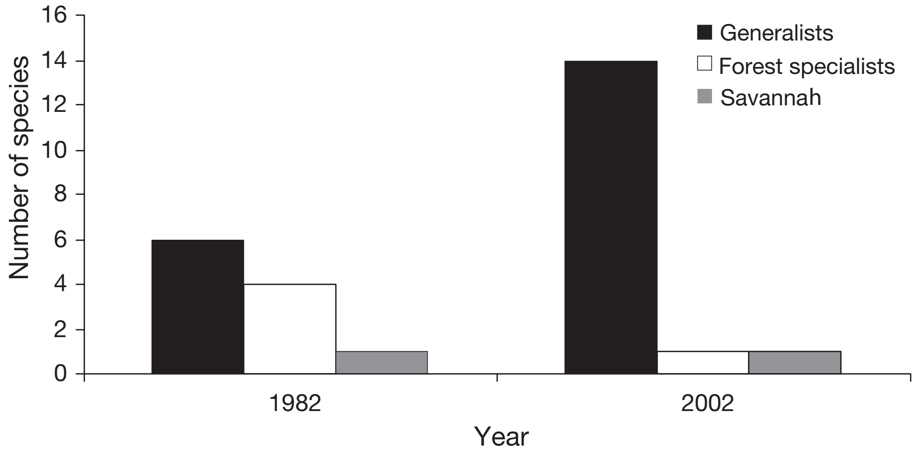

Figure 3. — Classification of anuran species at Etiope River, Abraka (Niger Delta) (see Lea *et al*., 2003) according to whether they are: 1) *forest specialists*; 2) *generalists* (reported to occur in wide range of habitats); 3) *savannah* species. The figure shows that there has been a significant rise in the number of generalist species and a fall in the number of forest specialists between the survey periods (cf. numbers of forest sp. & generalists across survey periods: $\chi^2 = 4.17$, df = 1, $p < 0.05$).

DISCUSSION

A rise in species with generalist habitat tolerances

A species-by-species account of the Obudu anurans should be taken cautiously because of the taxonomic confusion within West African frogs and hence the possibility of inter-observer differences in species identification. Indeed, in this paper we have considered *Hyperolius riggenbachi hieroglyphicus* and *H. r. riggenbachi* as conspecific (following Gartshore, 1986). Nevertheless, some clear changes in species composition are evident between old and recent surveys. First, although a similar number of species were caught in each Obudu survey, there has been a clear transition from a predominance of forest specialists in the 1960's and 1980's to a predominance of generalist species in 2002 (see Fig. 2). This is especially noticeable if we consider that the three unknown species in the 1960's were two *Cardioglossa* spp. and one *Arthroleptis* spp. and these are also likely to be forest specialists. Secondly, these results parallel the changes seen in the Etiope River (Niger Delta, Lea *et al*., 2003) where, although there are the expected differences (cf. to Obudu) in assemblage composition (i.e. lowland vs. montane fauna), there was again a significant shift from forest specialists to generalists that accompanied the degradation of rainforest (see Table VI and Fig. 3). This parallelism is even more remarkable when we consider the wide differences between the two habitats. That is to say, the Etiope River environment is a seasonally flooded lowland, whilst Obudu is a montane environment with a cooler climate and much better drainage. Nowadays, the Etiope has become a mosaic of fields, shrub, immature and mature secondary forest, whilst Obudu now consists of small fingers of secondary forest and large grassland areas interspersed with fields and human settlements. What they share in common is that the two sites (approx. 400 km linearly apart) were both originally stable, dense, closed canopy forest but have both nowadays become highly fluctuating disturbed environments. This may help to explain the extremely similar pattern of herpetofaunal succession that we see at each site. Below, we set out the details of the specific changes in the anuran fauna that have occurred at Obudu.

Bufonidae

Bufo maculatus now appears at village sites close to the cattle ranch hotel. The hotel has recently supplied electricity to surrounding villages and it is perhaps the electric lights that have attracted this toad, which commonly hunts insects close to human settlements. The disappearance of *B. regularis* is surprising since it is found in a wide range of pristine and disturbed habitats, including montane grassland, and so is expected to persist at Obudu (LeBreton, 1999). As *B. maculatus* and *B. regularis* are morphologically similar it is possible that previous records of the latter were actually specimens of the former. The disappearance of the other Bufonidae, *Werneria mertensi* and *Woltersdorffina parvipalmata*, may reflect a decline in or disturbance to their preferred habitats, which are listed as: undisturbed forest (*W. parvipalmata*) (Gartshore, 1986); mountain foothills (restricted range) and dense forest (*Werneria mertensi*) (Amiet, 1986; Gartshore, 1986). Both these apparently extirpated species are therefore obvious forest specialists.

RANIDAE

The Ranidae, in general, have persisted well at Obudu. Two new species have appeared, *Petropedetes parkeri* and *Ptychadena oxyrhynchus*, while *Phrynobatrachus aelleni* is now the most abundant of all anurans and *Phrynobatrachus wernei* remains common (see Table V). *P. parkeri* is reported by Amiet (1986) to be a forest species, although Lawson (1993) describes it as a generalist that often inhabits disturbed areas. The eggs of this species are laid in arboreal leaf nests and guarded by the adults (see Lawson, 1993). This behaviour, together with the large terrestrial component and rapid development of the tadpoles, may help explain the success of this species compared to species that abandon their eggs, which may well be swept away during the process of sand extraction, for example. *P. oxyrhynchus* is said to prefer open landscapes (Rödel, 2000) and disturbed areas when in forests (Lawson, 1993), which fits with current observations (i.e. species found in roadside puddles, lacking vegetation and bordering a cut-grass field). The success of *P. oxyrhynchus* is attributable in part to its incredible jumping and swimming abilities (Lamotte, 1998), high fecundity (3476 ± 1542 eggs/clutch, Barbault, 1984), rapid development, prolonged breeding and within-season clutch partitioning (in different ponds, to bet-hedge *sensu* Murphy, 1968 — see Rödel, 2000). In addition, *P. oxyrhynchus* is a generalist feeder (Eniang *et al*., 2003) and is therefore adaptable to changing circumstances. *P. aelleni* was observed in almost every habitat surveyed in 2002 (Tables IV and V) and interviews with local people suggest that it breeds throughout the rainy season and can even be heard calling in the dry season. *P. wernei* is another adaptable species that has maintained its widespread occurrence in many habitat types, as has previously been reported (Gartshore, 1986). *P. cricogaster* and *P. steindachneri* were not found in 2002. The former was found only in undisturbed forest beforehand (Perret, 1959; Gartshore, 1986; Lawson, 1993) and its present day absence is therefore unsurprising; the latter, however, is to be expected in elevated savannah (Perret, 1959, 1966) and should still therefore be present at Obudu. The general success of ranids such as *Phrynobatrachus* and *Ptychadena* in this altered environment is similar to what we have found before (Lea *et al.,* 2003) and this is discussed further below.

HYPEROLIIDAE

Concerning the hyperoliids, *H. riggenbachi* has persisted well in both disturbed and protected areas (Table IV), and indeed is expected to occur in both gallery forests and wetlands in montane grasslands (Gartshore, 1986), which are the typical habitats of Obudu. In contrast, *Leptopelis modestus* has disappeared from Obudu and we suggest that this may be as a consequence of its habit of burying its eggs in soil near water and the slow development of its larvae; it may therefore be very susceptible to sand excavations around the edges of water bodies and to general disturbance of watercourses.

ARTHROLEPTIDAE

For the Arthroleptidae, the genus *Cardioglossa* has shown the greatest reduction in species diversity in recent years, with only *C. melanogaster* persisting and C. *gracilis, C. pulchra, C. schioetzi* and *C. trifasciata* having disappeared. Also, *Astylosternus montanus*, *Leptodactylodon albiventris*, *L. polyacanthus* and *L. bicolor* are no longer found. All the above (eight) species are reported to be montane forest specialists (Schiøtz, 1963; Amiet, 1986; Gartshore, 1986; Lawson, 1993) and their disappearance may again reflect severe habitat fragmentation and a loss of suitable breeding sites. However, *Astylosternus diadematus, Cardioglossa melanogaster*, *Leptodactylodon ovatus* and *Trichobatrachus robustus* are also forest species but they have persisted at Obudu. Unfortunately, their current range may be severely restricted to undisturbed forest patches. For example, in 2002 *A. diadematus* was found along streams but only in small, protected forested areas (although it was locally abundant there) (Table IV). Forest streams are also the preferred habitat of *A. montanus* (Sanderson, 1936; Perret, 1966), and we searched all such streams intensively. This raises the question, why has *A. diadematus* persisted and *A. montanus* foundered? The same question arises for the *Cardioglossa*; why is *C. melanogaster* the only one remaining out of five *Cardioglossa* species that were previously present at Obudu despite them all having comparable habitat requirements (Gartshore, 1986)? Similarly, we need more ecological data concerning *L. ovatus* to be able to understand why it has outcompeted its congeners. One species that has persisted throughout the forty years since the first survey, despite the fact that it is a local delicacy (at least in Cameroon, Lawson, 1993), is *Trichobatrachus robustus*. A possible reason for its success (as with *P. parkeri*) could be the fact that males habitually guard the eggs, using their dermal appendages to remain underwater for considerable time (Perret, 1966). The final Arthroleptid found in 2002 is *Arthroleptis variabilis*, and this species has also probably persisted well at Obudu since the record of *Arthroleptis* spp. in the 1960's could well be *A. variabilis* (Rödel, pers. com). *Arthroleptis variabilis* is again a generalist species that has previously been found in both cultivated areas (Sanderson, 1936) and forest (Amiet, 1986; Lawson, 1993).

CONCLUSIONS

Overall, our results here are similar to what we have shown elsewhere (Lea *et al.,* 2003) i.e. that forest destruction in Nigeria does not necessarily lead to a reduction in species diversity, but that there can be a successional change in species composition with the generalists (esp. Ranidae) becoming more speciose at the expense of the forest specialists. In our previous study (Lea *et al.,* 2003) we actually saw an increase in overall amphibian species diversity (esp. Ranidae) despite massive destruction of lowland riparian forest, and we suggested that this was because the new mosaic landscape provides more ecotypes for adaptable species that can switch between a variety of habitats depending upon prevailing conditions (see also "spatial heterogeneity hypothesis': Pianka, 1966; Barbault, 1981, 1991). The situation at Obudu is different from the lowland case cited above in that there are essentially only two macrohabitat types (montane forest and grassland) and the remaining forest patches are very small and widely dispersed. So, in such a fragmented environment (i.e. with a lack of corridors) the utilization of more than one habitat type may not be possible for many species. In the past, Obudu species may well have been able to utilize both grassland and forest at different times of the year. However, the burning of grassland has created a sharp demarcation with the remnant forest patches and destroyed transitional environments, which has probably affected the dispersal of species that would traditionally leave the forest to breed and return again after spawning (e.g. *Wernia* spp., Gartshore, 1986). The species that are nowadays the most successful at Obudu (and also in lowland Nigeria, Lea *et al.*, 2003) include those that are highly mobile, have wide habitat tolerances and are opportunistic (e.g. *Ptychadena* and *Phrynobatrachus*); these species cope well with changing landscapes.

Other reasons for the failure of certain forest specialists can also be related to environmental degradation. First, there has been major disturbance to Obudu watercourses from sand dredging and agricultural run-off (i.e. pesticides and herbicides used on cattle and on the new golf course), which has led to increased siltation and eutrophication as well as unpredictable waterflow. Indeed, interviews with local women indicate that the number and quality of water sources have declined drastically in recent years (Rodenkirchen, 2002). This has no doubt affected tadpole survival and adult recruitment in many species, especially considering that montane tadpoles are generally rheophilic and can only breed in clear, fast-flowing perennial streams (Stebbins & Cohen, 1995). Again, the species that have persisted despite this disturbance include those that show some form of egg-guarding behaviour (*T. robustus* and *P. parkeri*) or perhaps produce very large clutches (e.g. *Ptychadena*). Secondly, the massive forest clearance that has occurred at Obudu has probably led to reduced cloud cover locally and therefore increased insolation, and a drier, less humid environment is particularly detrimental to specialized montane amphibians.

It is possible to generalize the results of our current study even further. This is because the pattern of species succession in both lowland and montane anuran assemblages in Southern Nigeria mirrors that found in cobras from the same study region. That is to say, there is again an ongoing shift in species dominance from the forest specialists (dominant until the 1980's) to the generalists, which are now dominant almost everywhere (Luiselli, 2001, 2002). And, exactly as in the case of the cobras, a particularly interesting question would be to explore the costs and benefits to generalist species of invading recently deforested or secondarily forested areas. For example, invading species may have some suboptimal adaptations to the new habitats (Luiselli, 2002) or, conversely, they may be successful colonizers because of the "exaptation" of pre-existing characteristics (Gould & Vrba, 1982). These adaptive hypotheses should be tested by *ad-hoc* experiments, and may provide a very fertile area for further research.

Finally, the Obudu plateau contains many amphibians endemic to the Cameroon-Gabon area, including *T. robustus, Astylosternus* spp., *Petropedetes* spp., *H. riggenbachi, C. melanogaster* and *G. seraphini* (Parker, 1936; Gartshore, 1986), and the montane areas of Nigeria and Cameroon may contain up to 75 endemic species, which are not closely related to other montane forms (Gartshore, 1986). Because of this restricted range there is a real danger that further environmental degradation may lead to the extinction of the less adaptable of these species — and indeed, it is a real possibility that this has already occurred in some cases. The unique and highly interesting amphibian fauna of Obudu urgently needs to be protected. Future work needs to be done to ascertain the factors that determine community composition (see Tables IV and V) and the specific ecological requirements of the Obudu amphibians in order to 1) better understand why some species have persisted while others have foundered and 2) plan conservation (or even reintroduction) measures.

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