



SPECIES RICHNESS AND VARIATION IN THE COMMUNITY COMPOSITION OF AMPHIBIANS AND REPTILES IN FOUR SITES OF THE DAHOMEY GAP IN BENIN, WEST AFRICA

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Abstract.

In order to analyze the community composition of herpetofauna in the Dahomey Gap area in West Africa, we studied the amphibians and reptiles of distinct sites in Benin. Our aims were to highlight whether these communities are homogeneous (as can be predicted by the fact that the Dahomey Gap is a relatively homogeneous vegetation zone) or whether there are remarkable site-specific differences. In particular, we tested the hypothesis that there should be significant differences in community composition between savannah and the open forest remnants or gallery forests along the riverine sites, by applying a Visual Encounter Survey protocol. We found that the herpetological species were typically those of the West African savannahs, with no species belonging to another ecosystem different from the Guinean and Sudanian savannahs. Anthropophilic species were also frequently observed. Our study also documented that the community composition may vary considerably in terms of species richness by site within the Dahomey Gap main habitats, whereas the bulk of the communities of both taxa remain the same. Habitat mosaics and remnant forest patches should be considered the most important habitat type for the conservation and management of herpetofauna species in the Dahomey Gap.

Key Words: Amphibia; Reptilia; West Africa; savannah; community structure; biodiversity

INTRODUCTION

Benin, a tiny country in West Africa, is part of the so-called «Dahomey Gap» (Salzmann and Hoelzmann, 2005; Demenou et al., 2018). This is a human-derived vegetation zone that is characterized by relatively small forest patches and gallery forests interspersed within a wide matrix of herbaceous savannah-like, that is currently heavily altered by urban settlements and plantations (Salzmann and Hoelzmann, 2005; Demenou et al., 2018). The Dahomey gap is ecologically very important as it subdivides the Guinea-Congolian rainforest belt into two distinct ecological zones, the Upper Guinean and the Lower Guinean forest blocks (Salzmann and Hoelzmann, 2005 ; Demenou et al., 2018).

The ecology of the Dahomey Gap has not received sufficient attention by researchers, and, whilst several studies have investigated the taxonomy of species and the composition of species' assemblages, very few have examined the community ecology and functional structure of

these animal communities. Interestingly, it has been shown that the freshwater turtles communities exhibit near-constant species compositions and relative abundances (Luiselli et al., 2020), also presenting similarly to those from the Guinean dry forests of Ghana (Gbewaa et al., 2021), indicating that the resource availability are likely similar across the Dahomey Gap. Conversely, in lizards there was evident variation in the community structure in relation to the habitat gradients available in the region, thus showing that the same assembly rules do not correspond across taxa (Luiselli et al., 2022).

From a herpetological point of view, Benin is one of the least studied countries in West Africa (Ullénbruch et al., 2010). Overall, 51 species of amphibians are known nationally (Nago, 2011), and 94 species of reptiles (Ullénbruch et al., 2010). However, it can be anticipated that several species should occur inside Benin as the field herpetological research has been far less intense than in the neighbouring Togo and Nigeria (e.g., Segniangbeto et al.,

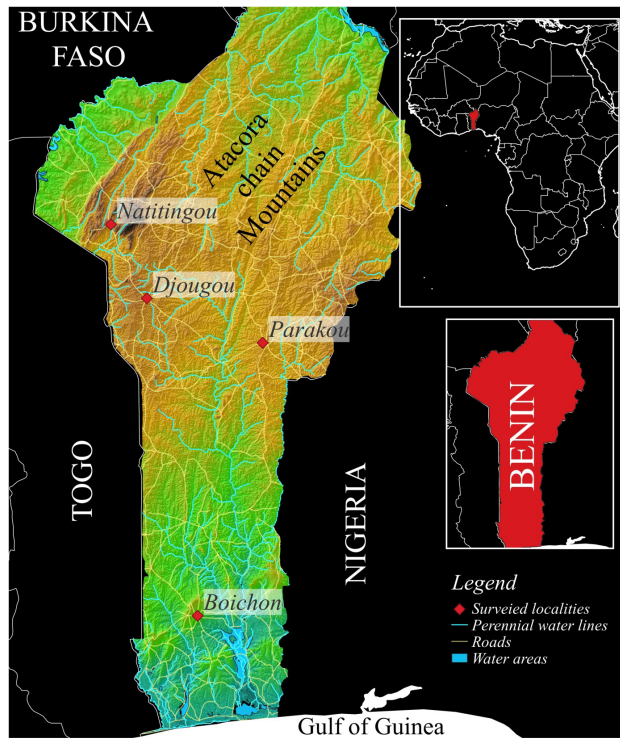


Fig. 1. Map of Benin showing the four study areas

2007, 2011, 2014, 2015). In particular, very little is known concerning the community composition of herpetofaunas in distinct sites, and on the variability of the species richness across sites and microhabitats in Benin.

The main objective of this study is to analyze the community composition and the amphibian and reptile species richness of distinct sites in Benin, in order to highlight whether these communities are homogeneous (as can be predicted by the fact that the Dahomey Gap is a relatively homogeneous vegetation zone) or whether there are remarkable site-specific differences. In particular, we anticipate that significant differences should occur between savannah and the open forest remnants or gallery forests along the riverine sites. This paper also addresses the issue of conserving the Dahomey Gap biodiversity by reporting some considerations on the status and abundance of some species.

MATERIALS AND METHODS

Study areas. The field study was carried out, during September – October 2021, at four distinct sites of Benin, West Africa (Figure 1).

Site 1 (Parakou) The Parakou site ($9^{\circ}15'N - 2^{\circ}22'E$) is essentially dominated by shrub savannah. Its flora and structure suggest that it is derived from the degradation of wooded and tree savannahs. A remnant of the tree stratum was sometimes observed, consisting of *Daniellia oliveri*, *Ekebergia capensis*, *Cussonia arborea* and *Vitellaria paradoxa*. This shrub savannah has developed behind a

forest gallery dominated by *Diospyros mespiliformis*, *Berlinia grandiflora*, and *Vitex doniana*. There are also fallows, plantations and farms.

Site 2 (Djougou) The Djougou site ($9^{\circ}22'N - 1^{\circ}30'E$) is essentially a fallow land characterized by young shoots of shrubs, mainly *Daniellia oliveri*. There are also few stands of *Sarcocephalus latifolius* and *Vitellaria paradoxa*. There are also cashew tree plantations with an undergrowth characterized by grasses. Between the site of the photovoltaic plant and the highway RNIE3, there is a marshy area dominated by grasses, temporarily waterlogged. This site is home to numerous amphibian species typical of African savannahs.

Site 3 (Natitingou) the Natitingou site ($10^{\circ}N - 1^{\circ}12'E$) is made up of a mosaic of ecosystems. Different types of habitats can be distinguished, notably gallery forests, dense dry forests, wooded savannahs, tree savannahs, shrub savannahs, fallows, plantations and fields. The vegetation landscape, relatively degraded overall, is remarkably dominated by savannahs, fallows and fields. The best-preserved natural plant formations are represented by relics of dense dry forest, gallery forest and wooded savannah. The site belongs to the Sudanian savannah domain; *Isoberlinia doka* and *Isoberlinia tomentosa* are only found locally in pockets (White 1983, Adomou et al., 2007). The gallery forest with the ecological characteristics of a semi-deciduous forest zone along the Atacora chain Mountains.

Site 4, the Bohicon ($7^{\circ}07'N - 2^{\circ}01'E$) site is a very degraded fallow land, marked by ox footprints. In places, there are fields of maize, beans and groundnuts. There is also a cashew nut plantations. At the entrance to the site, there is an excavated area probably used for road construction purposes. The abandoned excavated area serves as a collection site for run-off water where oxen come to drink. Vegetation has grown up around the excavated area, providing refuge for small mammals, reptiles and amphibians. This vegetation is characterized by *Azadirachta indica*, *Anacardium occidentale*, *Senna siamea*, *Hyptis suaveolens*, *Zanthoxylum zanthoxyloides*, etc.

Overall, the four study sites housed a remarkable suit of habitats that, on the basis of the classification of White (1983), are presented in Table 1. The habitats encountered in the study area were also described and assessed in terms of quality in relation to their conservation status according to five classes (Table 2).

Protocol. This study is based on both careful literature surveys and field research in order to establish as much as possible the community composition of the herpetofauna of the four study areas.

Literature survey. – As part of the present study, a bibliographic work was carried out on the species of reptiles and amphibians of Benin and especially on the species potentially present on the four sites which were investigated during this study. We cannot list all the bibliography

Table 1. Habitats encountered at the study area, using White’s (1983) classification

Abréviations	Habitats	Description
FANT	Anthropic formation	Areas where natural vegetation has been completely removed over very large areas; they can be buildings, etc.
FC	Open forest	Open stand of trees reaching at least 8 m in height with ground cover of at least 40%; herbaceous stratum usually grass-dominant
FB	Bushy formation	Open stand of bushes generally between 3 and 7 m in height, with a cover of the crowns of not more than 40%.
F	Thicket	Closed stand of bushes and climbing plants generally between 3 and 7 m in height
FA	Shrubland	Open or closed stand of shrubs up to 2 m in height.
FD	Dense forest	Continuous stand of trees up to at least 10 m tall, with interpenetrating crowns
FH	Grassland	Land covered with grasses or other grasses, either devoid of woody plants or with a covering of the latter not exceeding 10%
FHB	Wooded grassy formation	Land covered with grasses and other grasses, either devoid of woody plants or with a covering of the latter not exceeding 10%. Includes grassy vegetation of temporary marshes.
FVAED	Freshwater aquatic plant formation	Aquatic and freshwater marshy herbaceous vegetation

Table 2. Definition of the various classes of habitat quality as used in the present study

Quality classes	Description
Pristine	No trace of human activity is noticeable.
Almost pristine	Very little human activity is visible (example: selective removal of a tree).
Moderately degraded	Habitat in which human action has affected a very small part of its diversity, its structure (stratum), and which still provides goods and services
Degraded	Habitat that has lost certain segments of its structure and whose production of goods and services has become limited
Heavily degraded	Habitat whose entire segments of its structure have disappeared due to the action of man. Its ability to produce goods and services has become weak to zero. Almost all or all species have been destroyed.

that was used for the realization of this study. However, they are of two kinds. The first concerns guides or books that take into account all the herpetological fauna of West Africa. In this group, we can mention for the amphibians Schiøtz (1967, 1999), Rödel (2000), Channing and Rödel (2019), and Rödel et al. (2021); and for reptiles the works like Trape et al. (2012), Trape and Mané (2006), Chippaux (2006). In the second group, we have some specific data on Benin, Togo and Burkina Faso including the work of Nago et al. (2006 and 2010), Segniagbeto et al. (2007), Ayoro et al. (2020) on amphibians and reptiles, the work of Segniagbeto et al. (2011, 2014 and 2015), Baurer et al. (2006), de Ullenbruch et al. (2010), Kpera et al. (2011), Toudonou

et al. (2011a, 2011b) for the reptiles. Apart from these different works, some study reports have also been consulted to establish the diversity of reptiles and amphibians of the four study sites, and additional data were obtained from museum vouchers and unpublished field data obtained by one of the authors (GHS) during the last 20 years. In all cases, we considered as present in a given area only those species for which a voucher or a clear photo was available for the grey literature reports.

Field research. – Visual Encounter Surveys (VES) were carried during 12 days from 30th September to 11th October 2021. Fieldwork was carried out by three persons on each field day. In total, each of these three-team mem-

ber spent 38 hours observing all four sites. The total field effort of the team was 38 hours x 3 = 114 hours. This field effort allowed to (i) assess the specific richness of reptiles and amphibians at the four study sites, (ii) determine species communities at the local level, and (iii) estimate in a preliminary way the relative abundances of species within a community (Crump and Scott, 1994).

For reptiles the research techniques consisted of a visual scan of the terrain and the inspection of potential shelters: leaves, trunks and branches of trees for arboreal species, water bodies for aquatic species, all potential shelters of terrestrial species (plant debris, trees, burrows), ground shelters for burrowing species. Other evidence of presence was also recorded (e.g., moults, shells, skeletons). The search for reptiles took place day and night, with a significant portion of reptile species having nocturnal activity. For amphibians, fieldwork was concentrated mainly in habitats including the presence of water, in particular spots where small ponds are accessible as the sites are degraded savannahs. The different individuals were noted opportunistically during the visual surveys, but also male calls at night were used for species identification. The search for amphibians took place day and night (using flashlights). In most cases, the species were directly identified in the field based on our experience on amphibians. Some specimens with unresolved taxonomic status were collected, humanely sacrificed, fixed and identified at the Laboratory of Ecology and Ecotoxicology of the University of Lomé on the basis of taxonomic characters. The identifications of the

different species were performed using Chippaux (2006) and Trape and Mané (2006) for snakes, Trape et al. (2012) for other reptiles, and Channing and Rödel (2019) for amphibians. Taxonomy of amphibians follows Frost (2021).

At the different sites, each observation was recorded in an Excel database gathering the following information: (i) species name, (ii) date of observation, (iii) number of individuals, (iv) age and sex (if determinable), (v) habitat and habitat quality, (vi) sign of presence (seen/heard), (vii) GPS coordinates, (viii) photograph number if the individual was photographed, etc.

RESULTS

Overall, we observed 635 individuals of amphibians and reptiles during our surveys, with a Whittaker plot showing a long right tail (Fig. 2), thus indicating that several species were rarely sampled during our surveys. Indeed, eight singletons and three doubletons were observed (Fig. 2). We did not analyze the quantitative data on the number of individuals recorded by site separately because of the too small sample sizes also concerning species that are normally abundant (for instance, *Trachylepis maculilabris*, *Trachylepis affinis*, etc)

The species richness of amphibians per site varied more (19-33) than that of reptiles (53-64), with similar patterns of variation: Natitingou was the site housing the highest species richness and Bohicon the lowest species richness of both taxa (Table 3).

In Parakou (Fig. 3 and Fig. 4), the most abundant

Fig. 2. Whittaker plot showing the abundance of the various species of amphibians and reptiles (all study areas being pooled) ranked from the most frequently observed to the least frequently observed during the field surveys in Benin

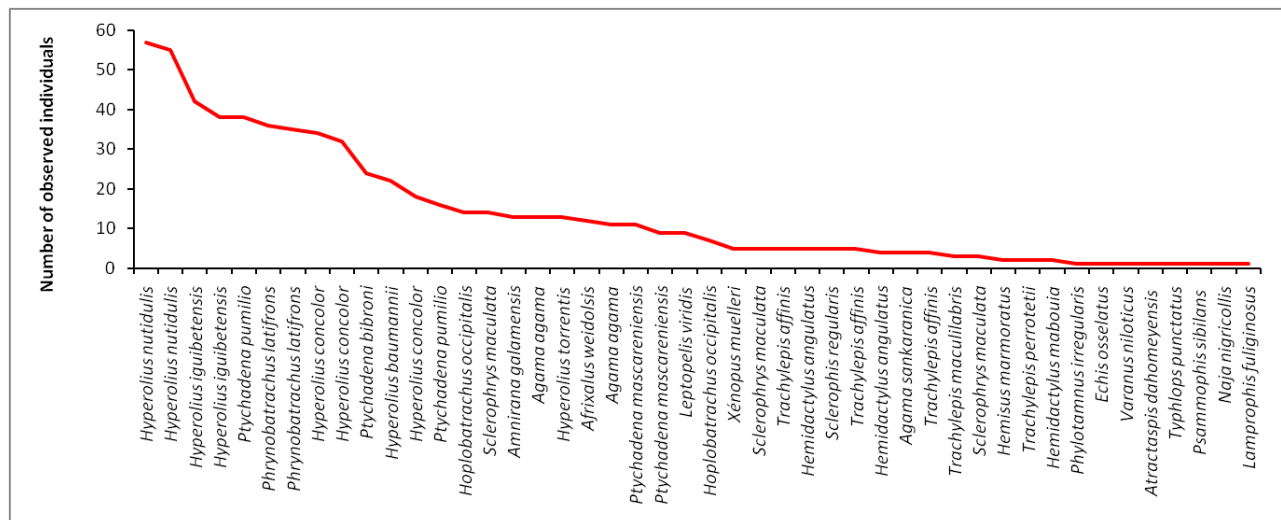


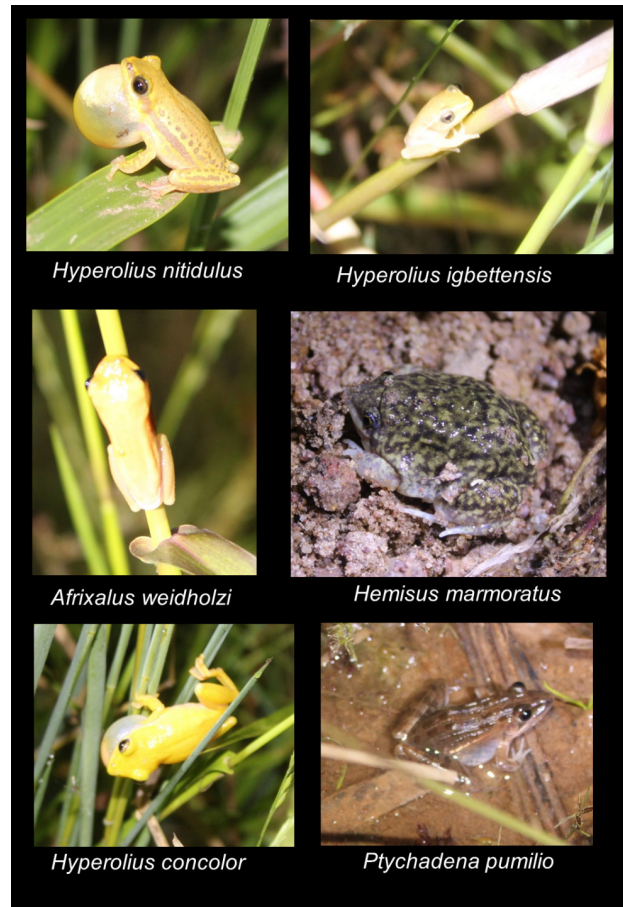
Table 3. List of the amphibians and reptiles occurring at the four study areas in Benin. Legend: O = Species whose specimens have been observed in the field, E = Species reported by village surveys, B = Species reported by bibliography, x = presence of a given species in a given site.

	Presence	Observation type	Presence	Observation type	Presence	Observation type	Presence	Observation type
	Parakou		Djougou		Natitingou		Bohicon	
Amphibia								
<i>Arthroleptis poecilonotus</i>	x	O	x	O	x	O	x	O
<i>Sclerophrys maculatus</i>	x	O	x	O	x	O	x	B
<i>Sclerophrys regularis</i>	x	O	x	O	x	O	x	O
<i>Hemisis marmoratus</i>	x	O	x	B	x	B		
							x	O
<i>Afrixalus vittiger</i>	x	B	x	B	x	B	x	O
	x	O	x	O	x	B		
<i>Hyperolius baumanni</i>					x	O		
<i>Hyperolius concolor</i>	x	O	x	O	x	O	x	O
<i>Hyperolius igbettensis</i>	x	O	x	O	x	B		
<i>Hyperolius nitidulus</i>	x	O	x	O	x	O		
					x	B		
					x	O		
<i>Kassina cassinoides</i>	x	B	x	B	x	B		
<i>Kassina fusca</i>	x	B	x	B	x	B		
<i>Kassina senegalensis</i>	x	B	x	B	x	B	x	O
			x	B	x	O		
<i>Leptopelis viridis</i>	x	O	x	O	x	O	x	O
<i>Leptopelis spiritusnoctis</i>	x	B	x	B	x	O	x	O
<i>Phrynomantis microps</i>	x	B	x	B	x	B	x	B
<i>Phrynobatrachus latifrons</i>	x	O	x	O	x	O	x	O
					x	B		
			x	B	x	B		
<i>Phrynobatrachus natalensis</i>	x	B	x	B	x	B	x	B
<i>Xenopus tropicalis</i>	x	B	x	B	x	B		
<i>Xenopus fischbergi</i>	x	O	x	O	x	B	x	B
					x	B		
<i>Hylarana galamensis</i>	x	B	x	O	x	B	x	B
<i>Hoplobatrachus occipitalis</i>	x	O	x	O	x	O	x	O
<i>Ptychadena bibroni</i>	x	O	x	O	x	O	x	O
<i>Ptychadena mascareniensis</i>	x	O	x	O	x	O	x	O
<i>Ptychadena oxyrhynchus</i>	x	B	x	B	x	B	x	B
<i>Ptychadena pumilio</i>	x	O	x	O	x	O	x	O
<i>Ptychadena tellinii</i>	x	B	x	B	x	B		
	26		28		33		19	

Reptilia								
<i>Pelusios castaneus</i>	x	O	x	E	x	E	x	O
<i>Pelomedusa subrufa olivacea</i>	x	O	x	E	x	E	x	O
<i>Kinixys nogueyi</i>	x	E	x	E	x	E	x	E
<i>Cyclanorbis senegalensis</i>	x	E			x	E		
<i>Amblyodipsas unicolor</i>	x	B	x	B	x	B		
<i>Atractaspis dahomeyensis</i>	x	B	x	B	x	B	x	B
<i>Atractaspis aterrima</i>	x	B	x	O	x	B	x	B
<i>Atractaspis irregularis</i>	x	B	x	B	x	B	x	B
<i>Afronatrix anoscopus</i>	x	B	x	B	x	B		
<i>Chamaelycus fasciatus</i>	x	B	x	B	x	B	x	B
<i>Crotaphopeltis hotamboeia</i>	x	B	x	B	x	B	x	B
<i>Dasypeltis fasciata</i>	x	B	x	B	x	B	x	B
<i>Dasypeltis gansi</i>	x	B	x	B	x	B	x	B
<i>Lamprophis fuliginosus</i>	x	B	x	B	x	O	x	B
<i>Lamprophis lineatus</i>	x	B	x	B	x	B	x	B
<i>Lycophidion irroratum</i>	x	B	x	B	x	B	x	B
<i>Lycophidion semicinctum</i>	x	B	x	B	x	B	x	B
<i>Mehelya crossi</i>	x	B	x	B	x	B	x	B
<i>Mehelya poensis</i>	x	B	x	B	x	B	x	B
					x	B		
<i>Meizodon coronatus</i>	x	B	x	B	x	B	x	B
<i>Meizodon regularis</i>	x	B	x	B	x	B	x	B
					x	B		
<i>Philothamnus irregularis</i>	x	O	x	B	x	B	x	B
<i>Philothamnus semivariegatus</i>	x	B	x	B	x	B	x	B
<i>Prosymna meleagris</i>	x	B	x	B	x	B	x	B
<i>Psammophis sibilans</i>	x	B	x	O	x	B	x	B
<i>Psammophis elegans</i>	x	B	x	B	x	B	x	B
<i>Psammophis phillipsi</i>	x	B	x	B	x	B	x	O
<i>Rhamnophis aethiopissa</i>	x	B	x	B	x	B	x	B
<i>Rhamphiophis oxyrhynchus</i>	x	B	x	B	x	B	x	B
<i>Rhamphiophis togoensis</i>	x	B	x	B	x	B	x	B
<i>Scaphiophis albopunctatus</i>	x	B	x	B	x	B	x	B
					x	B		
<i>Telescopus variegatus</i>	x	B	x	B	x	B	x	B
<i>Toxicodryas blandingii</i>	x	B	x	B	x	B	x	B
<i>Toxicodryas pulverulenta</i>	x	B	x	B	x	B	x	B
<i>Dendroaspis viridis</i>	x	E	x	B	x	B	x	E
<i>Elapsoidea semiannulata</i>	x	B	x	B	x	B	x	B
<i>Naja melanoleuca</i>	x	E	x	E	x	E	x	E
<i>Naja nigricollis</i>	x	O	x	E	x	E	x	E

<i>Leptotyphlops bicolor</i>	x	B	x	B	x	B	x	B
<i>Python regius</i>	x	E	x	B	x	B		E
<i>Python sebae</i>	x	E	x	B	x	B		
<i>Typhlops punctatus</i>	x	B	x	O	x	B	x	B
<i>Bitis arietans</i>	x	E	x	B	x	E	x	E
<i>Causus maculatus</i>	x	E	x	B	x	B	x	E
<i>Echis ocellatus</i>	x	O	x	B	x	B	x	E
<i>Crocodylus suchus</i>	x	E	x	E	x	E		
<i>Agama agama</i>	x	O	x	O	x	O	x	O
<i>Agama sankaranica</i>	x	O	x	O	x	O	x	E
<i>Chamaeleo senegalensis</i>	x	E	x	E	x	E	x	O
<i>Cnemaspis spinicollis</i>	x	B			x	B		
<i>Hemidactylus angulatus</i>	x	O	x	O	x	O	x	O
<i>Hemidactylus mabouia</i>	x	O	x	O	x	O	x	B
<i>Hemidactylus albituberculatus</i>	x	B					x	O
<i>Hemitheconyx caudicinctus</i>	x	E					x	E
<i>Ptylodactylus raggazii</i>					x	O		
<i>Heliobolus nitida</i>	x	E	x	B	x	B	x	E
<i>Panaspis togoensis</i>	x	B			x	B		
<i>Trachylepis affinis</i>	x	O	x	O	x	O	x	O
<i>Trachylepis maculilabris</i>	x	O	x	O	x	O	x	O
<i>Trachylepis perrotetii</i>	x	O	x	O	x	O	x	O
<i>Trachylepis quinquetaeniata</i>	x	O	x	O	x	O	x	O
<i>Varanus exanthematicus</i>	x	E	x	E	x	E	x	O
<i>Varanus niloticus</i>	x	O	x	E	x	E	x	E
TOTAL	62		57		64		53	

Fig. 3. Some of the amphibian species encountered at Parakou in Benin.



amphibian species were *Hyperolius concolor*, *Hyperolius nitidulus*, *Hyperolius igbettensis*, *Arthroleptis poecilonotus*, *Ptychadena pumilio*, *Sclerophrys regularis* et *Hoplobatrachus occipitalis* (none being of IUCN conservation concern or protected in Benin), and the most frequently encountered reptiles were *Varanus niloticus*, *Echis ocellatus*, *Trachylepis affinis*, *Trachylepis maculilabris*, *Agama sankaranica*. Three reptile species are VU (IUCN, 2024): *Kinixys nogueyi*, *Cyclanorbis senegalensis* and *Crocodylus suchus*.

In Djougou (Fig. 4 and Fig. 5), the most common amphibian species were *Hyperolius nitidulus*, *Hyperolius concolor*, *Hyperolius igbettensis*, *Afraxalus weidholzi*, *Ptychadena pumilio*, *Ptychadena mascareniensis*, *Ptychadena bibroni*, *Sclerophrys maculatus*, and the most common reptile species were *Trachylepis affinis*, *Trachylepis maculilabris*, *Psammophis sibilans*, *Typhlops punctatus*.

Natitingou site had a higher diversity of species compared to the two previous sites (Table 3), with the most frequently observed amphibians (Fig. 6) being *Hyperolius torrentis*, *Hyperolius baumanni*, *Hyperolius nitidulus*, *Leptopelis viridis*, *Leptopelis spiritusnoctis*, *Arthroleptis poecilonotus*, *Sclerophrys maculatus*, *Sclerophrys regularis*, *Ptychadena bibroni*, *Ptychadena mascareniensis*, *Ptychadena pumilio*. Among these amphibian species, there were mainly forest forms including *Hyperolius torrentis* (VU according to IUCN, 2022) and *Hyperolius baumanni* which are endemic species throughout the Atacora chain shared by Ghana, Togo and Benin. For the

Fig. 4. Some of the reptile species encountered at Parakou and Djougou, in Benin.

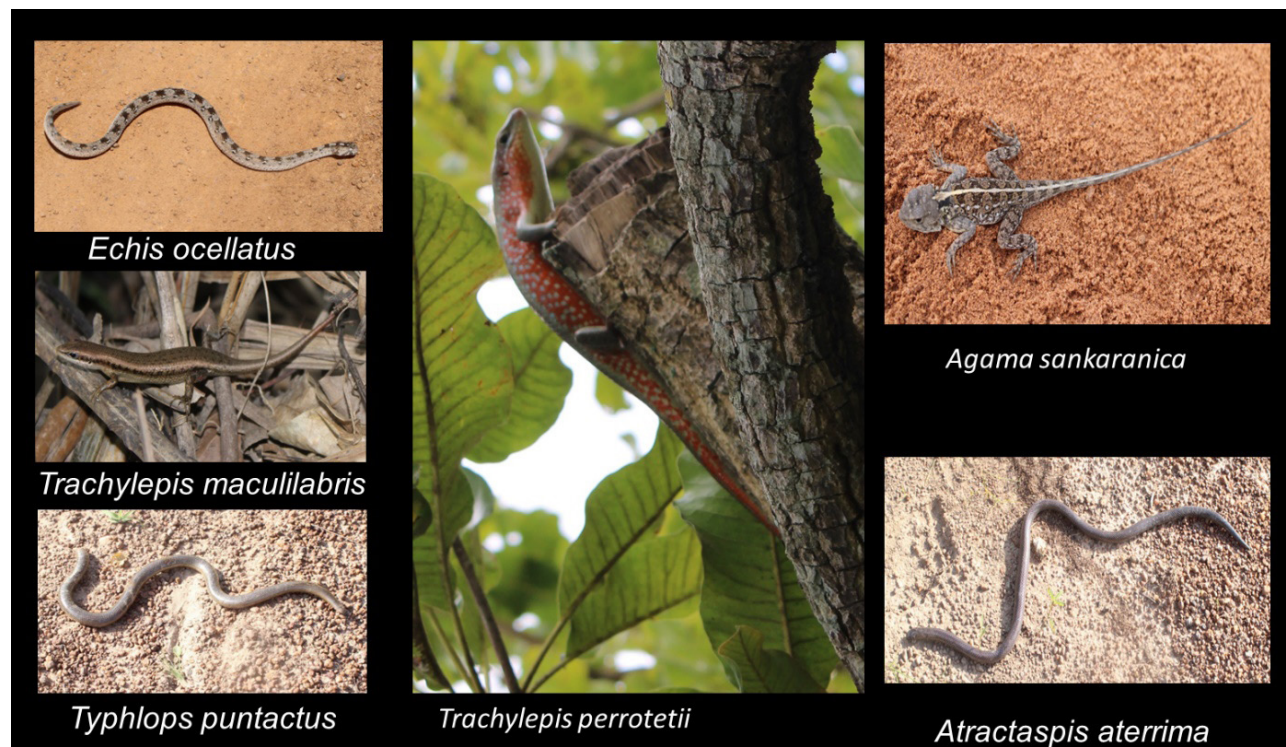


Fig. 5. Some of the amphibian species encountered at Djougou in Benin.



Fig. 6. Some of the amphibian species encountered at Natitingou in Benin. Note that for *Hyperolius baumanni* this is the first record for Benin.

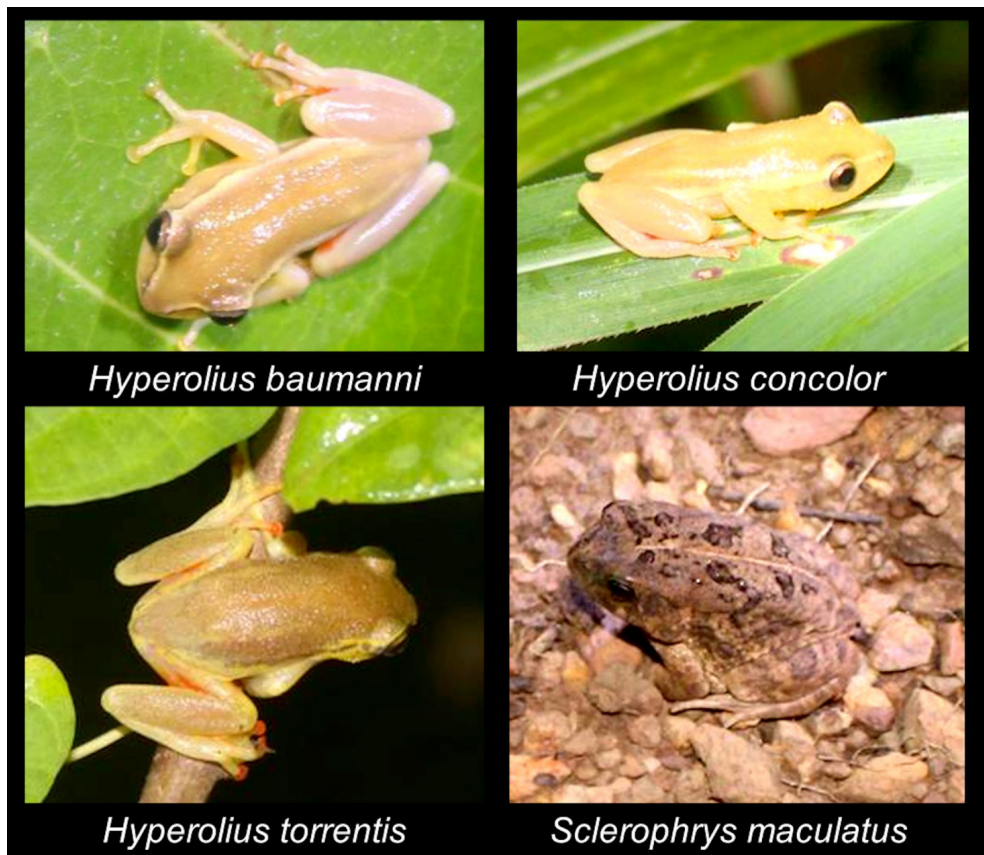


Fig. 7. Some of the reptile species encountered at Natitingou and Bohicon, in Benin.

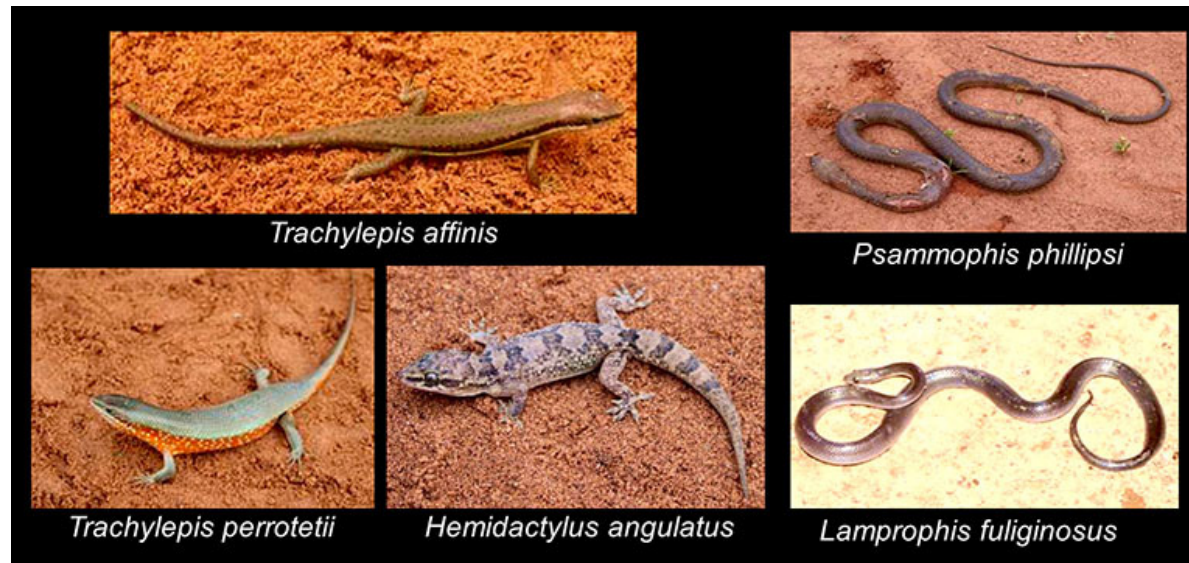
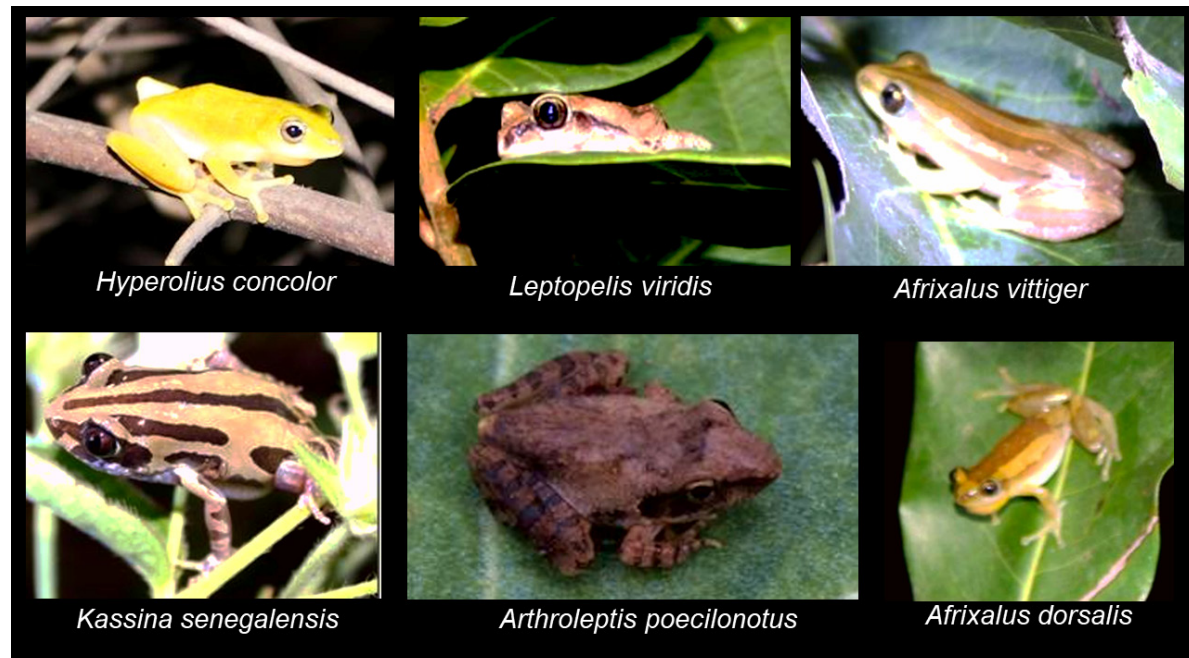


Fig. 8. Some of the amphibian species encountered at Bohicon, in Benin.



specific case of *Hyperolius baumanni*, this is the first time that the species has been reported in Benin (Fig. 6). For reptiles (Fig. 7), the most frequently encountered species were *Trachylepis affinis*, *Trachylepis maculilabris*, *Trachylepis perrotetii* and *Lamprophis fuliginosus*.

In Bohicon (Fig. 7 and Fig. 8), the most abundant amphibian species were *Arthroleptis poecilonotus*, *Sclerophrys regularis*, *Afrixalus dorsalis*, *Afrixalus vittiger*, *Hyperolius concolor*, *Kassina senegalensis*, *Leptopelis viridis* et *Hoplobatrachus occipitalis*, and the most abundant reptile species were *Pelusios castaneus*, *Psammophis phillipsi*, *Hemidactylus angulatus*, *Hemidactylus albitu-*

berculatus, *Trachylepis affinis*, *Trachylepis maculilabris*, *Trachylepis perrotetii* and *Varanus exanthematicus*.

DISCUSSION

Our surveys provided the first comprehensive lists of amphibian and reptile species of four study areas in Benin that were explored for a relatively prolonged time. Nonetheless, these lists are no doubt incomplete given that we were able to make our surveys only during a single season, whereas the activity of tropical reptiles and amphibians is highly related to the seasons and the community of species encountered at a site varies over the seasons depending

on the biological activity of the species (e.g., Vonesh, 2001; Prahdan et al., 2014; Leyte-Manrique et al., 2016), including in West Africa (Akani et al., 2010, 2013). Moreover, although VES is a good start for any herpetological surveys, the inclusion of additional survey methods (e.g., pitfall traps, drift fences, and acoustic monitoring) could have improved species detection, particularly for cryptic or nocturnal species. Unfortunately, this was not possible during our surveys due to logistics and time-schedule issues. Because of the above-mentioned methodological limitations, we recorded several singletons and doubletons, and a few number of individuals in general also for the apparently most common species. For these reasons, it is necessary to implement several field studies intersecting the different seasons to understand the specific overall herpetological richness of a site. Therefore, additional species of both taxa may well occur at the study sites but remained undetected.

In general, the herpetological fauna species identified are West African savannah species if we refer to the work of Roëdel (2000), Segniagbeto et al. (2011 and 2015), Trape and Mané (2006) and Trape et al. (2012). No species belonging to another ecosystem different from the Guinean and Sudanian savannahs were identified. They are sometimes anthropophilic and coexist with human activities. From the point of view of the observed amphibian and reptile species, therefore, the Dahomey Gap does not show substantial differences with the large sub-Saharan savannahs of West Africa, and indirectly confirms that the entire vegetation zone has no real ecological differences from the other savannahs. However, this consideration is valid if we consider the general population of the amphibian and reptile faunas of the Dahomey Gap, while, going down to the local scale, the general pattern becomes considerably more complicated. Indeed, our study documented that the community composition may vary considerably in terms of species richness by site within the Dahomey Gap main habitats, whereas the bulk of the communities of both taxa remain the same. So, whilst the range of encountered species varied substantially by site (more in amphibians than in reptiles), there were many species that were found in all sites. Including also bibliographic data, in amphibians 15 out of 34 species (44.1%) were observed at all sites (i.e. *Arthroleptis poecilnotus*, *Sclerophrys maculatus* and *S. regularis*, *Afraxalus vittiger*, *Hyperolius concolor*, *Kassina senegalensis*, *Leptopelis viridis*, *Leptopelis spiritusnoctis*, *Phrynomantis microps*, *Phrynobatrachus latifrons*, *Phrynobatrachus natalensis*, *Xenopus fischbergi*, *Hylarana galamensis*, *Hoplobatrachus occipitalis*, and four species of *Ptychadena*) with only four (11.7%) species (*Afraxalus dorsalis*, *Hyperolius torrentis*, *Phrynobatrachus calcaratus*, *Hylarana albolabris*) being observed at a single site. The same pattern was even stronger in reptiles: 52 out of 66 total species (78.8%) were observed at all sites (i.e. *Pelusios castaneus*, *Pelomedusa subrufa olivacea*, *Kinixys nogueyi*, *Atractaspis da-*

homeyensis, *Atractaspis aterrima*, *Atractaspis irregularis*, *Chamaelycus fasciatus*, *Crotaphopeltis hotamboea*, *Dasipeltis gansi*, *Dasipeltis fasciata*, *Lamprophis fuliginosus*, *Lamprophis lineatus*, *Lycophidion irroratum*, *Lycophidion semicinatum*, *Mehelya crossii*, *Mehelya poensis*, *Meizodon coronatus*, *Meizodon regularis*, *Philothamnus irregularis*, *Philothamnus semivariatus*, *Prosymna meleagris*, three *Psammophis* species, *Rhamnophis aethiops*, *Rhamphiphis oxyrhynchus*, *Rhamphiphis togoensis*, *Scaphiophis albopunctatus*, *Telescopus variegatus*, *Toxicodryas blandingii*, *Toxicodryas pulverulenta*, *Dendroaspis viridis*, *Elapsoidea semiannulata*, *Naja melanoleuca*, *Naja nigricollis*, *Leptotyphlops bicolor*, *Typhlops punctatus*, *Bitis arietans*, *Causus maculatus*, *Echis ocellatus*, *Agama agama*, *Agama sankaranica*, *Chamaeleo senegalensis*, *Hemidactylus angulatus*, *Hemidactylus mabouia*, *Heliobolus nitida*, four *Trachylepis* species and two *Varanus* species) and only four (6.1%) occurred in only one site (*Natriciteres variegata*, *Hapsidophrys smaragdinus*, *Thelotornis kirtlandii*, *Ptylodactylus raggazii*). However, interestingly most gecko species occurred at two sites only, thus showing that their community structure tend to vary at a smaller scale than that of other reptilian groups. It is possible that this difference may depend on a strong interspecific competition among geckos (Harmon et al., 2007; Cole and Harris, 2011; Nguyen et al., 2020), but further studies should confirm this hypothesis. Evidence of interspecific competition have already been documented in West African gecko communities from forest areas using null models and Monte Carlo simulations (Luiselli et al., 2007; Rugiero et al., 2007). The same methodology should be used also for gecko assemblages of the Dahomey Gap, but we do not have the data in this article to try answering to this noteworthy point.

The main source of variation in herpetofaunal assemblage composition by study area was certainly the availability of dry forested, gallery forest residual patches and habitat mosaics. Indeed, (i) some of the species found at a single site (for instance *Thelotornis kirtlandii*) tend to be more abundant in sites with high vegetation than in grasslands areas, and (ii) the highest species richness was found in the area characterized by the highest vegetation complexity and habitat mosaics (Natitingou) whereas the least diversity was found in Bohicon, the site most degraded and with more homogeneous vegetation. Thus, the presence of residual fragments of forest is surely correlated with a higher diversity of species at the landscape scale. This fact should be deeply considered for conservation and management (see below).

Conservation considerations. Although the great majority of the recorded species do not have any conservation concern according to IUCN (2024), some of them are exploited for local consumption, these are *Varanus exanthematicus*, *Varanus niloticus*, *Bitis arietans*, *Pelusios castaneus*, *Pelomedusa subrufa olivacea* et *Kinixys*

nogueyi. Given the disappearance of the taboos and ritual practices of traditional religion, the totemic character of *Python regius* is also no longer so much respected, with many individuals of this species being collected and exploited in international trade. The populations of these intensely exploited species should be monitored in the years to come in order to prevent any serious decline.

The four sites sampled are in an advanced state of degradation. These are often cashew tree plantations or corn fields surrounded by fallow lands. The Natitingou site is essentially fallow. There are sometimes rivers (Parakou) or ponds (Bohicon and Djougou) that are home to amphibian populations. These rivers or ponds are also very degraded, especially that of the Bohicon site. In Bohicon and Parakou, there is a strong hunting activity including on reptile species. Thus, careful monitoring of herpetofauna populations in general is strongly urged for the whole region. However, priority attention should be given to the appropriate management and conservation of the relictual forest patches and of the gallery forest strips, as these are the habitats with the highest diversity of species of the whole Dahomey Gap region. For the future, we recommend longer-term studies across different seasons and more extensive geographic areas within the Dahomey Gap and beyond, in order to properly understand the ecological characteristics and the conservation needs of amphibians and reptiles in this part of Africa.

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Adomou, A. C., Akoègninou, A., Sinsin, B., de Foucault, B., & van der Maesen, L. J. (2007). Notulae Florae Beninensis, 13—Biogeographical analysis of the vegetation in Benin. *Acta Botanica Gallica*, 154(2), 221-233.

Akani G. C., Ebere N., Franco D., Eniang E. A., Petrozzi F., Politano E., and Luiselli L. (2013), Correlation between annual activity patterns of venomous snakes and rural people in the Niger Delta, southern Nigeria, *Journal of Venomous Animals and Toxins including Tropical Diseases*, 19, 1-8.

Akani G. C., Luiselli L., Ogbeibe A. E., Onwuteaka J. N., Chuku E., Osakwe J. A., ... and Gijo H. A. (2010), Aspects of species richness and seasonality of amphibians and reptiles in the coastal barrier island of Brass (Nigeria), *Revue d'Ecologie, Terre et Vie*, 65, 151-161.

Ayoro H. J., Segniagbeto G.H., Hema E.M., Penner J., Oueda A., Dubois A., Rödel M-O, Kabré G. B., Ohler A. (2020), Amphibian species (Vertebrata, Tetrapoda) of Burkina Faso: a commented list, *Zoosystema*, 42 (28): 547 – 582.

Bauer A. M., Tchiboza S., Pauwels O. S. G. and Lenglet G. (2006), A review of the gekkotan lizards of Bénin, with the description of a new species of *Hemidactylus* (Squamata: Gekkonidae), *Zootaxa*, 1242, 1-20.

Channing, A., and Rödel M.-O. (2019), *Field Guide to the Frogs and other Amphibians of Africa*, Struik Nature, Cape Town, 408 pp.

Chippaux J.-P. (2006), *Les serpents d'Afrique Occidentale et Centrale*, Collection Faune et Flore tropicales, Paris, IRD Éditions 35: 311 p.

Cole N. C., and Harris S. (2011), Environmentally-induced shifts in behavior intensify indirect competition by an invasive gecko in Mauritius, *Biological Invasions*, 13, 2063-2075.

Crump M.L., and Scott N.J. Jr. (1994), Visual encounter survey. In Heyer, W.R., Donnelly, M.A.; McDiarmid, R.W., Donnelly, Heyek, L.C., and Foster, M.S. (Eds) *Measuring and monitoring Biological diversity, Standard Methods for Amphibians*, Smithsonian Institution Press, Washington D.C: pp 84-91.

Deménu B.B., Doucet J.L., and Hardy O.J. (2018), History of the fragmentation of the African rain forest in the Dahomey Gap: insight from the demographic history of *Terminalia* system, *Heredity*, 120, 547–561.

Frost D. R. (2021), *Amphibian Species of the World: an Online Reference*. Version 6.1 (Date of access). Electronic Database accessible at <https://amphibiansoftwareworld.amnh.org/index.php>. American Museum of Natural History, New York, USA. doi.org/10.5531/db.vz.0001.

Gbewaa S. B., Oppong S. K., Horne B. D., Tehoda P., Petrozzi F., Dendi D., ... and Luiselli L. (2021), Community characteristics of sympatric freshwater turtles from savannah waterbodies in Ghana, *Wetlands*, 41, 1-13.

Harmon L. J., Harmon L. L., and Jones C. G. (2007), Competition and community structure in diurnal arboreal geckos (genus *Phelsuma*) in the Indian Ocean, *Oikos*, 116, 1863-1878.

IUCN (2024), the IUCN Red List of Threatened Species, available at www.iucnredlist.org, last accessed on 28th May 2024.

Kpera G. N., Mensah G.A., and Sinsin B. (2011), Crocodiles: In Neuenschwander, P., Sinsin, B. and Goergen, G. (eds). *Protection de la Nature en Afrique de l'Ouest: Une Liste Rouge pour le Bénin*, Nature Conservation in West Africa, Red List for Benin. International Institute of Tropical Agriculture, Ibadan, Nigeria, p: 157 – 163.

- Leyte-Manrique A., Morales-Castorena J. P., and Escobedo-Morales L. A.** (2016), Variación estacional de la herpetofauna en el cerro del Veinte, Irapuato, Guanajuato, México, *Revista mexicana de biodiversidad*, **87**, 150-155.
- Luiselli L., Akani G. C., Ajong S. N., George A., Di Vittorio M., Eniang E. A., Dendi D., Hema E. M., Petrozzi F., and Fa J. E.** (2020), Predicting the structure of turtle assemblages along a megatransect in West Africa, *Biol. J. Linn. Soc.*, **130**, 296-309.
- Luiselli L., Dendi D., Petrozzi F., Segniagbeto G.H.** (2022), Lizard community structure and spatial resource use along a forest-savannah-urban habitat gradient in the Dahomey Gap (West Africa), *Urban Ecosystems*, <https://doi.org/10.1007/s11252-022-01215-w>.
- Luiselli L., Eniang E. A., and Akani G. C.** (2007), Non-random structure of a guild of geckos in a fragmented, human-altered, African rainforest, *Ecological Research*, **22**, 593-603.
- Nago S. G. A., Grell O., Sinsin B., and Rödel M.-O.** (2006) The amphibian fauna of the Pendjari National Park and surroundings, northern Benin, *Salamandra*, **42**: 93-108.
- Nago G.** (2011) Amphibiens, In Neuenschwander, P., Sinsin, B. and Goergen, G. (eds). *Protection de la Nature en Afrique de l'Ouest: Une Liste Rouge pour le Bénin. Nature Conservation in West Africa*, Red List for Benin. International Institute of Tropical Agriculture, Ibadan, Nigeria, p: 149 – 156.
- Neuenschwander P., Sinsin B., and Goergen G. (eds).** (2011), *Protection de la Nature en Afrique de l'Ouest: Une Liste Rouge pour le Bénin. Nature Conservation in West Africa*, Red List for Benin. International Institute of Tropical Agriculture, Ibadan, Nigeria. 365 pages.
- Nguyen H. N., Hung C. M., Yang M. Y., and Lin S. M.** (2020), Sympatric competitors have driven the evolution of temporal activity patterns in *Cnemaspis* geckos in Southeast Asia, *Scientific reports*, **10**, 1-8.
- Pradhan S., Mishra D., and Sahu K. R.** (2014), Seasonal variation and abundance of herpetofauna in the Gandhamardan Hills range, Western Orissa, India, *International Journal of Research in Zoology*, **4**, 51-54.
- Rödel, M.-O.** (2000), *Herpetofauna of West Africa. Vol 1. Amphibians of the West African savana*. Frankfurt am Main, Chimaira.
- Rödel M.-O, G. B. Adum, E. Aruna, N. E. Assemian, M. F. Barej, R. Bell, T. Doherty-Bone, M. Burger, J. Doumbia, R. Ernst, N. L. G., A. Hillers, M. Hirschfeld, N. G. Kouamé, T. F. Kpan, M. Mohnke, G. A. Nago, C. Ofori-Boateng, A. Onadeko, O. S.G. Pauwels, L. Sandberger-Loua, G. H. Segniagbeto, A.M. F. Tchassem, B. Tohé, B. Zimkus, and J. Penner** (2021), Diversity, threats and conservation of western and central African amphibians (Senegal, The Gambia, Guinea Bissau, Mali, Guinea, Sierra Leone, Liberia, Ivory Coast, Burkina Faso, Ghana, Togo, Benin, Nigeria, Niger, Cameroon, Gabon, São Tome and Principe, Equatorial Guinea, Central African Republic, Chad, Republic of the Congo, Democratic Republic of the Congo, northern Angola). In *Amphibian Biology*, Volume 11, Part 7, Status of Conservation and Decline of Amphibians: Eastern Hemisphere (Status and threats of Afrotropical Amphibians – Sub-Saharan Africa, Madagascar, Western Indian Ocean Islands). Publisher: Frankfurt Contributions to Natural History, Vol. 78, Edition Chimaira, Frankfurt/M.
- Rugiero L., Luiselli L., Eniang E. A., and Akani G. C.** (2007), Diet of a guild of geckos in a fragmented, human-altered African rainforest, *African Journal of Herpetology*, **56**, 91-96.
- Salzmann U., and Hoelzmann P.** (2005), The Dahomey Gap: an abrupt climatically induced rain forest fragmentation in West Africa during the late Holocene, *The Holocene*, **15**, 190-199.
- Schiotz A.** (1967), Tree frogs (Rhacophoridae) of West Africa. *Spolia Zool. Mus. Haun.*, **25**, 1-346.
- Schiotz A.** (1999), *Treefrogs of Africa*, Frankfurt am Main, Chimaira.
- Segniagbeto G. H., Trape J-F., Afiademanyo K, Rödel M.-O., Ohler A., Dubois A., David P., Meirte D., Glitho A., Petrozzi F., and Luiselli L.** (2015), Checklist of the lizards of Togo, (West Africa), with comments on systematics, distribution, ecology, and conservation, *Zoosystema*, **37**, 381 – 402.
- Segniagbeto G. H., Bour R., Ohler A., Dubois A., Rödel M.-O., Trape J-F., Fretey J., Petrozzi F. Aidam A., and Luiselli L.** (2014), Turtles and tortoises of Togo: historical data, distribution, ecology and conservation., *Chelonian Conservation and Biology*, **13**, 152 – 165.
- Segniagbeto G. H., Trape J.-F., David P., Ohler A.-M., Dubois A., and Glitho, I. A.** (2011), The snake fauna of Togo: systematics, distribution, and biogeography, with remarks on selected taxonomic problems. *Zoosystema*, **33**, 325-360.
- Segniagbeto G. H., Bowessidjaou J. E., Dubois A., and Ohler, A.** (2007), Les Amphibiens du Togo : état actuel des connaissances. *Alytes*, **24**, 72-90.
- Trape J.-F., and Mané Y.** (2006), *Guide des serpents d'Afrique occidentale (savane et désert)*, IRD Éditions, Paris, 226 p.
- Trape J.-F., Trape S., and Chirio L.** (2012), *Lézards, crocodiles et tortues d'Afrique occidentale et du Sahara*, IRD éditions, Marseilles: 1-503.
- Toudonou A. S. C.** (2011a), Serpents. In Neuenschwander, P., Sinsin, B. and Goergen, G. (eds). *Protection de la Nature en Afrique de l'Ouest: Une Liste Rouge*

- pour le Bénin. Nature Conservation in West Africa: Red List for Benin. International Institute of Tropical Agriculture, Ibadan, Nigeria, p: 186 – 197.*
- Toudonou A. S. C.** (2011b), Varans et caméléons. *In* Neuenchwander, P., Sinsin, B. and Goergen, G. (eds). *Protection de la Nature en Afrique de l'Ouest: Une Liste Rouge pour le Bénin. Nature Conservation in West Africa: Red List for Benin. International Institute of Tropical Agriculture, Ibadan, Nigeria, p: 198 – 203.*
- Ullénbruch K., Grell O., and Böhme W.** (2010), Reptiles from southern Benin, West Africa, with the description of a new Hemidactylus (Gekkonidae), and a country-wide checklist, *Bonn zoological Bulletin*, **57**, 31–54.
- Vonesh J. R.** (2001), Patterns of Richness and Abundance in a Tropical African Leaf-litter Herpetofauna 1. *Biotropica*, **33**, 502-510.
- White F.** (1983), The vegetation of Africa. Vol. 20.