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Biogeographic analysis of the composition of the mammalian fauna of Togo (West Africa)

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Abstract: The Dahomey Gap in West Africa is a human-derived savannah-like vegetation zone interspersed by patches of moist forest, with large rainforest blocks at both West (Upper Guinean Forest) and East (Lower Guinean Forest) of its limits. Togo is a tiny country situated in the middle of the Dahomey Gap. In this paper, a biogeographic analysis of the composition of the mammalian fauna of Togo is presented, by classifying each species on the basis of five distinct ecological distribution patterns. The greatest proportion of species were Pan-African (88.0%). Excluding the Pan-African species from the analysis, the mammalian fauna appeared to be affiliated similarly to both Upper Guinean and Lower Guinean Forest blocks. Only three endemic species were observed, all of them being rodents: *Cryptomys zechi* (Batyergidae), *Funisciurus substriatus* (Sciuridae), and *Leimacomys buettneri* (Muridae). Considering only the multispecies genera, the great majority did not show any barrier effect by the Dahomey Gap on their own species, as all of them did occur on both sides of Togo. A barrier effect by the Dahomey Gap was uncovered in 8 genera; overall, the Dahomey Gap apparently showed a barrier effect on 28.6% of the multispecies genera. It is emphasized that the full understanding of the role of the Dahomey Gap as a biogeographic barrier and of its island forests as centers of endemism is impeded by the lack of biogeographic reviews and meta-analyses on the composition of faunal and floral groups of the entire region.

Key words: West Africa; Dahomey Gap; ecology; distribution patterns; Mammalia; endemism.

Introduction

In modern biogeography, an ‘area of endemism’ is defined as a geographic region comprising the distributions of two or more monophyletic taxa, that exhibit a phylogenetic and distributional congruence, and have their respective relatives occurring in other such defined regions (Harold and Mooi 1994). Therefore, the areas of endemism are characterized by non-random distributional congruence among different taxa’ (e.g., see Morrone 1994).

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However, their precise definition is still controversial from a statistical point of view (Amori and Luiselli 2019).

The Dahomey Gap in West Africa is a human-derived savannah-like vegetation zone interspersed by patches of moist forest, with large rainforest blocks at both West (Upper Guinean Forest) and East (Lower Guinean Forest) of its limits (Demenou et al. 2016, 2018; Salzmann and Hoelzmann 2005). Functionally speaking, the Dahomey Gap breaks the Guinea-Congolian rainforest block, thus causing isolation and speciation for forest taxa living in the Upper (= Western African) versus the Lower (= Central African) Guinean forests (Booth 1958; Mayr and O'Hara 1986). The isolation effect of the Dahomey Gap has been uncovered in a suite of different organisms, including both invertebrates and vertebrates (e.g., Houngbédji et al. 2012; Leaché et al. 2020). For instance, in the Giant beetle genus *Goliathus* Lamarck, 1801, two species (*Goliathus cacicus* (Olivier, 1789) and *G. regius* Klug, 1835) have their eastern-most distribution limit in Togo whereas *Goliathus goliatus* (Linnaeus, 1771) occurs exclusively east of Togo (Croizat 1994; De Palma et al. 2020); in reptiles, the Gaboon viper *Bitis gabonica* (Duméril, Bibron & Duméril, 1854) occurs in central African forests with its westernmost limit being western Nigeria, whereas the ecologically equivalent *Bitis rhinoceros* (Schlegel, 1855) occurs in the Upper Guinean forests eastwards up to Togo (Segniagbeto et al. 2011). The forest islands within the Dahomey Gap can therefore be considered centers of endemism for varied fauna and flora (Leaché et al. 2020). Unfortunately, there has been a continued shortage of knowledge on vertebrates in the Dahomey Gap countries of West Africa (Amori et al. 2011, 2012; Luiselli et al. 2012).

Togo, which is, with Benin, the core country of the Dahomey Gap, is an important area for biodiversity studies because the evolutionary biogeographic origin of its fauna is still quantitatively unknown, despite the fact that several comprehensive checklists of its vertebrate fauna are available (Leaché et al. 2006; Segniagbeto et al. 2014a, 2014b, 2015), as well as more quantitative studies on their ecological communities (e.g., Luiselli et al. 2022). Togo is positioned roughly in the center of the Dahomey Gap. It has a tiny, latitudinally elongated shape that includes several vegetation zones, from forest to dry savannah in the north (Amori et al. 2016). Therefore, because of i) its peculiar position within the African continent and ii) its variety of vegetation zones, it is likely that many distribution patterns of animal species may overlap in the country. For instance, it can be predicted that Togo may be a land bridge where species with wide African distribution, or inhabiting either side of the Dahomey Gap, or even distributed in the nearby Sahel region in the north, do coexist. Therefore, the study of the distribution patterns of Togolese animal coenoses is especially interesting from the biogeographic point of view.

In this paper, we specifically investigated the following key questions:

a) Is the Togolese fauna mostly derived from Eastern Africa or Western African forests/savannahs, or is it a mixture of both?
b) Did the Dahomey Gap act as a barrier to the spreading of taxa?
c) Are forest islands important centers of endemism for the fauna of the Dahomey Gap, as suggested by previous literature (see above)?

We answer the three above questions by using the Mammalian fauna as a study case, because i) the comprehensive checklist of the Togolese species is available with precise distribution records (Amori et al. 2016), and ii) the distribution of all species is reasonably well known (Kingdon et al. 2013).

Materials and Methods

Study area

Togo is a tiny country situated along the Gulf of Guinea, West Africa. It is characterized by five main ecological zones (Amori et al. 2016) (Figure 1): – EZ I consists of Sudanese savannahs with dominant leguminous plants of the family Mimosoideae (*Acacia* spp.) or Combretaceae (*Terminalia* spp., *Combretum* spp.), with dry forest patches dominated by *Anogeissus* spp., gallery forests, and grasslands; – EZ II includes essentially dense dry and open forest hills bordered by Guinean savannah areas; – EZ III is represented by Guinean savannah and characterized by a relatively rich flora dominated by Combretaceae and Andropogoneae; – EZ IV consists of a wet tropical climate and originally was largely covered with true tropical dense wet forests or semi-deciduous forests. Currently, the remaining high tropical forests of Togo are entirely located inside ecological zone IV (Amori et al. 2016); – EZ V is restricted to the littoral area, and is characterized by a highly disturbed landscape of littoral bushes, marshy grasslands, and mangroves.

Protocol

The list of taxa considered in this paper comes from Amori et al. (2016), with nomenclatural updates from Kingdon et al. (2013). We also added the newly described species for Togo after the year 2016. Each mammal species was classified, on the basis of its overall distribution pattern, as:

a) Endemic (END): only found in the Dahomey Gap (Togo and Benin).
b) Upper Guinean (UGU): found in Togo and the countries situated west of Togo, from Ghana to Senegal.
c) Lower Guinean (LGU): found in the Dahomey Gap and the countries situated east of Benin, from Nigeria to East Africa.
d) Pan-African (south of the Sahara; PAN): found throughout sub-Saharan Africa, either very widespread or with many small isolated populations.
e) Sahelian (SAH): found only in the arid savannah of Sahel, just north of the Dahomey Gap (i.e., in Burkina Faso, Mali, and Niger).

Each species in Togo was allocated to one pattern only. When a given species did not fit exactly into any of the above-mentioned biogeographic patterns, the best fitting pattern was selected. For each species, we also determined its presence within the five ecological zones of Togo, by using the database provided in Appendix 1 of Amori et al. (2016).

In order to verify whether the Dahomey Gap may have acted as a barrier to the spreading of mammalian taxa, for our analyses, we only considered those genera with two or more species (excluding the endemics from this count). We then calculated the number of taxa within each genera occurring only West or East of Togo, thus showing that their distribution pattern was clearly affected by the presence of the Dahomey Gap. In all cases, the statistical differences in the frequencies of occurrence of the various biogeographic patterns were assessed by the observed vs expected X^2 test. Statistical analyses were performed by PAST 4.0 statistical software, with alpha set at 5%.

Results

The list of the species classified according to the five biogeographic patterns is reported in Table 1. Considering the whole number of the species (n=175) there were significant differences in the frequencies of the five biogeographic patterns (X^2=498.8, df=4, p<0.0001).

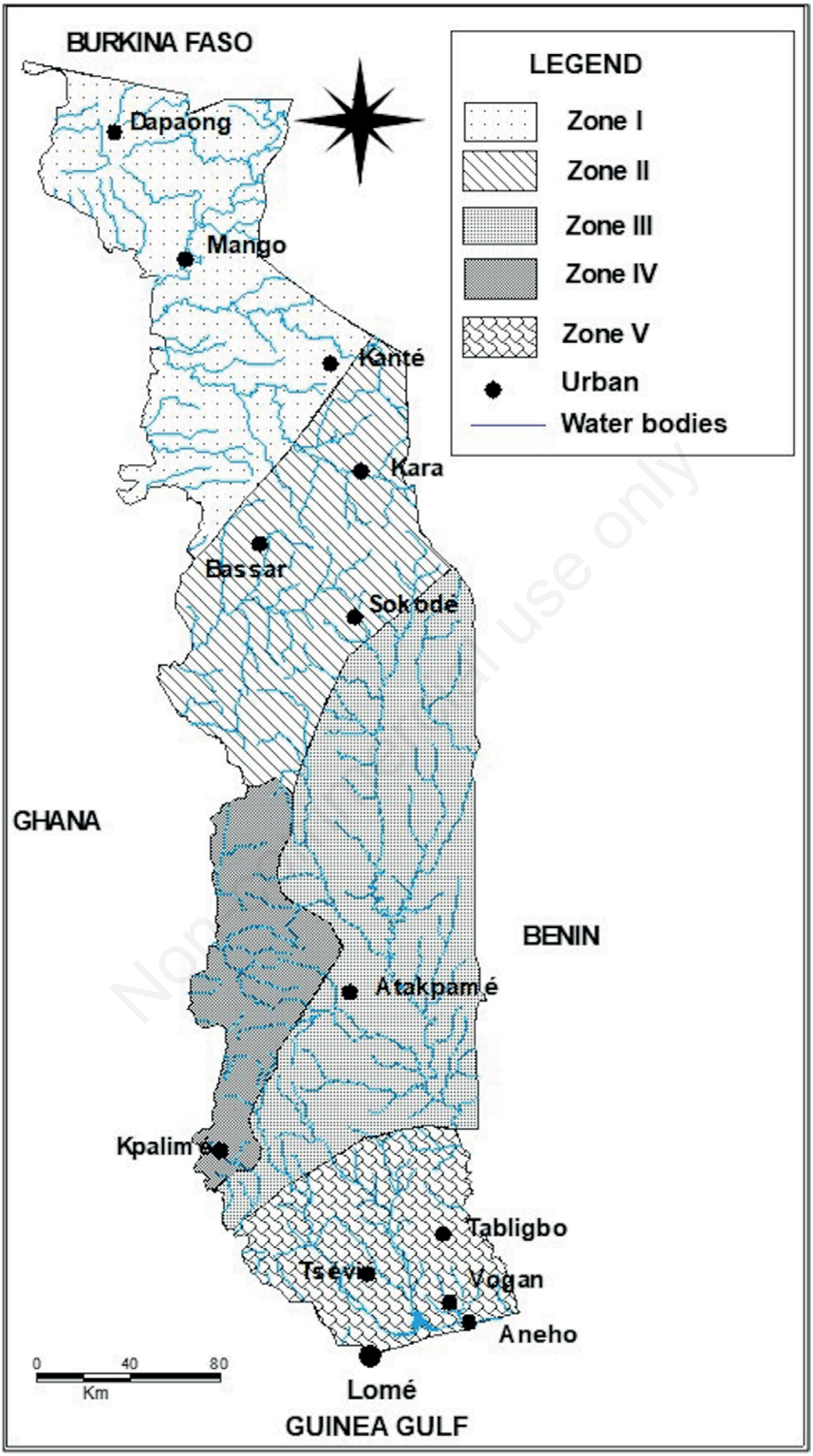

Figure 1. Map of Togo, showing the five ecological zones.

Table 1. List of the Togo mammals, classified according to their biogeographic pattern.

Species	Order	Family	Distribution pattern
Funisciurus substriatus de Winton, 1899	Rodentia	Sciuridae	a
Leimacomys buettneri Matschie, 1893	Rodentia	Muridae	a
Cryptomys zechi (Matschie, 1900)	Rodentia	Bathyergidae	a
Cercopithecus petaurista (Schreber, 1774)	Primates	Cercopithecidae	b
Colobus vellerosus (I. Geoffroy, 1834)	Primates	Cercopithecidae	b
Procolobus verus (Van Beneden, 1838)	Primates	Cercopithecidae	b
Crocidura theresae Heim de Balsac, 1968	Soricomorpha	Soricidae	b
Tadarida spurrelli (Dollman, 1911)	Chiroptera	Molossidae	b
Scotophilus nigrita (Schreber, 1774)	Chiroptera	Vespertilionidae	b
Cephalophus dorsalis dorsalis Gray, 1846	Artiodactyla	Bovidae	b
Cephalophus niger Gray, 1846	Artiodactyla	Bovidae	b
Philantomba walteri Colyn et al., 2010	Artiodactyla	Bovidae	b
Gerbilliscus guineae (Thomas, 1910)	Rodentia	Muridae	b
Mus baoulei (Vermeiren & Verheyen, 1980)	Rodentia	Muridae	b
Cercopithecus erythrogaster Gray, 1866	Primates	Cercopithecidae	c
Chlorocebus tantalus (Ogilby, 1841)	Primates	Cercopithecidae	c
Tragelaphus spekii Speke, 1863	Artiodactyla	Bovidae	c
Dendromus messorius (Thomas, 1903)	Rodentia	Nesomyidae	c
Praomys misonnei van der Straeten & Dieterlen, 1987	Rodentia	Muridae	c
Stochomys longicaudatus (Tullberg, 1893)	Rodentia	Muridae	c
Lophuromys sikapusi (Temminck, 1853)	Rodentia	Muridae	d
Orycteropus afer (Pallas, 1766)	Tubulidentata	Orycteropidae	d
Dendrohyrax interfluvialis Oates et al., 2022	Hyracoidea	Procaviidae	a
Procavia capensis (Pallas, 1766)	Hyracoidea	Procaviidae	d
Loxodonta africana (Blumenbach, 1797)	Proboscidea	Elephantidae	d
Trichechus senegalensis Link, 1795	Sirenia	Trichechidae	d
Perodicticus potto (Müller, 1766)	Primates	Lorisidae	d
Galago senegalensis E. Geoffroy, 1796	Primates	Galagidae	d
Galagoides demidovii Fischer, 1908	Primates	Galagidae	d
Cercopithecus mona (Schreber, 1774)	Primates	Cercopithecidae	d
Erythrocebus patas (Schreber, 1775)	Primates	Cercopithecidae	d
Papio anubis (Lesson, 1827)	Primates	Cercopithecidae	d
Pan troglodytes (Blumenbach, 1775)	Primates	Hominidae	d
Lepus microtis Heuglin, 1865	Lagomorpha	Leporidae	d
Atelerix albiventris (Wagner, 1841)	Erinaceomorpha	Erinaceidae	d
Crocidura crossei Thomas, 1895	Soricomorpha	Soricidae	d
Crocidura foxi Dollman, 1915	Soricomorpha	Soricidae	d
Crocidura fuscomurina (Heuglin, 1865)	Soricomorpha	Soricidae	d
Crocidura grandiceps Hutterer, 1983	Soricomorpha	Soricidae	d
Crocidura lamottei Heim de Balsac, 1968	Soricomorpha	Soricidae	d
Crocidura olivieri (Lesson, 1827)	Soricomorpha	Soricidae	d
Crocidura poensis (Fraser, 1843)	Soricomorpha	Soricidae	d
Crocidura viaria (I.Geoffroy, 1834)	Soricomorpha	Soricidae	d
Suncus megalura (Jentink, 1888)	Soricomorpha	Soricidae	d

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Table 1. Continued from previous page.

Species	Order	Family	Distribution pattern
Eidolon helvum (Kerr, 1792)	Chiroptera	Pteropodidae	d
Epomophorus gambianus (Ogilby, 1835)	Chiroptera	Pteropodidae	d
Epomops franqueti (Tomes, 1860)	Chiroptera	Pteropodidae	d
Hypsignathus monstrosus H. Allen, 1861	Chiroptera	Pteropodidae	d
Lissonycteris angolensis (Bocage, 1898)	Chiroptera	Pteropodidae	d
Megaloglossus azagnyi Nesi, Kadjo & Hassanin, 2012	Chiroptera	Pteropodidae	d
Micropteropus pusillus (Peters, 1868)	Chiroptera	Pteropodidae	d
Myonycteris torquata (Dobson, 1878)	Chiroptera	Pteropodidae	d
Nanonycteris veldkampii (Jentink, 1888)	Chiroptera	Pteropodidae	d
Rousettus aegyptiacus (E. Geoffroy, 1810)	Chiroptera	Pteropodidae	d
Rhinolophus alcyone Temminck, 1853	Chiroptera	Rhinolophidae	d
Rhinolophus fumigatus Rüppell, 1842	Chiroptera	Rhinolophidae	d
Rhinolophus landeri Martin, 1838	Chiroptera	Rhinolophidae	d
Hipposideros abae J.A. Allen, 1917	Chiroptera	Hipposideridae	d
Hipposideros beatus K. Andersen, 1906	Chiroptera	Hipposideridae	d
Hipposideros caffer (Sundevall, 1846)	Chiroptera	Hipposideridae	d
Hipposideros cyclops (Temminck, 1853)	Chiroptera	Hipposideridae	d
Hipposideros gigas (Wagner, 1845)	Chiroptera	Hipposideridae	d
Hipposideros ruber (Noack, 1893)	Chiroptera	Hipposideridae	d
Lavia frons (E. Geoffroy, 1810)	Chiroptera	Megadermatidae	d
Taphozous mauritianus E. Geoffroy, 1818	Chiroptera	Emballonuridae	d
Taphozous nudiventris Cretzschmar, 1830	Chiroptera	Emballonuridae	d
Taphozous perforatus E. Geoffroy, 1818	Chiroptera	Emballonuridae	d
Coleura afra (Peters, 1852)	Chiroptera	Emballonuridae	d
Nycteris arge Thomas, 1903	Chiroptera	Nycteridae	d
Nycteris gambiensis (K. Andersen, 1912)	Chiroptera	Nycteridae	d
Nycteris grandis Peters, 1865	Chiroptera	Nycteridae	d
Nycteris hispida (Schreber, 1775)	Chiroptera	Nycteridae	d
Nycteris macrotis Dobson, 1876	Chiroptera	Nycteridae	d
Nycteris nana (K. Andersen, 1912)	Chiroptera	Nycteridae	d
Nycteris thebaica E. Geoffroy, 1818	Chiroptera	Nycteridae	d
Tadarida major (Troussart, 1897)	Chiroptera	Molossidae	d
Tadarida nigeriae Thomas, 1913	Chiroptera	Molossidae	d
Tadarida pumilus (Cretzschmar, 1826)	Chiroptera	Molossidae	d
Tadarida condylura (A. Smith, 1833)	Chiroptera	Molossidae	d
Tadarida thersites (Thomas, 1903)	Chiroptera	Molossidae	d
Nycticeinops schlieffeni (Peters, 1859)	Chiroptera	Vespertilionidae	d
Scotophilus dinganii (A. Smith, 1833)	Chiroptera	Vespertilionidae	d
Scotophilus leucogaster (Cretzschmar, 1830)	Chiroptera	Vespertilionidae	d
Scotophilus viridis (Peters, 1852)	Chiroptera	Vespertilionidae	d
Glauconycteris poensis (Gray, 1842)	Chiroptera	Vespertilionidae	d
Glauconycteris variegata (Tomes, 1861)	Chiroptera	Vespertilionidae	d
Mimetillus moloneyi (Thomas, 1891)	Chiroptera	Vespertilionidae	d
Pipistrellus capensis (A. Smith, 1829)	Chiroptera	Vespertilionidae	d

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Table 1. Continued from previous page.

Species	Order	Family	Distribution pattern
Pipistrellus guineensis (Bocage, 1889)	Chiroptera	Vespertilionidae	d
Pipistrellus nanus (Peters, 1852)	Chiroptera	Vespertilionidae	d
Pipistrellus rendalli (Thomas, 1889)	Chiroptera	Vespertilionidae	d
Pipistrellus somalicus (Thomas, 1901)	Chiroptera	Vespertilionidae	d
Pipistrellus tenuipinnis (Peters, 1872)	Chiroptera	Vespertilionidae	d
Myotis bocagii (Peters, 1870)	Chiroptera	Vespertilionidae	d
Manis tricuspis Rafinesque, 1821	Pholidota	Manidae	d
Acinonyx jubatus (Schreber, 1775)	Carnivora	Felidae	d
Caracal aurata (Temminck, 1827)	Carnivora	Felidae	d
Caracal caracal (Schreber, 1776)	Carnivora	Felidae	d
Felis silvestris Schreber, 1777	Carnivora	Felidae	d
Leptailurus serval (Schreber, 1776)	Carnivora	Felidae	d
Panthera leo (Linnaeus, 1758)	Carnivora	Felidae	d
Panthera pardus (Linnaeus, 1758)	Carnivora	Felidae	d
Civettictis civetta (Schreber, 1776)	Carnivora	Viverridae	d
Genetta genetta (Linnaeus, 1758)	Carnivora	Viverridae	d
Genetta maculata (Gray, 1830)	Carnivora	Viverridae	d
Genetta thierryi Matschie, 1902	Carnivora	Viverridae	d
Crossarchus obscurus F.G. Cuvier, 1825	Carnivora	Nandiniidae	d
Nandinia binotata (Gray, 1830)	Carnivora	Nandiniidae	d
Atilax paludinosus (G. [Baron] Cuvier, 1829)	Carnivora	Herpestidae	d
Galerella sanguinea (Rüppell, 1835)	Carnivora	Herpestidae	d
Herpestes ichneumon (Linnaeus, 1758)	Carnivora	Herpestidae	d
Ichneumia albicauda (G. [Baron] Cuvier, 1829)	Carnivora	Herpestidae	d
Mungos gambianus (Ogilby, 1835)	Carnivora	Herpestidae	d
Mungos mungo (Gmelin, 1788)	Carnivora	Herpestidae	d
Crocuta crocuta (Erxleben, 1777)	Carnivora	Hyaenidae	d
Canis adustus Sundevall, 1847	Carnivora	Canidae	d
Lycaon pictus (Temminck, 1820)	Carnivora	Canidae	d
Aonyx capensis (Schinz, 1821)	Carnivora	Mustelidae	d
Hydrictis maculicollis (Lichtenstein, 1835)	Carnivora	Mustelidae	d
Ictonyx striatus (Perry, 1810)	Carnivora	Mustelidae	d
Mellivora capensis (Schreber, 1776)	Carnivora	Mustelidae	d
Hylochoerus meinertzhageni Thomas, 1904	Artiodactyla	Suidae	d
Phacochoerus africanus (Gmelin, 1788)	Artiodactyla	Suidae	d
Potamochoerus porcus (Linnaeus, 1758)	Artiodactyla	Suidae	d
Hippopotamus amphibius Linnaeus, 1758	Artiodactyla	Hippopotamidae	d
Alcelaphus major (Blyth, 1869)	Artiodactyla	Bovidae	d
Cephalophus rufilatus Gray, 1846	Artiodactyla	Bovidae	d
Cephalophus silvicultor (Afzelius, 1815)	Artiodactyla	Bovidae	d
Damaliscus korrigum (Ogilby, 1837)	Artiodactyla	Bovidae	d
Eudorcas rufifrons (Gray, 1846)	Artiodactyla	Bovidae	d
Ourebia ourebi quadriscopa (C.H. Smith, 1827)	Artiodactyla	Bovidae	d
Sylvicapra grimmia (Linnaeus, 1758)	Artiodactyla	Bovidae	d

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Table 1. Continued from previous page.

Species	Order	Family	Distribution pattern
Hippotragus equinus (E. Geoffroy Saint-Hilaire, 1803)	Artiodactyla	Bovidae	d
Syncerus brachyceros (Gray, 1837)	Artiodactyla	Bovidae	d
Tragelaphus derbianus (Gray, 1847	Artiodactyla	Bovidae	d
Tragelaphus eurycerus (Ogilby, 1837)	Artiodactyla	Bovidae	d
Tragelaphus phaleratus (C.H. Smith, 1827)	Artiodactyla	Bovidae	d
Kobus ellipsiprymnus (Ogilby, 1833)	Artiodactyla	Bovidae	d
Kobus kob (Erxleben, 1777)	Artiodactyla	Bovidae	d
Redunca redunca (Pallas, 1767)	Artiodactyla	Bovidae	d
Funisciurus leucogenys (Waterhouse, 1842)	Rodentia	Sciuridae	d
Funisciurus pyrropus (F. Cuvier, 1833)	Rodentia	Sciuridae	d
Heliosciurus gambianus (Ogilby, 1835)	Rodentia	Sciuridae	d
Heliosciurus rufobrachium (Waterhouse, 1842)	Rodentia	Sciuridae	d
Protoxerus stangeri (Waterhouse, 1842)	Rodentia	Sciuridae	d
Xerus erythropus (E. Geoffroy, 1803)	Rodentia	Sciuridae	d
Graphiurus crassicaudatus (Jentink, 1888)	Rodentia	Gliridae	d
Graphiurus kelleni (Reuvens, 1890)	Rodentia	Gliridae	d
Graphiurus nagtaglasii Jentink, 1888	Rodentia	Gliridae	d
Cricetomys gambianus Waterhouse, 1840	Rodentia	Nesomyidae	d
Steatomys caurinus Thomas, 1912	Rodentia	Nesomyidae	d
Uranomys ruddi Dollman, 1909	Rodentia	Muridae	d
Gerbilliscus kempi (Wroughton, 1906)	Rodentia	Muridae	d
Taterillus gracilis (Thomas, 1892)	Rodentia	Muridae	d
Arvicanthis niloticus (E. Geoffroy, 1803)	Rodentia	Muridae	d
Arvicanthis rufinus (Temminck, 1853)	Rodentia	Muridae	d
Dasymys rufulus Miller, 1900	Rodentia	Muridae	d
Grammomys kuru (Thomas & Wroughton, 1907)	Rodentia	Muridae	d
Hylomiscus alleni (Waterhouse, 1838)	Rodentia	Muridae	d
Lemniscomys striatus (Linnaeus, 1758)	Rodentia	Muridae	d
Lemniscomys zebra (Heuglin, 1864)	Rodentia	Muridae	d
Mastomys erythroleucus (Temminck, 1853)	Rodentia	Muridae	d
Mastomys natalensis (Smith, 1834)	Rodentia	Muridae	d
Mus haussa (Thomas & Hinton, 1920)	Rodentia	Muridae	d
Mus minutoides Smith, 1834	Rodentia	Muridae	d
Mus muscoloides Temminck, 1853	Rodentia	Muridae	d
Mus setulosus Peters, 1876	Rodentia	Muridae	d
Praomys daltoni (Thomas, 1892)	Rodentia	Muridae	d
Praomys derooi Van der Straeten & Verheyen, 1978	Rodentia	Muridae	d
Praomys tullbergi (Thomas, 1894)	Rodentia	Muridae	d
Anomalurus derbianus (Gray, 1842)	Rodentia	Anomaluridae	d
Atherurus africanus Gray, 1842	Rodentia	Hystricidae	d
Hystrix cristata Linnaeus, 1758	Rodentia	Hystricidae	d
Thryonomys swinderianus (Temminck, 1827)	Rodentia	Thryonomyidae	d
Acomys johannis Thomas, 1912	Rodentia	Muridae	e

a, Endemic (END); b, Upper Guinean (UGU); c, Lower Guinean (LGU); d, Pan-African (PAN); e, Sahelian (SAH).

The greatest proportion of species are PAN (87.4%), followed by UGU (6.3%), LGU (3.4%), END (2.3%, n=4), and SAH (0.6%, n=1). The PAN species live in many habitats and ecosystem species and are some of the most 'successful' species in Sub-Saharan Africa. In addition, excluding the PAN species from the analysis, the mammalian fauna appeared to be affiliated similarly to both 'UGU' and 'LGU' (X^2=1.47, df=1, p=0.225).

Remarkably, three out of four END species were rodents: *Cryptomys zechi* (Bathyergidae), *Funisciurus substriatus* (Sciuridae), and the enigmatic *Leimacomys buettneri* (Muridae), which is known from only two individuals from over 100 years ago. These three species differed remarkably in terms of their ecological distribution: one species (*Leimacomys buettneri*) occurs only in dense tropical forests (ecological zone IV), one species (*Cryptomys zechi*) only in dry Sudanese savannahs (I), and one species (*Funisciurus substriatus*) is widespread across habitats (I to IV). Thus, there was no evidence that any specific habitat/vegetation zone represented a center for the evolution of endemism within the Dahomey Gap. The fourth species is the Dahomey Gap tree hyrax (*Dendrohyrax interfluvialis*) that inhabits both forests and savannahs (Oates et al. 2022).

Concerning the UGU species (n=11), two species were only from the Sudanese savannah, one species from open forests (ecological zone II), one species from dense tropical forests, and eight species (72.7%) were habitat generalists, found in at least three different ecological zones of Togo. With regard to the LGU species (n=6), two species were exclusive of the dense tropical forests, one of the altered coastal bushlands (ecological zone V), and three were found in at least three ecological vegetation zones. The only species belonging to the category SAH (i.e., *Acomys johannis*) was expectedly found only in Sudanese savannahs.

Considering only the multispecies genera (n=28), 71.4% did not show any barrier effect by the Dahomey Gap on their own species, as all of them did occur on both sides of Togo. The remaining genera (n=8) revealed a barrier effect by the Dahomey Gap (Table 2). In these genera, the number of species for which the Dahomey Gap represented a barrier turned out to be identical both in the west and east of the considered region (n=5 on both sides). Conversely, the number of species for which the Dahomey Gap did not act as a barrier was 26 (Table 2). Overall, the Dahomey Gap apparently showed a barrier effect on 28.6% of the multispecies genera, and may have caused the speciation of ten species. Out of these ten species, nine are forest dwellers, and one (*Crocidura theresae*) is found in Sudanese savannahs.

Table 2. Synopsis of the taxa that are affected by the Dahomey Gap as a barrier. Only genera with multiple species occurring in Togo are considered. Endemic taxa are excluded from this Table.

Genus	Total number of species	East of Togo	West of Togo	Both sides
Cephalophus C.H. Smith, 1827	4	2	0	2
Tragelaphus de Blainville, 1816	4	1	0	3
Cercopithecus Linnaeus, 1758	3	1	1	1
Crocidura Wagler, 1832	9	0	1	8
Gerbilliscus Thomas, 1897	2	0	1	1
Praomys Thomas, 1915	4	1	0	3
Scotophilus Leach, 1821	4	0	1	3
Tadarida Rafinesque, 1814	6	0	1	5
Total	36	5	5	26

Discussion

Our study confirmed that the mammalian fauna of Togo was basically influenced by Pan-African taxa, with a moderate contribution of species occurring only in the Upper Guinean forests, Lower Guinean forests, or even endemic of the Dahomey Gap. The preponderance of Pan-African species (accounting for more than 85% of taxa) and the similar percentage of species from either Upper or Lower Guinean forests clearly shows that Togo is a "confluence area" for faunas with different biogeographic patterns, and not an area with high endemism rates. From the ecological point of view, this is not surprising given that the majority of the Togolese territory consists of varied types of savannahs, from the wet Guinean to the dry Sudanese categories (Ern 1979), and these vegetation types are widespread throughout West and Central Africa thus giving the widespread savannah species easy access to the Dahomey Gap. The similar percentage of species occurring within the Dahomey Gap from either Upper or Lower Guinean forests does not mirror previous studies. For instance, in the Cetoniinae beetles, the number of shared species is highest between Ghana and Ivory Coast (i.e., Upper Guinean forests, n=114) than between Ghana and Benin (Lower Guinean forests, n=74), with Ivory Coast and Benin having 82 species in common (Philips et al. 2022).

Although most Togolese species showed a Pan African distribution, our analyses on multispecific genera highlighted a barrier effect by the Dahomey Gap, as 28% of the species in these genera were distributed only eastwards or westwards of the considered region. These species were almost exclusively forest-dwellers (90%), showing that, as expected, the Dahomey Gap acted as a barrier only for forest taxa. This fact confirms previous studies documenting the role of the Dahomey Gap as an ecological interruption between the Upper and Lower Guinean Forest blocks (e.g., Luiselli et al. 2019; Mallon et al. 2015).

Conversely, we did not uncover any clear effect of forest islands within the Dahomey Gap as sources of endemism, although some cases of invertebrate (e.g., the gasteropod *Archachatina puylaerti* (A.R. Mead, 1998), see Mead 1998; Le Gall et al. 2002) and of vertebrate species endemic to the remnant forests in this region are known (for instance, the frog *Conraua derooi* Hulselmans, 1972, see Segniagbeto et al. 2017). Indeed, concerning the mammalian fauna, only *Leimacomys buettneri* was endemic to the Dahomey Gap Forest islands. These data mirror those provided by Philips et al. (2022) on Cetoniinae beetles. According to these authors, with a total number of species in each country ranging from 130 to 189, the number of species uniquely occurring in the Dahomey Gap was very low (Ghana = 11 species; Benin = 34 species, with no known endemic species). According to Philips et al. (2022), the absence of endemics was due to the generally broad east-west orientation of habitats within West Africa. We hypothesize that the non-effect of the forest patches as endemism centers in the Dahomey Gap was due to i) the small number of remnant forest patches interspersed within the savannah matrix, ii) their relative size (24% of the territory of Togo according to MEDDPN 2020) as well as iii) its likely anthropogenic origin. The areas of forest concentration are the protected areas, including Fazao-Malfakassa, Togodo, Abdoulaye, Assoukoko, and some related ecosystems. These factors may not be an obstacle to the speciation of small-sized species with reduced vagility, such as amphibians (e.g., Segniagbeto et al. 2017), gasteropods (Mead 1998) and arthropods (Le Gall 2010; Usher 1985).

The full understanding of the role of the Dahomey Gap as a biogeographic barrier and of its island forests as centers of endemism is impeded by the lack of biogeographic reviews and meta-analyses on the composition of faunal and floral groups of the entire region. We would urge to focus further research on statistically documenting the frequencies of occurrence of the various biogeographic patterns within different taxonomical groups in order to uncover the general picture of the biogeography of the Dahomey Gap organisms.

Authors' contributions

GA and LL planned the research, made the analyses, and wrote the text; GHS collected part of the data, quantified the areas of interest, and drafted the map; all authors reviewed and approved the final version to be published.

Conflict of interest

The authors declare no potential conflict of interest.

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Availability of data and materials

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References

Amori G, Chiozza F, Rondinini C, Luiselli L. 2011. Country-based patterns of total species richness, endemicity, and threatened species richness in African rodents and insectivores. *Biodiversity and Conservation.* 20:1225–1237. https://doi.org/10.1007/s10531-011-0024-1

Amori G, Luiselli L. 2019. A scale-dependent 'functional' assessment of the concept of endemism. *Biological Journal of the Linnean Society*. 127:900–911. https://doi.org/10.1093/biolinnean/blz059

Amori G, Masciola S, Saarto J, Gippoliti S, Rondinini C, Chiozza F, Luiselli L. 2012. Spatial turnover and knowledge gap of African small mammals: using country checklists as a conservation tool. *Biodiversity and Conservation.* 21:1755–1793. https://doi.org/10.1007/s10531-012-0275-5

Amori G, Segniagbeto GH, Decher J, Assou D, Gippoliti S, Luiselli L. 2016. Non-marine mammals of Togo (West Africa): an annotated checklist. *Zoosystema.* 38:201–244. https://doi.org/10.5252/z2016n2a3

Booth AH. 1958. The Niger, the Volta and the Dahomey Gap as geographic barriers. *Evolution.* 1958:48–62. https://doi.org/10.1111/j.1558-5646.1958.tb02927.x

Croizat L. 1994. Observations on the biogeography of the genus *Goliathus* (Insecta: Coleoptera). *National Herbarium & Botanic Garden.* 1994:141–155.

Demenou BB, Doucet JL, Hardy OJ. 2018. History of the fragmentation of the African rain forest in the Dahomey Gap: insight from the demographic history of *Terminalia superba*. *Heredity*. 120:547–561. https://doi.org/10.1038/s41437-017-0035-0

Demenou BB, Piñeiro R, Hardy OJ. 2016. Origin and history of the Dahomey Gap separating West and Central African rain forests: insights from the phylogeography of the legume tree *Distemonanthus benthamianus*. *Journal of Biogeography*. 43:1020–1031. https://doi.org/10.1111/jbi.12688

De Palma M, Takano H, Leonard P, Bouyer T. 2020. Barcoding analysis and taxonomic revision of *Goliathus* Lamark, 1802 (Scarabaeidae, Cetoniinae). *Entomologia Africana*. 25:11–32.

Ern H. 1979. Die Vegetation Togos. Gliederung, Gefährdung, Erhaltung. *Willdenowia.* 9:295–312.

Harold AS, Mooi RD. 1994. Areas of endemism: definition and recognition criteria. *Systematic Biology.* 43:261–266. https://doi.org/10.1093/sysbio/43.2.261

Houngbédji MG, Djossa BA, Adomou AC, Dakpogan SC, Sinsin B, Mensah GA. 2012. Conservation status of the Red-bellied Guenon (*Cercopithecus erythrogaster erythrogaster*) in the western Dahomey Gap in southwestern Benin and the adjacent Togodo Forest Reserve, South Togo. *African Primates*. 7:184–192.

Kingdon J, Happold D, Butynski T, Hoffmann M, Happold M, Kalina J. (eds) 2013. *Mammals of Africa* (6 vols). Bloomsbury Publishing, London, UK. 3500 pp.

Leaché AD, Oaks JR, Ofori-Boateng C, Fujita MK. 2020. Comparative phylogeography of West African amphibians and reptiles. *Evolution*. 74:716–724. doi: 10.1111/evo.13941

Leaché AD, Rödel MO, Linkem CW, Diaz RE, Hillers A, Fujita MK. 2006. Biodiversity in a forest island: reptiles and amphibians of the West African Togo Hills. *Amphibian and Reptile Conservation*. 4:22–45.
Le Gall P. 2010. Affinités biogéographiques des Insectes du" Dahomey gap": présence d'une population de *Goliathus goliatus* Linné, 1771, au Bénin (Coleoptera, Scarabaeidae, Cetoniinae). *Bulletin de la Société entomologique de France*. 115:17–21. https://doi.org/10.3406/bsef.2010.2821
Le Gall, P., Goergen, G., Neuenschwander, P. 2002. Les insectes et le sillon dahomeen: fragmentation et refuges forestiers. *Biosystema*. 20:73–80.
Luiselli L, Civetta F, Masciola S, Milana G, Amori G. 2012. Spatial turnover and knowledge gaps for African chelonians mirror those of African small mammals: conservation implications. *Tropical Conservation Science*. 5:365–380. https://doi.org/10.1177/194008291200500310
Luiselli L, Dendi D, Eniang EA, Fakae BB, Akani GC, Fa JE. 2019. State of knowledge of research in the Guinean forests of West Africa region. *Acta Oecologica.* 94:3–11. https://doi.org/10.1016/j.actao.2017.08.006
Luiselli L, Dendi D, Petrozzi F, Segniagbeto GH. 2022. Lizard community structure and spatial resource use along a forest-savannah-urban habitat gradient in the Dahomey Gap (West Africa). *Urban Ecosystems.* 25:1015–1026. https://doi.org/10.1007/s11252-022-01215-w
Mallon DP, Hoffmann M, Grainger MJ, Hibert F, Van Vliet N, McGowan PJ. 2015. An IUCN situation analysis of terrestrial and freshwater fauna in West and Central Africa. *Occasional paper of the IUCN Species Survival Commission*. 54:40. https://doi.org/10.2305/IUCN.CH.2015.SSC-OP.54.en
Mayr E, O'Hara RJ. 1986. The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. *Evolution*. 40:55–67. doi: 10.1111/j.1558-5646.1986.tb05717.x.
Mead AR. 1998. A new species of *Archachatina* in the Dahomey Gap of West Africa and its implications in phylogeny (Pulmonata. Achatinidae). *Journal of African Zool*ogy. 112:123–145.
MEDDPN (Ministère de l'Environnement, du Développement Durable et de la Protection de la Nature). 2020. Niveau de référence des Forêts (NRF) du Togo. Rapport National RED+. 80 pp.
Morrone JJ. 1994. On the identification of areas of endemism. *Systematic Biology*. 43:438–441. https://doi.org/10.1093/sysbio/43.3.438
Oates JF, Woodman N, Gaubert P, Sargis EJ, Wiafe ED, Lecompte E, Dowsett-Lemaire F, Dowsett RJ, Gonedelé Bi S, Ikemeh RA, Djagoun CA. 2022. A new species of tree hyrax (Procaviidae: *Dendrohyrax*) from West Africa and the significance of the Niger–Volta interfluvium in mammalian biogeography. *Zoological Journal of the Linnean Society*. 194:527–552.
Philips TK, Mudge AD, Orozco J, Neidlinger R, Beinhundner G, Joly C. 2022. A rich and diverse fauna: an illustrated guide to the cetoniines of Ghana with comparisons to Ivory Coast and Benin (Coleoptera: Scarabaeidae: Cetoniinae). *Zootaxa*. 5150:151–188. doi: 10.11646/zootaxa.5150.2.1.
Salzmann U, 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. https://doi.org/10.1191/0959683605hl799rp
Segniagbeto GH, Assou D, Dendi D, Rödel MO, Ohler A, Dubois A, Luiselli L. 2017. The distribution and local density of the critically endangered frog *Conraua derooi* Hulselmans, 1972 in Togo, West Africa. *Herpetological Bulletin.* 141:23–27.
Segniagbeto GH, Bour R, Ohler A, Dubois A, Rödel MO, Trape JF, Fretey J, Petrozzi F, Luiselli L. 2014a. Turtles and tortoises of Togo: historical data, distribution, ecology, and conservation. *Chelonian Conservation and Biology.* 13:152–165.
Segniagbeto G, Trape JF, Afiademanyo KM, Rödel MO, Ohler A, Dubois A, David P, Meirte D, Glitho IA, Petrozzi F, Luiselli L. 2015. Checklist of the lizards of Togo (West Africa), with comments on systematics, distribution, ecology, and conservation. *Zoosystema*. 37:381–402. https://doi.org/10.5252/z2015n2a7
Segniagbeto GH, Trape JF, David P, Ohler A, Dubois A, Glitho IA. 2011. The snake fauna of Togo: systematics, distribution and biogeography, with remarks on selected taxonomic problems. *Zoosystema*. 33:325–360. https://doi.org/10.5252/z2011n3a4
Segniagbeto GH, Van Waerebeek K, Bowessidjaou JE, Ketoh K, Kpatcha TK, Okoumassou K, Ahoedo K. 2014b. Annotated checklist and fisheries interactions of cetaceans in Togo, with evidence of Antarctic minke whale in the Gulf of Guinea. *Integrative Zoology*. 9:1–13. doi: 10.1111/1749-4877.12011.
Usher MB. 1985. The species of *Henotesia* Butler (Lepidoptera: Nymphalidae, Satyrinae) in western West Africa. *Insect Systematics & Evolution*. 16:259–264.